

1 Learning and attention reveal a general relationship between neuronal variability and perception

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7 The trial-to-trial response variability that is shared between pairs of neurons (termed
8 spike count correlations¹ or r_{SC}) has been the subject of many recent studies largely because it
9 might limit the amount of information that can be encoded by neuronal populations. Spike count
10 correlations are flexible and change depending on task demands²⁻⁷. However, the relationship
11 between correlated variability and information coding is a matter of current debate²⁻¹⁴. This
12 debate has been difficult to resolve because testing the theoretical predictions would require
13 simultaneous recordings from an experimentally unfeasible number of neurons. We hypothesized
14 that if correlated variability limits population coding, then spike count correlations in visual
15 cortex should a) covary with subjects' performance on visually guided tasks and b) lie along the
16 dimensions in neuronal population space that contain information that is used to guide behavior.
17 We focused on two processes that are known to improve visual performance: visual attention,
18 which allows observers to focus on important parts of a visual scene¹⁵⁻¹⁷, and perceptual learning,
19 which slowly improves observers' ability to discriminate specific, well-practiced stimuli¹⁸⁻²⁰.
20 Both attention and learning improve performance on visually guided tasks, but the two processes
21 operate on very different timescales and are typically studied using different perceptual tasks.
22 Here, by manipulating attention and learning in the same task, subjects, trials, and neuronal
23 populations, we show that there is a single, robust relationship between correlated variability in
24 populations of visual neurons and performance on a change-detection task. We also propose an
25 explanation for the mystery of how correlated variability might affect performance: it is oriented
26 along the dimensions of population space used by the animal to make perceptual decisions. Our
27 results suggest that attention and learning affect the same aspects of the neuronal population
28 activity in visual cortex, which may be responsible for learning- and attention-related
29 improvements in behavioral performance. More generally, our study provides a framework for

- 30 leveraging the activity of simultaneously recorded populations of neurons, cognitive factors, and
- 31 perceptual decisions to understand the neuronal underpinnings of behavior.

32 We investigated the relationship between the activity of neuronal populations and
33 behavioral performance by manipulating attention and perceptual learning simultaneously in two
34 rhesus monkeys (*Macaca mulatta*). We recorded from neuronal populations in visual area V4
35 with chronically implanted microelectrode arrays as the monkeys practiced an orientation
36 change-detection task that manipulated spatial attention (**Fig. 1a**). The monkey's task was to
37 detect a subtle change in the orientation of either of two Gabor stimuli that flashed on and off
38 simultaneously, one at a location that overlapped the receptive fields (RFs) of the recorded
39 neurons and the other in the opposite hemifield (**Fig. 1b**).

40 Before recording, the monkeys were briefly trained on the behavioral task so that they
41 were familiar with the task structure. Each monkey was trained to report 90° changes with the
42 attention cue in place: the cued stimulus would change on 80% of trials and the uncued stimulus
43 would change on 20% of trials. We began recording after 2-5 days of training on the full version
44 of the task (see Methods), with performance on cued trials matched between the two stimuli.

45 We designed our experiment to allow us to simultaneously measure attention and
46 perceptual learning in the same behavioral trials and neuronal responses. We quantified the
47 behavioral effects of attention (comparing attended trials (RF stimulus cued) and unattended
48 trials (RF stimulus uncued) within each session) or learning (across sessions) by quantifying the
49 monkey's detection sensitivity for a fixed orientation change (d' ; other behavioral measures gave
50 qualitatively similar results; see **Supplementary Fig. 1**) at the RF location (**Fig. 1c**).

