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Neural correlates of perceptual learning in a sensory-motor, but not a sensory, cortical area

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This study aimed to identify neural mechanisms that underlie perceptual learning in a visual-discrimination task. We trained two monkeys (*Macaca mulatta*) to determine the direction of visual motion while we recorded from their middle temporal area (MT), which in trained monkeys represents motion information that is used to solve the task, and lateral intraparietal area (LIP), which represents the transformation of motion information into a saccadic choice. During training, improved behavioral sensitivity to weak motion signals was accompanied by changes in motion-driven responses of neurons in LIP, but not in MT. The time course and magnitude of the changes in LIP correlated with the changes in behavioral sensitivity throughout training. Thus, for this task, perceptual learning does not appear to involve improvements in how sensory information is represented in the brain, but rather how the sensory representation is interpreted to form the decision that guides behavior.

Training can induce long-lasting improvements in our ability to detect, discriminate or identify sensory stimuli[1]. Despite the prevalence of this phenomenon, called perceptual learning, our understanding of the underlying neural plasticity is incomplete. Changes in early sensory areas of the cortex have been inferred from psychophysical studies[2] (but see refs. 3,4) and identified in monkeys trained on auditory[5] and somatosensory[6] tasks. However, monkeys trained on visual tasks show only moderate or no change in early visual cortex[7–11]. Changes in higher stages of processing, including those that contribute to decision-making and attention, have also been inferred from psychophysical and physiological studies[4,8,12–14]. However, such changes have not been identified directly in the brain. We sought to identify experience-dependent changes in visual processing in two different cortical areas, one in extrastriate visual cortex and the other in parietal cortex, and to determine their relative contributions to perceptual learning.

We trained monkeys to determine the direction of motion of a random-dot stimulus and to indicate their direction decision with an eye movement. Most neurons in area MT of extrastriate visual cortex are tuned for the location and direction of moving visual stimuli[15]. In trained monkeys, MT responses can be as sensitive to random-dot motion signals as the monkey's behavioral reports and are weakly predictive of the monkey's choices on the discrimination task[16,17]. Moreover, MT lesions degrade performance[18] and MT microstimulation biases performance on the task[19]. Therefore, MT provides at least some of the motion information used to form the direction decision.

Neurons in area LIP of parietal cortex, which has been implicated in a variety of cognitive and visuomotor functions, including attention, intention, reward anticipation and decision-making[20–23], also respond while monkeys carry out the discrimination task. These responses are modulated by the strength and duration of the motion stimulus and can be strongly predictive of the monkey's saccadic choices[24,25]. LIP microstimulation can bias performance on a reaction-time version of the task[26]. Therefore, area LIP appears to be involved in transforming motion information into a saccadic choice, although that role might be shared among several oculomotor regions, including the frontal eye field (FEF) and superior colliculus, that show similar responses during task performance[27,28].

We recorded the activity of individual MT and LIP neurons while two naive monkeys were trained on the direction-discrimination task. Behavioral sensitivity to weak motion signals improved continuously during training, long after monkeys had acquired the stimulus-response association. This improvement in behavioral sensitivity corresponded to changes in the responses of neurons in LIP, but not in MT, during motion viewing. The results are consistent with a model in which perceptual improvements result from changes in how sensory evidence is interpreted and used to instruct behavior, as reflected in LIP, but not in changes to the representation of the evidence itself in MT.

RESULTS

Discrimination threshold improved with training

We trained two rhesus monkeys on a one-interval, two-alternative direction-discrimination task (monkey C, 165 sessions over 645 d; monkey Z, 155 sessions over 473 d; **Fig. 1a**). Each daily training session began by introducing recording electrodes into MT and/or LIP (**Fig. 1b**). As in previous studies, quantifying the relationship between behavioral and neuronal performance depended on matching the visual stimulus to the properties of the neuron(s) being recorded[16,25]. Under this constraint, we sought to minimize changes in the stimulus configuration across sessions by selecting neurons with consistent
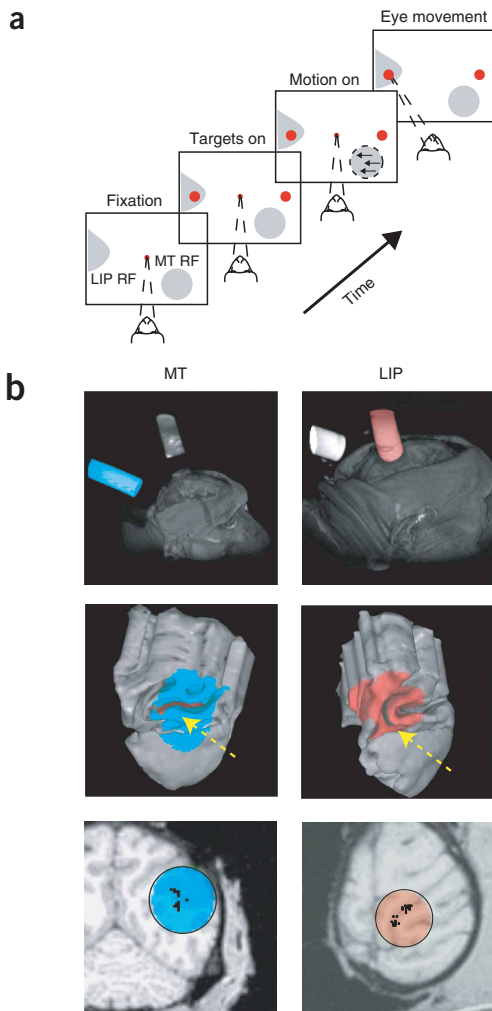
Figure 1 Task and anatomical localization. (**a**) Direction-discrimination task. The motion stimulus matched the RF location and preferred direction (and its 180° opposite) of the middle temporal area (MT) neuron being recorded or the modal values from previous sessions if no MT neuron was found. One target was placed in the response field of the LIP neuron being recorded or the modal location from previous sessions if no LIP neuron was found, and the other was placed in the opposite visual hemifield. (**b**) Anatomical localization of recording site locations in areas MT (left, cyan) and LIP (right, red) using magnetic resonance imaging. Top, volume rendering using the AFNI[49] render plugin showing the three-dimensional orientation of the recording cylinders relative to the head. Middle, partial reconstruction of the cortical surface along with the projection of the recording cylinder using Caret and SureFit[50] (http://brainmap.wustl.edu/caret) and custom software. The yellow arrow in the left panel points to the location of area MT (red) along the superior temporal sulcus. The yellow arrow in the right panel points to the location of area LIP (brown) along the intraparietal sulcus. Bottom, partial penetration maps of successful recording sites (black points) superimposed on planes of sections perpendicular to the long axis of the recording cylinder. MT sites (top) ranged in depth from 6–9 mm from the dura mater. LIP sites (bottom) ranged in depth from 4–7 mm from the dura mater. These images were generated with previously described methods (Kalwani, R.M., Bloy, L., Hulvershorn, J., Elliot, M.A. & Gold, J.I. *Soc. Neurosci. Abstr.* **454.14**, 2005).