51 Attention and perceptual learning affected performance in similar ways. Both processes
52 were associated with improvements in behavioral sensitivity (**Fig. 2a, h**), albeit on different
53 timescales (attention is the difference between the solid and dashed lines in **Fig. 2a** and **h**, and
54 learning is the change in performance across time). Consistent with other perceptual learning

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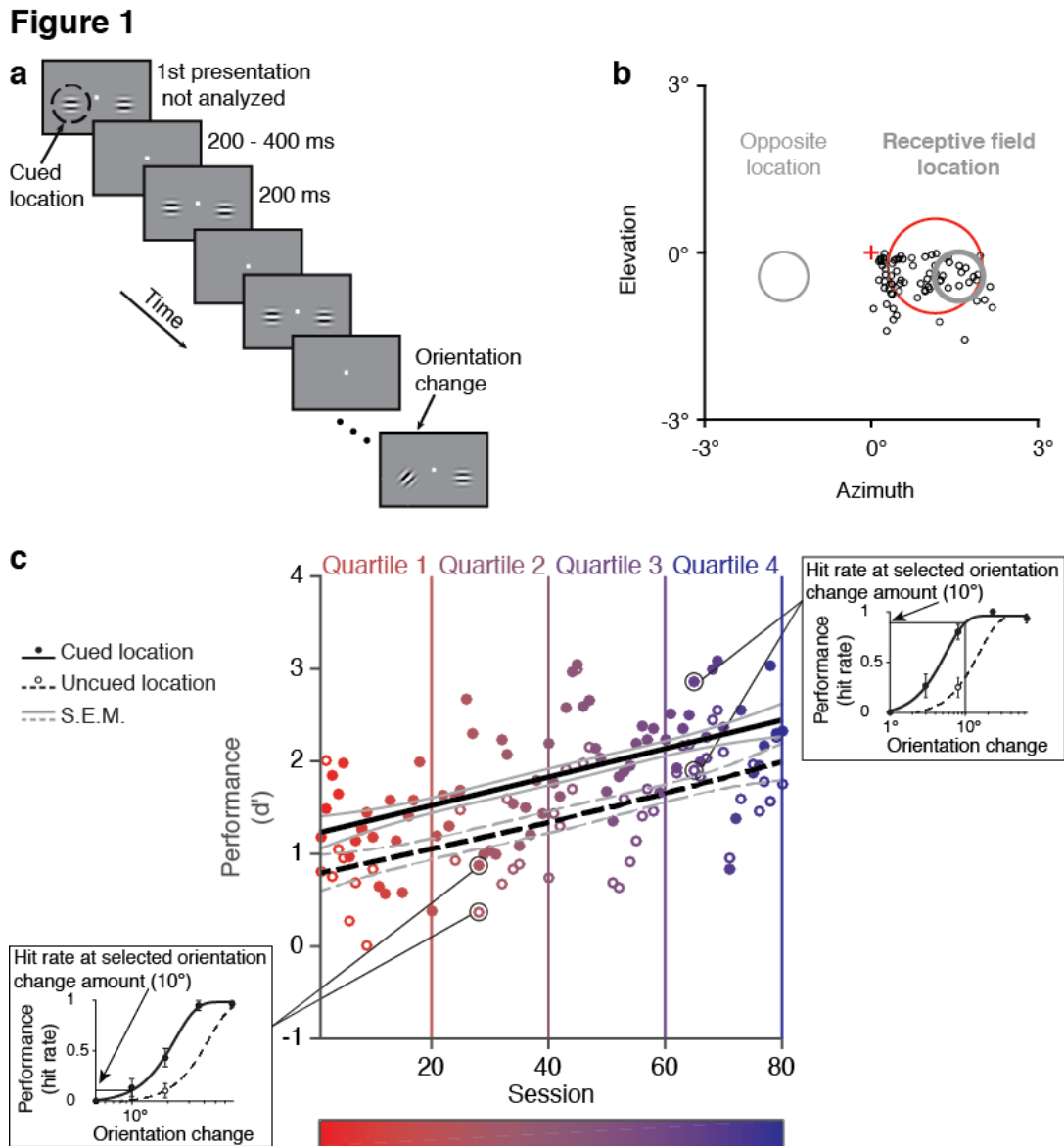