tuning properties, including the receptive field (RF) location and direction preference of MT neurons and the response field location of LIP neurons (**Supplementary Fig. 1** online). After finding the appropriate neuron(s), we placed the motion stimulus in the MT RF (or in its modal location if no MT neuron was found) and one of the two choice targets in the LIP response field (or in its modal location if no LIP neuron was found). Training occurred only while the responses of at least one MT or LIP neuron were isolated and recorded, allowing us to make direct, session-by-session comparisons of behavioral and neuronal performance as training progressed.

Behavioral performance improved steadily for both monkeys with training (**Fig. 2**). In early sessions, we trained monkeys on a simplified version of the task using only the strongest motion stimulus (99% coherence) to reinforce the association between motion direction and saccade target. After their performance on this easy condition improved to well above chance (> ∼75% correct), we introduced more difficult stimuli using randomly interleaved motion coherences and viewing durations (indicated as session 1 in **Fig. 2c**). Nevertheless, we continued to randomly interleave trials with 99% coherence in each session throughout training (**Fig. 2c**). For both monkeys, declining error rates on these high-coherence trials as a function of session were fit by a single-exponential function with a lower asymptote of zero (mean ± s.e.m., initial value = 0.51 ± 0.02 for monkey C,

0.48 ± 0.01 for monkey Z; time constant = 3.6 ± 0.4 sessions for monkey C, 30.4 ± 1.1 sessions for monkey Z). Thus, both monkeys learned how to perform the task in early sessions and were soon able to express the visuomotor association for high-coherence stimuli with few or no errors.

In addition to learning the association, the monkeys learned to better discriminate weaker and weaker motion signals at shorter viewing times. We examined the performance of monkey C in two sample sessions, one early and one late in training (**Fig. 2a**). For nearly all coherences and viewing times, the percentage of correct responses was greater in the later session than in the earlier session. Indeed, throughout training, performance improved significantly for all nonzero coherences for monkey C and for 12.8–99.9% coherence for monkey Z (linear regression of percent correct per coherence with training session; H_0: slope = 0, $P < 0.05$).

To further quantify improvements in performance with training, we used a time-dependent cumulative Weibull function (equation (1) and solid lines in **Fig. 2a,b**) to estimate the discrimination threshold, which is the motion strength at which the monkey correctly discriminated the direction of motion ∼82% of the time for a 1-s viewing duration, for each session. This function takes into account associative (high-coherence) errors (λ in equation (1)) and can therefore indicate changes in threshold that are distinct from changes in associative learning or lapses of attention (**Supplementary Fig. 2** online). Thresholds improved from ∼67% to ∼15% coherence for monkey C and from ∼68% to ∼19% coherence for monkey Z, with a time course that was substantially longer than that for the associative improvements (mean ± s.e.m., time constants of single-exponential solid curves = 24.6 ± 0.4 sessions for monkey C and 58.5 ± 2.5 sessions for monkey Z, final value = 14.7 ± 0.1% coherence for monkey C and 19.3 ± 0.4% coherence for monkey Z, **Fig. 2c**; improvements in high-coherence errors were limited to early sessions, whereas improvements in threshold were apparent throughout most of training; **Fig. 2d**). Other behavioral parameters, including the shape and time dependence of the psychometric function, did not show similar systematic changes with training (**Supplementary Table 1** online). The goal of this study was to identify changes in the response properties of MT and LIP neurons that accompanied the improvements in discrimination threshold.
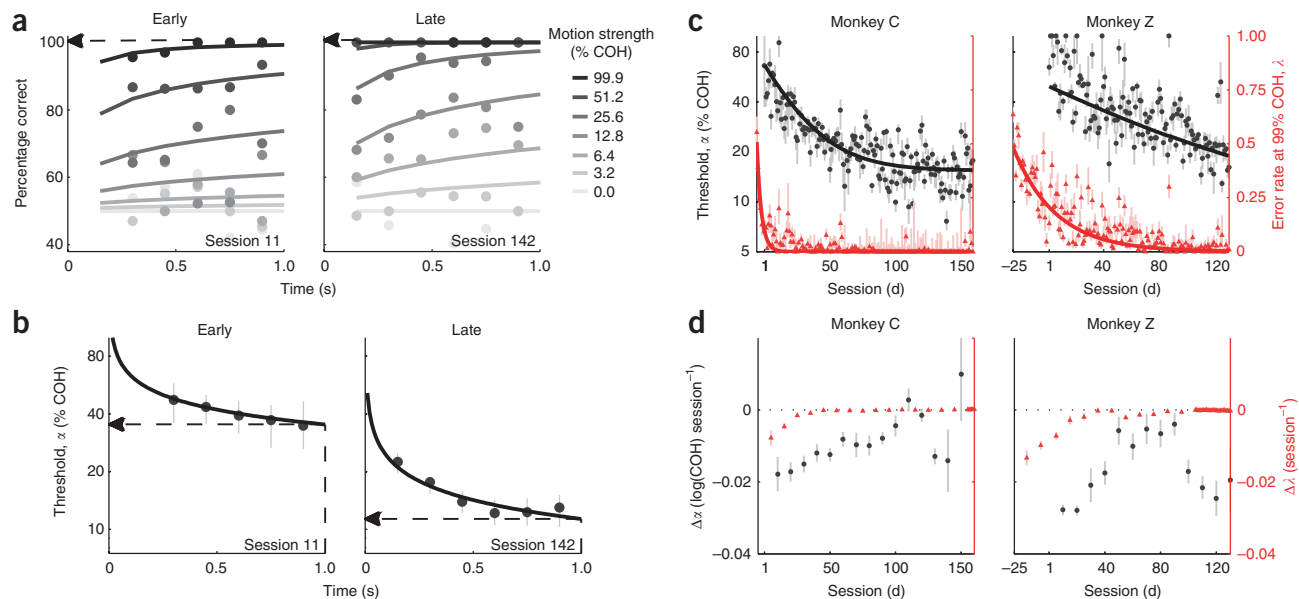
Figure 2 Behavior. (**a**,**b**) Behavioral performance (**a**) and discrimination threshold (**b**, best fits and 68% confidence intervals, CIs) as a function of viewing time (0.3-s-wide bins in 0.15-s intervals) for different motion strengths (see legend) from two representative sessions, early (left) and late (right) in training. Discrimination thresholds in **b** were computed for each time bin using a cumulative Weibull function[16]. Solid lines in **a** and **b** represent behavioral performance and discrimination thresholds computed from a time-dependent cumulative Weibull function (equation (1) fit to each dataset; not binned by viewing duration), respectively. We report error rates at 99.9% coherence (COH; dashed arrows in **a**, ▲ in **c** and **d**) and discrimination thresholds at 1-s viewing duration from the fits (dashed arrows in **b**, ● in **c** and **d**). (**c**,**d**) Discrimination threshold (● ; note the logarithmic scale on the left ordinate) and error rate at 99.9% coherence (▲; linear scale on the right ordinate) with 68% CIs plotted as a function of training session for the two monkeys. Prior to session 1, monkeys were trained mostly with 99.9% coherence motion. Solid lines are best-fitting single exponential functions. (**d**) Learning rates (best fits and s.e.m.) of discrimination thresholds (●) and errors at 99.9% coherence (▲) during training for the two monkeys. The learning rate was computed as the slope of a linear fit to the behavioral data (log discrimination thresholds or errors at 99.9% coherence) in a 41-session-wide bin. A negative learning rate implies that the behavioral parameter improved during that particular epoch of training.