Figure 1 Methods and behavior. **a**, Orientation change-detection task with cued attention². **b**, Centers of visual receptive fields for the recorded units from one monkey (*black circles*). The monkey fixated a central point (*red cross*) while two Gabor stimuli were presented, one overlapping the neuronal receptive fields (*thick gray circle*) and one in the opposite hemifield (*thin gray circle*). The red circle illustrates a representative receptive field size. **c**, Our method for quantifying attention- and learning-related changes in detection sensitivity (d') as a function of session number (one session = 125 trials in each attention condition; multiple sessions per day; see Methods). The best fitting exponential functions are plotted for cued (*solid black line fit to filled circles*) vs. uncued (*dashed black line fit to empty circles*) performance, with S.E.M. indicated (cued: *solid gray lines*; uncued: *dashed gray lines*). The heat map illustrates the session number and learning quartiles, which we used throughout the paper to illustrate learning phase. Insets: Psychometric curves (hit rate as a function of orientation change amount) for two example sessions to illustrate how we calculated hit rate at one selected orientation change amount for each animal (Monkey 1: 29° , Monkey 2: 10°).

56 paradigms^{21,22}, the behavioral improvements associated with learning were specific to the
57 trained stimulus location (**Supplementary Fig. 2**).

58 Both attention and perceptual learning had profound effects on the variability of neuronal
59 responses in V4. Even though the trial-averaged evoked response of individual units did not
60 change consistently with learning^{21,23-27} (**Fig. 2b, i**), attention and learning were associated with
61 decreases in the mean-normalized trial-to-trial variance (Fano factor) of individual units and the
62 correlated variability (r_{SC}) between pairs of units (**Fig. 2c, d, j, k**; see **Supplementary Fig. 3** for
63 eye movement analysis). These decreases in variability appear to be task-specific, as variability
64 in the responses of the same neurons to visual stimuli presented during passive fixation was
65 constant throughout the recording period (**Fig. 2f, g, m, n**). The data also suggest that the
66 monkeys had already learned to attend during the initial training period and they were improving
67 sensitivity at orientation change-detection rather than learning to attend during the recording
68 period. The perceptual learning-related increase in behavioral sensitivity across sessions was not
69 accompanied by changes in the signatures of attention across sessions (**Supplementary Fig. 4**).

70 Task-related changes in response variability (particularly correlated response variability)
71 have attracted considerable attention because they have the potential to change the amount of
72 sensory information encoded in a population of neurons, which might limit performance. In
73 theoretical studies, however, the relationship between response variability and population coding
74 is a matter of active study^{8-11,28,29}. The fundamental concern is that correlated variability should
75 only affect information coding if it lies along the dimensions in neuronal population space along
76 which task related information is read out^{10,14}. However, determining whether the correlated
77 variability would affect an optimal decoder based on the thousands of neurons that respond to
78 any stimulus is nearly impossible with experimentally tractable data sets.