MT responses did not change with training

We recorded the responses of individual MT neurons to the motion stimulus both before and during training (monkey C, $n = 50$ MT neurons recorded during a passive viewing condition before discrimination training began and $n = 92$ during training; monkey Z, $n = 47$ before and $n = 60$ during training; **Fig. 3**). MT responses before and during training showed a pattern of activation similar to that reported in trained monkeys[16]. Motion in the preferred direction elicited an increase in spike rate and motion in the opposite direction elicited a decrease in spike rate to relatively constant values that depended on motion strength and were sustained throughout motion viewing (**Fig. 3a**). To quantify these responses and test for changes with training, we fitted a simple linear model to the normalized responses of individual neurons. This model describes the neural responses in terms of the baseline firing rate and three stimulus-based terms: a dependence on motion coherence that does not change with viewing time, a dependence on viewing time that does not change with motion coherence and a dependence on the (multiplicative) interaction between coherence and viewing time that is consistent with an accumulation of motion information over time[29] (equation (3), **Fig. 3b** and **Supplementary Fig. 3** online). For both monkeys, only the coherence-alone term was typically > 0, consistent with the idea that MT responses provide evidence about motion direction that depends only on stimulus strength and not on viewing time. Moreover, none of the three terms changed significantly with training (linear regression versus session, computed separately for each term and monkey, before and during training, H_0: slope $= 0$, $P > 0.05$ for all conditions).

We also quantified the motion sensitivity of individual MT neurons by computing a 'neurometric' discrimination threshold using the same time-dependent cumulative Weibull function that was used to estimate behavioral threshold (equation (1), **Supplementary Fig. 4** online). Neurometric thresholds were, on average, $\sim 4\%$ better during training than before training, but the differences were not significant (monkey C: geometric mean threshold coherence before training $= 25.9\%$, during training $= 21.0\%$, Mann-Whitney U test $P = 0.20$; monkey Z: before $= 21.1\%$; during $= 18.4\%$, $P = 0.48$). Moreover, the neurometric thresholds of the whole population or of the most-sensitive 50% of the MT neurons did not change systematically as a function of session either before or during training (linear regression, H_0: slope of log threshold versus session $= 0$; before training: monkey C $P = 0.76$, monkey Z $P = 0.95$; during training: monkey C, whole population $P = 0.95$, 50% most sensitive $P = 0.99$, monkey Z, whole population $P = 0.89$, 50% most sensitive $P = 0.95$). Notably, this lack of long-term changes across sessions occurred despite the short-term changes that occurred within sessions, as has been reported previously[30] (geometric mean $\pm$ s.e.m. ratio of psychometric thresholds in the second 200 versus the first 200 trials, 0.92 ± 0.22 in monkey C and 0.84 ± 0.29 in monkey Z; ratio of neurometric thresholds in MT in the second 200 versus the first 200 trials, 0.87 ± 0.23 in monkey C and 0.98 ± 0.29 in monkey Z). Other response properties, including the width of directional tuning, were unaffected by training (**Fig. 3** and **Supplementary Table 1**).

There was, however, a slight strengthening with training of the relationship between the trial-by-trial variability of MT responses and the monkeys' choices. This analysis, called choice probability, has
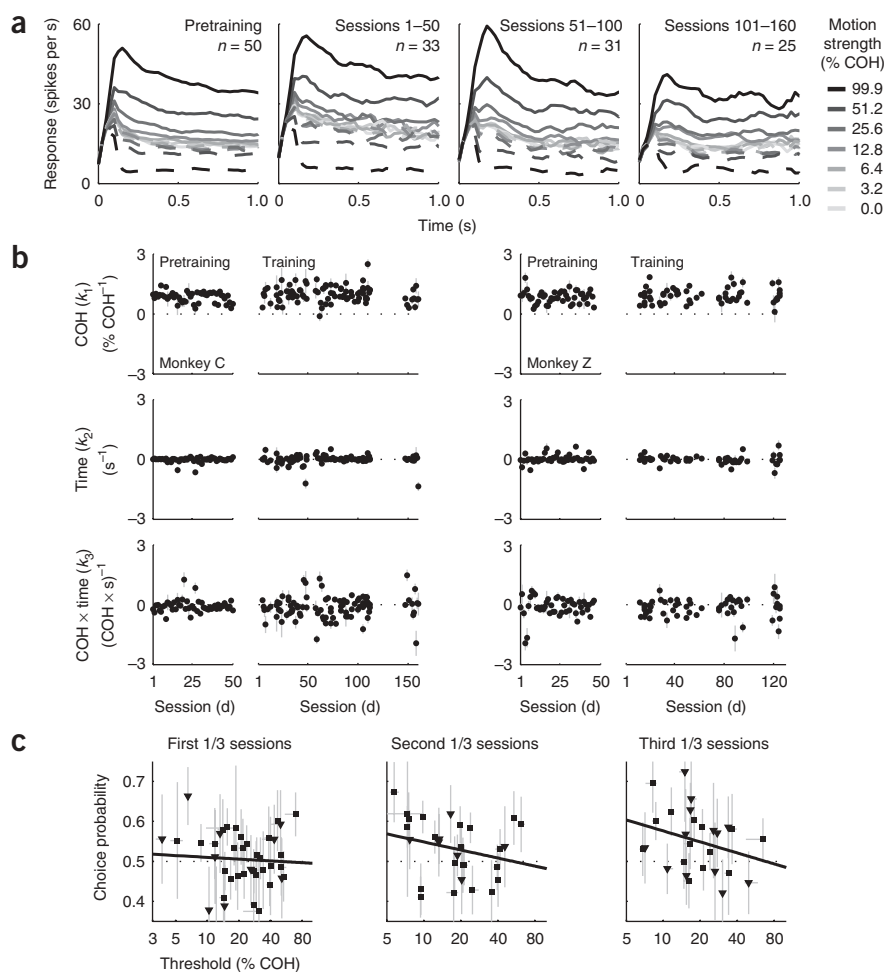
Figure 3 MT responses. (**a**) Average activity of MT neurons as a function of viewing time (using 0.1-s-wide time bins with 0.025-s increments) for different motion strengths (see legend) for each neuron's preferred (solid line) and null (dashed line) motion during different training periods for monkey C. Pretraining refers to responses to the motion stimulus measured while the monkey was rewarded for simply fixating a central spot, before being trained on the discrimination task. (**b**) Coherence, viewing time and coherence × viewing time dependence (equation (3) of individual MT neurons before and during training for monkeys C, left, and Z, right). Error bars are 68% CIs. (**c**) Relationship between neurometric threshold and choice probability for individual MT neurons during different training periods for monkeys C (■) and Z (▼). Error bars are 68% CIs. Solid lines are linear fits.

LIP responses changed with training

The responses of individual LIP neurons during motion viewing were recorded throughout training (monkey C, $n = 123$; monkey Z, $n = 99$ LIP neurons recorded during training). We determined the average spike rates of the population of LIP neurons recorded from monkey C aligned to motion onset and saccade onset for different training epochs (**Fig. 4a**). Throughout training, in trials in which the monkey selected the saccade target in the neuron's response field, LIP activity tended to increase gradually during motion viewing, stay elevated during the subsequent delay period and then increase just before saccade onset. In trials in which the other target was selected, LIP activity tended to decrease gradually during motion viewing and then remain below baseline levels until after the saccade. The perisaccadic activity tended to be smaller in the first 15 sessions (average activity from –0.5 to –0.1 s before saccade onset was 18.6 spikes s^{-1} from sessions 1–15 and 31.3 spikes s^{-1} from sessions 16–160, t-test, $P = 0.02$ for monkey C; 27.0 spikes s^{-1} from sessions 1–15 and 48.6 spikes s^{-1} from sessions 16–130, $P < 0.01$ for monkey Z), but then remained relatively stable throughout the rest of the training (linear regression, H_0: slope of average activity versus session was 0, $P = 0.12$ for monkey C; $P = 0.31$ for monkey Z). In contrast, the responses during motion viewing changed substantially throughout training, with the rates of rise and fall becoming steeper and increasingly dependent on motion strength (higher coherences corresponding to steeper slopes).

To quantify the effects of training on the coherence-dependent LIP responses, we fit spike-rate data from individual neurons to the same linear model that we used for the MT responses (**Fig. 4b**). For both monkeys, the coherence- and time-alone terms tended to be near zero throughout training (although the coherence term decreased slightly with training to small negative values in both monkeys, and the time term increased slightly with training to small positive values in monkey C). A larger effect was seen in the coherence × time interaction term, which began near zero, indicating that there was little or no influence of the motion stimulus on the LIP responses at the beginning of training, and progressed steadily to more positive values. Because these neurons were selected on the basis

shown that MT neurons predict choice slightly, but reliably, in fully trained monkeys ($\sim$0.55, where 0.5 is chance and 1.0 is perfect; ref. 17), which is the relationship expected for elements in a pool of weakly correlated neurons that provide noisy evidence for the decision[31]. Choice probability increased as a function of training session (combined data from both monkeys, mean ± s.e.m., choice probability of 0.493 ± 0.011 for the first 30% and 0.549 ± 0.018 for the last 30% of sessions). Moreover, the relationship between choice probability and motion sensitivity in the MT changed systematically over the course of training such that more-sensitive neurons became more predictive of the monkey's direction decision as training progressed (correlation coefficient between choice probability and neurometric thresholds of MT neurons in the first one-third of the sessions, $r = 0.02$, H_0: $r = 0$, $P = 0.56$; second one-third of the sessions, $r = -0.23$, $P = 0.11$; third one-third of the sessions, $r = -0.34$, $P = 0.04$; **Fig. 3c**).

In principle, the increases in choice probability could arise from an increase in correlated firing among MT neurons. In a small number of simultaneously recorded pairs of MT neurons, however, preliminary evidence indicated that the degree of correlation was similar before (mean ± s.e.m., correlation coefficient $r = 0.16 ± 0.06$, $n = 8$) and during ($r = 0.18 ± 0.04$, $n = 9$) training and did not increase over the course of training (linear regression, H_0: slope = 0, $P = 0.57$). Thus, the systematic change in choice probability probably reflects an increasingly selective readout of activity from MT neurons, particularly those most sensitive to the motion stimulus.
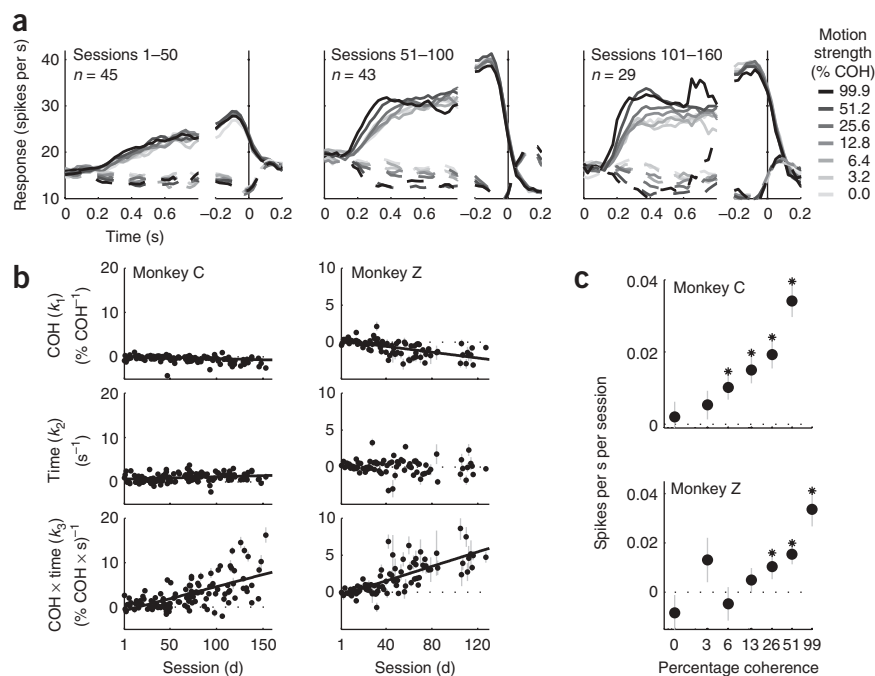
Figure 4 LIP responses. (**a**) Average activity of LIP neurons as a function of viewing time (using 0.1-s-wide time bins with 0.025-s increments) for different motion strengths (see legend) for saccades into (solid line) and out of (dashed line) each neuron's response field during different training periods for monkey C. Only correct trials were included. (**b**) Coherence, viewing time and coherence × viewing time dependence (equation (3)) of individual LIP neurons before and during training for monkeys C, left, and Z, right). Error bars are 68% CIs. Solid lines are significant linear fits ($P < 0.05$ for H_0: slope = 0). (**c**) Coherence-specific effects of training on the rate of rise of LIP activities during motion viewing for monkeys C (top) and Z (bottom). The rate of rise was estimated separately for each coherence using a piecewise-linear function (equation (6) with the coherence-dependence term, β_1, set to zero). Points and error bars are the slope and 68% CIs of a linear regression relating this rate of rise to session number (* indicates $P < 0.05$ for H_0: slope = 0).

of spatially tuned presaccadic activity (see Methods and **Supplementary Fig. 5** online), this result implies that training both established and then shaped the sensory-driven responses in these sensory-motor neurons.

The changes in sensory-driven LIP responses reflected the improvements in behavioral sensitivity to weak motion signals. The pattern of coherence-specific changes in LIP was similar to the pattern of coherence-specific behavioral improvements. Both the rate of the rise of stimulus-driven LIP responses and discrimination performance increased as a function of training session for most nonzero coherences, with greater increases for higher coherences (H_0, slope of a linear regression between session number and either average LIP rate of rise or percent correct for each coherence was 0, $P < 0.05$ for coherences $\geq 6.4\%$ for LIP data and $\geq 3.2\%$ for behavioral data for monkey C, and for coherences $\geq 25.6\%$ for LIP data and $\geq 12.8\%$ for behavioral data

for monkey Z; **Fig. 4c**). Moreover, LIP activity was correlated with behavioral threshold across sessions after taking into account the high-coherence errors (partial correlation $r_\alpha, (k3|\lambda) = -0.42$, H_0: $r = 0$ using Fisher's Z transformation, $P < 10^{-5}$ for monkey C; $r_\alpha, (k3|\lambda) = -0.35$, $P < 0.01$ for monkey Z; **Fig. 5**), but the converse was not true; there was no correlation between high-coherence errors and LIP activity after taking into account the changes in behavioral threshold ($r_\lambda(k3|\alpha) = 0.05$, $P = 0.62$ for monkey C; $r_\lambda(k3|\alpha) = -0.06$, $P = 0.60$ for monkey Z).

The changes in sensory-driven LIP responses with training also did not appear to reflect changes in other motor (**Fig. 5**, middle) or motivational parameters (**Fig. 5**, right) known to modulate LIP activity[21,22]. Some of these parameters changed with training, but none were consistently correlated with the changes in LIP responsiveness over the course of training for both monkeys (**Fig. 5** and **Supplementary Table 1**).
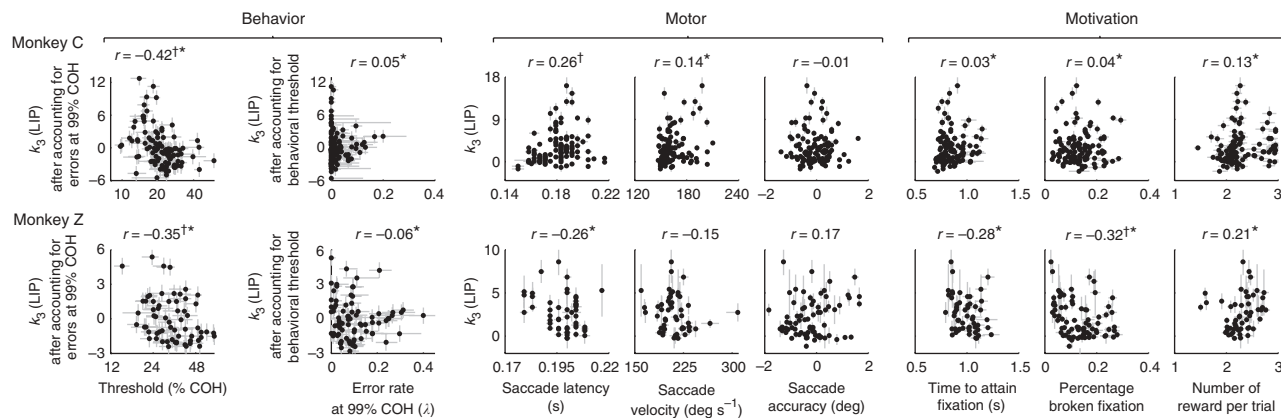

Figure 5 Relationship between the coherence- and time-dependent LIP responses (k_3, equation (3)) and various behavioral, motor and motivational parameters. The *r* values for the behavioral parameters (left two columns) are the partial correlations between each parameter and k_3 with the effect of the other parameter on k_3 removed. Other *r* values are the correlation coefficients between that behavioral parameter and k_3. † indicates a significant correlation between the behavioral parameter and k_3 ($P < 0.05$). * indicates that the behavioral parameter changed significantly as a function of training session (linear regression, $P < 0.05$; see **Supplementary Table 1**). Error bars are 68% CIs.
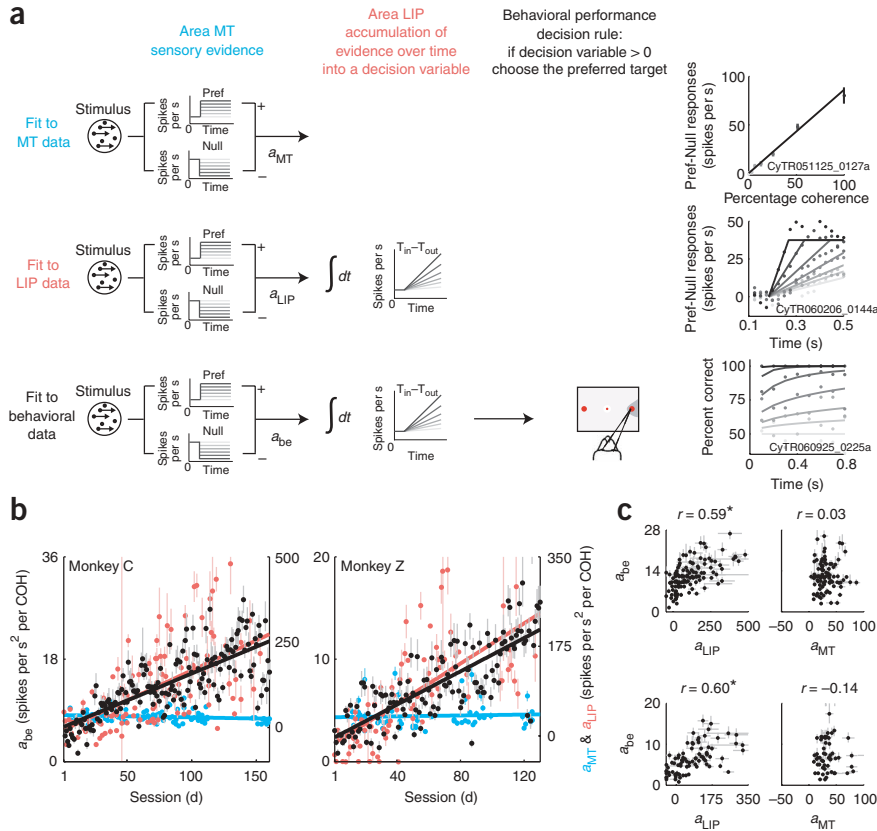
Figure 6 Decision model. (**a**) Schematic of the decision model and example fits to behavioral, MT and LIP data. The decision model assumes that MT represents the coherence-dependent sensory evidence, that LIP accumulates this sensory evidence over time into a decision variable and that the monkey's choice depends on the value of this decision variable. The model allowed us to fit separately data from MT, LIP and behavior, but to extract a common parameter: the coherence dependence of the sensory information represented in each stage of processing (*a* in equation (4)). (**b**) Coherence dependence (best fit values and 68% CIs) computed from behavioral (left axes, black symbols) and neural data (right axes, cyan symbols for MT data, red symbols for LIP data). Solid lines are linear fits (H_0: slope = 0; monkey C: behavior $P < 10^{-10}$, MT $P = 0.11$, LIP $P < 10^{-13}$; monkey Z: behavior $P < 10^{-10}$, MT $P = 0.63$, LIP $P < 10^{-13}$). (**c**) Relationship between *a* computed from behavioral data and neural data. * indicates a significant correlation ($P < 0.05$). Error bars are 68% CIs.

does not affect the representation of sensory evidence in MT directly, but effectively scales its output, providing increasingly sensitive evidence to the decision variable in LIP used to guide behavior.

Specificity of learning

Perceptual learning is typically specific to the stimulus attributes used during training, including motion direction in a direction-discrimination task[33]. This phenomenon helps to distinguish perceptual learning from cognitive or motor changes and has been used to argue that the underlying changes occur at early stages of sensory processing[2]. For our task, the stimulus configuration used in a given session depended on the characteristics of the MT and/or LIP neuron(s) being recorded, and thus varied slightly from session to session (a factor that can in itself affect the specificity of learning[34]). We tested for the specificity of learning by analyzing performance relative to the similarity of the current stimulus configuration to configurations used in previous sessions.

For both monkeys, discrimination performance depended on the familiarity of the axis of motion (**Fig. 7**). For each session, we calculated the difference between the motion sensitivity computed from behavioral data (*a* in equation (4)) and its 21-session running average. This quantity provides an estimate of discrimination performance relative to its current trend; a positive value implies that the performance was better than average, a negative value implies worse-than-average performance. For both monkeys, the value of this quantity was negatively correlated with the absolute *z* score of motion direction (monkey C: correlation coefficients, $r = -0.39$, H_0: $r = 0$ using Fisher's *Z* transformation, $P < 10^{-7}$; monkey Z: $r = -0.49$, $P < 10^{-9}$), indicating that performance tended to degrade when an unfamiliar stimulus was used. This specificity for the axis of motion was mirrored in neural activity in LIP (monkey C: $r = -0.37$, $P < 10^{-3}$; monkey Z: $r = -0.29$, $P = 0.02$; **Fig. 7b**), but not in MT (monkey C: $r = 0.09$, $P = 0.54$; monkey Z: $r = 0.22$, $P = 0.21$; **Fig. 7b**), which is consistent with the idea that perceptual learning can be specific by virtue of what is learned (in this case, the LIP decision variable) and need not involve changes in the sensory representation (direction-selective responses in area MT)[3].

Comparison of behavioral, MT and LIP data during training

In trained monkeys, MT and LIP are thought to have different, but complementary, roles in forming the direction decision; MT (possibly in tandem with other motion-sensitive areas such as the middle superior temporal area) provides sensory evidence used to form the decision, whereas LIP (possibly in tandem with other sensory-oculomotor areas such as the FEF and superior colliculus) accumulates and interprets the sensory evidence to form the categorical judgment that instructs behavior[23]. Our results suggest that the improvements in behavioral sensitivity result from changes not in the sensory representation, but rather in its interpretation.

To test this idea and to more directly compare the MT, LIP and behavioral data, we used a sequence of three nested models. The first model describes the coherence-dependent sensory evidence and was fit to the MT data. The second model builds on the first, describing the accumulation over time of the sensory evidence into a decision variable, and was fit to the LIP data. The third model builds on the second, describing the monkey's decisions in terms of the value of the LIP decision variable, and was fit to the behavioral data[29,32] (**Fig. 6a**). The advantage of this scheme is that the MT, LIP and behavioral data can be fit separately, but then compared directly via a term, common to the three models, describing how the sensory evidence used to form the decision scales with motion coherence (a_{MT}, a_{LIP} and a_{be} in **Fig. 6a**). For both monkeys, the value of this motion-sensitive term grew as a function of training session in a similar manner for data from behavior and LIP, but not from MT (monkey C: correlation coefficient between MT and behavior, $r = 0.03$, H_0: $r = 0$ using Fisher's *Z* transformation, $P = 0.79$; LIP and behavior, $r = 0.59$, $P < 10^{-12}$; monkey Z: MT and behavior, $r = -0.14$, $P = 0.29$; LIP and behavior, $r = 0.60$, $P < 10^{-9}$; **Fig. 6b,c**). A straightforward interpretation of this result is that training
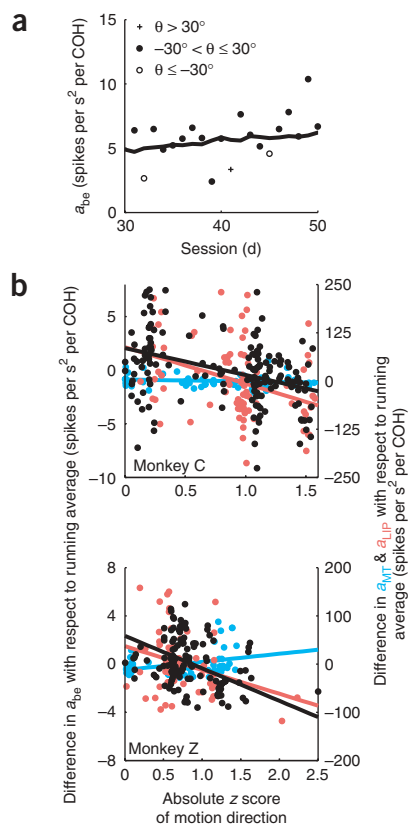
Figure 7 Specificity of learning. (**a**) The coherence dependence of the sensory information (a in equation (4)) estimated from behavioral performance from sessions 30–50 for monkey Z. The solid line is a 21-session running average. (**b**) The difference between the coherence dependence from a given session and its 21-session running average for behavior (black), MT (cyan) and LIP (red) responses are plotted against the absolute z score of motion direction for monkeys C (top) and Z (bottom). For a given session, the z score is computed using the distribution of motion directions used before that session. Thus, less frequently used motion directions will have larger z scores. Solid lines are linear fits.

DISCUSSION

Our results show that for monkeys trained to discriminate the direction of motion of noisy visual stimuli, improvements in discrimination threshold (that is, higher sensitivity to weak motion) corresponded to changes in sensory-driven responses in area LIP, but not in MT. In MT, individual neurons responded similarly to motion stimuli before and throughout training, with, on average, a sensitivity that was similar to that of trained monkeys. However, responses of the most sensitive MT neurons became increasingly predictive of the monkeys' choices with training. In LIP, neurons tuned for saccadic direction were insensitive to visual motion at the beginning of training, but developed responses that grew in an increasingly strong manner with motion strength and viewing time as performance on the task improved. The results suggest that the perceptual improvements corresponded to an increasingly selective readout of highly sensitive MT neurons by a decision process, represented in LIP, that instructed the behavioral response.

Because the motion sensitivity of MT neurons probably arises from their direct and indirect input from V1 (ref. 35), our results appear to rule out learning-induced changes in V1. This finding is consistent with electrophysiological studies in monkeys that found little or no changes in V1 with perceptual learning[7–9] (although larger effects have been

found in V1 of human subjects using functional magnetic resonance imaging[36]) and provides additional evidence that the stimulus specificity of perceptual learning does not necessarily imply changes in primary sensory cortex[3,4]. Our results also further distinguish early visual cortical areas from primary somatosensory and auditory cortices, which in both monkeys and humans can show marked changes with perceptual learning[5,6,37–39]. We cannot rule out the possibility that changes occurred in other parts of extrastriate visual cortex that carried appropriate motion signals, such as the middle superior temporal area[40]. Nevertheless, it is notable that we found no changes in MT sensitivity over the course of training, despite the established role of MT in task performance[16–19], the increase in MT choice probabilities with training (indicating an increasingly strong correspondence with behavior) and the fact that our recording and analysis methods could resolve within-session changes in MT sensitivity[30] that were smaller in magnitude than the longer-term changes that we would expect on the basis of behavior.

The changes that we report for LIP complement and extend previous findings. Learned sensory-motor associations have been shown to correspond to changes in LIP, but not MT[41,42]. Consistent with those findings, we found that motion-driven LIP responses appeared when the monkeys learned the association between motion direction and saccadic response. However, unlike previous studies, we showed that both behavior and LIP responses continued to evolve well after the visuomotor association was established, together reflecting improved sensitivity to weak motion. These results support the possibility that associative and perceptual learning might share common mechanisms[4,43]. Learning a stimulus-response association establishes functional connectivity between neurons that represent the sensory stimulus and neurons that control the motor response. Improvements in perceptual sensitivity might then involve refinement of this connectivity to provide a more selective readout of the most sensitive sensory signals associated with that response. Our results are consistent with such a refinement of direct or indirect ascending projections from MT to LIP[44], an idea that merits further testing.

We do not know the exact role that LIP has in task performance throughout training. In trained monkeys, multiple brain areas including LIP, the superior colliculus and parts of the prefrontal cortex, including the FEF, show similar sensory-motor responses during the performance of the discrimination task[24,25,27,28]. We do not know what, if any, differences exist between the contributions of these brain areas to task performance either during or after training. Moreover, LIP has a multitude of cognitive and sensory-motor roles that could, in principle, change during training and account for the changes in LIP responses during motion viewing[20–22]. However, we found no evidence for such modulation by numerous oculomotor and motivational parameters. Instead, the sensory-driven LIP responses changed in a manner that was consistent with a decision process that used increasingly sensitive motion evidence to determine the saccadic choice. These decision computations represented in LIP appear to be critical for the performance of trained monkeys, an idea that is supported by a close relationship between LIP responses and reaction times[25] and the ability to bias performance using electrical microstimulation of LIP[26]. Additional work is needed to establish similarly strong links between LIP activity, decision-making and behavior throughout training.

The results also further support a close relationship between learning and attention[12]. Of the learning-induced changes that have been found previously in V1, attentional modulation appears to have a primary role[8]. Attentional modulation might likewise account for the slight overall improvement in MT sensitivity in our data when comparing sessions before and during training or, as in several other studies,

within training sessions[30,45]. The changes in choice probabilities in MT and motion-driven responses in LIP might also be thought of in terms of improved attention to appropriate features of the motion representation used to form the decision. This idea is parsimonious with the widely reported role of LIP in spatial and feature-based attention[20,46] and the relationship between attention and perceptual learning in other tasks[12]. It remains to be seen how general a role this kind of mechanism has in different forms of perceptual learning, which can have much different time courses[47], attentional demands[12] and magnitudes[48].

METHODS

Behavioral task. The motion stimulus was a random-dot kinematogram that has been described previously[16,29]. Motion direction, coherence and duration (a random time between 0.1–1.4 s from an exponential distribution) were varied randomly from trial to trial. Correct responses and half of the 0% coherence trials elicited a juice reward of a variable amount (1–4 drops). Incorrect responses were followed by a 'time out' period lasting 1–5 s. Task difficulty was held relatively constant by adjusting the distributions of coherences and viewing times to give a correct response rate of ∼70–80% per session. This design kept the total reward per session roughly constant and helped to keep the monkeys motivated throughout training. Eye position was monitored using a video-based system (ASL) sampled at 240 Hz to enforce fixation during motion viewing and register the saccadic response.

Electrophysiology. Monkeys were prepared for the experiments by surgical implantation of a head-holding device and recording cylinders. Areas MT and LIP were targeted using stereotaxic information and magnetic resonance imaging (**Fig. 1b**). Neural activity was recorded using quartz-coated platinum-tungsten microelectrodes that were advanced using two Mini Matrix systems (Thomas Recording), one per recording cylinder. Spike waveforms were stored and sorted offline (Plexon). All training, surgical and experimental procedures were in accordance with the US National Institutes of Health Guide for the Care and Use of Laboratory Animals and were approved by the University of Pennsylvania Institutional Animal Care and Use Committee.

We searched for MT neurons with consistent spatial, direction and speed tuning, measured using a 99.9% coherence stimulus (**Supplementary Figs. 1** and **3**). We searched for LIP neurons using a delayed-saccade task and selected neurons with spatially tuned delay-period activity[25] and response fields in consistent locations (**Supplementary Figs. 1** and **5**).

Analysis of behavioral data. We fit behavioral data to a time-dependent cumulative Weibull function in which the discrimination threshold is a power function of time:

$$P(C,T) = 0.5 + (0.5 - \lambda) \times \left(1 - e^{-\left(\frac{C}{\alpha T^n}\right)^\beta}\right) \quad (1)$$

where P is the discrimination performance at motion strength C (in percent coherence) and viewing time T (in seconds), λ is the fraction of errors measured for stimuli of 99% coherence and viewing times > 0.4 s, and with fitted parameters α (threshold coherence at 1 s), n (time exponent) and β (shape parameter).

Analysis of MT and LIP data. To quantify the effects of motion coherence and viewing time on the responses of MT and LIP, we first normalized the responses of each neuron:

$$\hat{r}(C,T) = \frac{r(C,T) - r_{BL}}{r_{97.5} - r_{BL}} \quad (2)$$

where $r(C,T)$ is the difference between responses (in spikes s^{-1}) at coherence C and viewing time T to motion toward and away from the neuron's preferred direction (for MT) or preferred choice (for LIP), r_{BL} is the average baseline response (−0.2–0 s) before motion onset and $r_{97.5}$ is the 97.5 percentile response at 99.9% coherence preferred motion.

This normalized response (MT, from 0.1–1.0 s; LIP, from the beginning to the end of the ramp activity, which were estimated by fitting a piecewise-linear

function, equation (6), to the neuron's responses to 99.9% coherent motion) was then fit to a simple linear model:

$$\hat{r}(C,T) = k_0 + k_1 C + k_2 T + k_3 CT \quad (3)$$

with parameters that describe the effect of coherence (k_1), viewing time (k_2) and the coherence × time interaction (k_3) on the neuron's response.

In addition, we also computed the sensitivity (neurometric discrimination threshold)[16] and choice probability[17] of each MT neuron. Sensitivity was computed using a receiver-operating-characteristic analysis of distributions of MT responses separated by motion direction, computed separately for each motion strength and cumulative bins of viewing time from 0–1 s in 0.05-s steps, and fit to equation (1). Choice probability was computed from the distributions of MT responses to 0% coherence stimuli, separated by the monkey's choices.

Model of the decision variable. We modeled the decision variable as the accumulated difference in activity between noisy pools of motion sensors tuned to the correct (S_c) and incorrect (S_i) directions of motion[29]:

$$\begin{aligned} \langle S_c \rangle &= (R_0 + aC^m)T^n \\ \langle S_i \rangle &= R_0 T^n \end{aligned} \quad (4)$$

where C is fraction coherence, T is viewing time (s), R_0 is the response (in spikes s^{-1}) of MT neurons for 0% coherence, $\langle S \rangle$ denotes expectation, and a, m and n are fitted parameters. We assume that S_c and S_i are normally distributed with variances that scale with their mean $\phi = \frac{\text{Var}(S_c)}{\langle S_c \rangle} = \frac{\text{Var}(S_i)}{\langle S_i \rangle}$. A correct response results when $S_c > S_i$. If S_c and S_i are independent and normally distributed, then the probability of a correct response, P, is:

$$P(C,T) = \frac{1}{\sqrt{2\pi\sigma^2}} \int_0^\infty e^{-\frac{(x-\mu)^2}{2\sigma^2}} dx \quad (5)$$

where μ is the expected value of the accumulated difference, $\langle S_c - S_i \rangle = \langle S_c \rangle - \langle S_i \rangle$ and σ^2 is the sum of the variances of S_c and S_i.

We used different versions of the model to estimate the coherence-dependence of the decision variable (the parameter a in equation (4)) separately for the behavioral, MT and LIP data. For behavior, we fit equation (5) to performance. For the MT data, we estimated the linear dependence of preferred-null direction responses averaged over the full viewing duration, consistent with the difference between the time-independent portions of $\langle S_c \rangle$ and $\langle S_i \rangle$. For LIP data, we fit

$$F(C,T) = \begin{cases} \gamma & , \text{if } T < \tau \\ \gamma + (\beta_0 + \beta_1 C)(T - \tau) & , \text{if } T \geq \tau \\ \beta_2 & , \text{if } F(C,T) > \beta_2 \end{cases} \quad (6)$$

to the difference in activity between the neuron's preferred and null choices, letting β_0, β_1, β_2, τ and γ be free parameters and reporting β_1 as the coherence-dependent parameter (equivalent to a in the behavioral model). These estimates are expected to be offset from each other by an overall scale factor because of different pooling assumptions; we fit data from individual MT neurons, from individual LIP neurons that were assumed to pool from an unknown number of MT neurons and from behavioral data assumed to reflect both MT and LIP contributions (note the different axes in **Fig. 6** for behavioral and neural data). Nevertheless, these fits are useful for comparing how each estimate changes with training.

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

AUTHOR CONTRIBUTIONS
J.I.G. planned and supervised the study. C.L. conducted the experiments and data analyses. C.L. and J.I.G. wrote the manuscript together.

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