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Figure 2

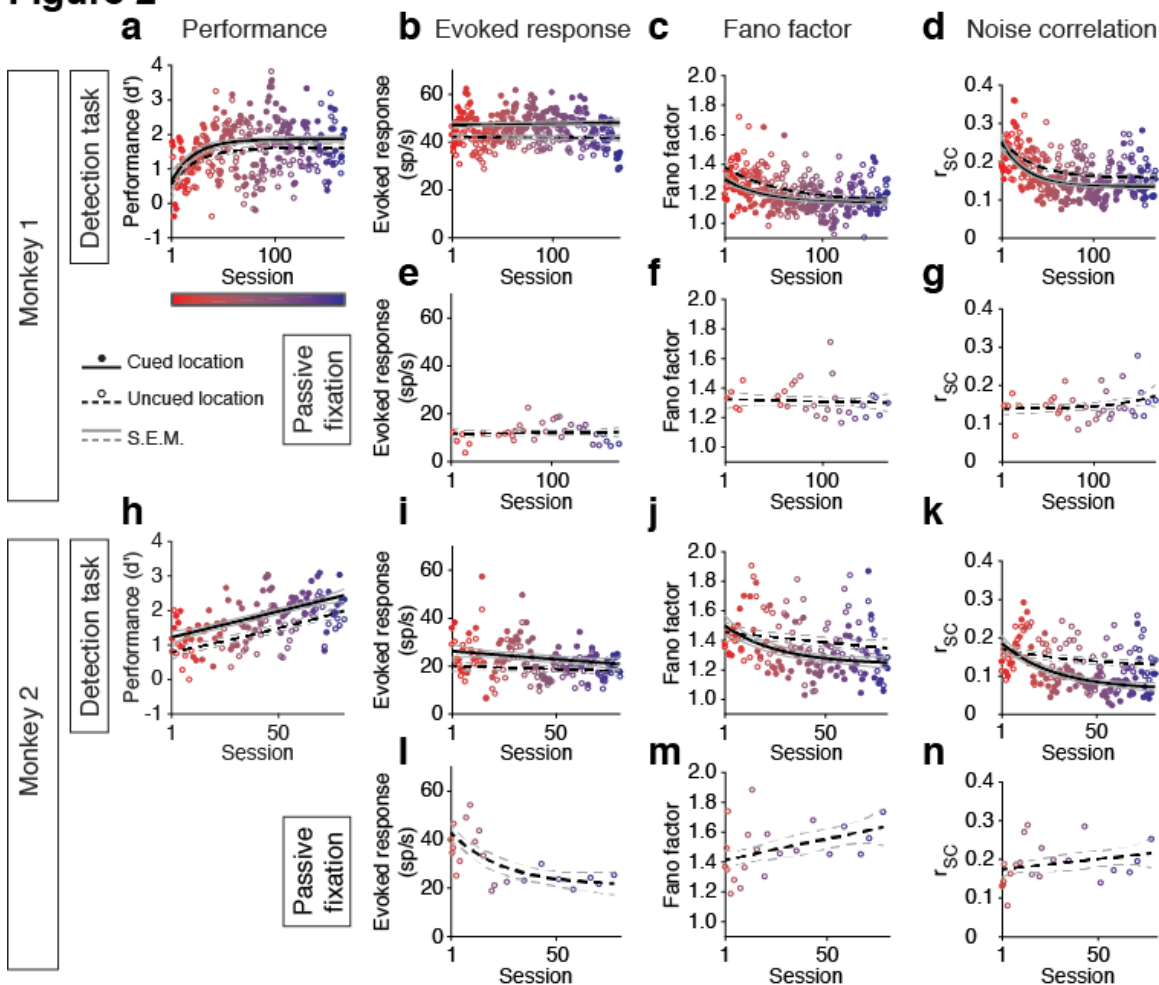


Figure 2 Summary of the behavioral and neuronal effects of attention and perceptual learning. Each plot follows the format of **Fig. 1c**. We quantified the effects of attention using a paired t-test comparing cued and uncued trials within each session and the effects of learning during the cued attention condition using a two-tailed t-test comparing sessions from the first vs. second half of the total training period, without assuming equal variances. Number of sessions: detection task: Monkey 1: $n = 150$, Monkey 2: $n = 78$; passive fixation: Monkey 1: $n = 35$, Monkey 2: $n = 22$. Mean number of single or multiunits per session: Monkey 1: $n = 34$, Monkey 2: $n = 15$. **a-g**, Monkey 1. **h-n**, Monkey 2. **a,h**, Sensitivity (d') increased with both attention (Monkey 1: $p < 10^{-8}$; Monkey 2: $p < 10^{-12}$) and learning (Monkey 1: $p < 10^{-4}$; Monkey 2: $p < 10^{-9}$). **b,e,i,l**, Evoked response (firing – baseline rate) increased with attention (Monkey 1: $p < 10^{-37}$; Monkey 2: $p < 10^{-14}$) but did not change consistently with learning or passive fixation (no change in Monkey 1, $p = 0.13$ learning, $p = 0.44$ fixation; decrease in Monkey 2, $p < 10^{-3}$ learning, $p < 10^{-3}$ fixation). **c,j**, Fano factor decreased with both attention (Monkey 1: $p < 10^{-5}$; Monkey 2: $p < 10^{-4}$) and learning (Monkey 1: $p < 10^{-5}$; Monkey 2: $p < 10^{-3}$). **f,m**, Fano factor decreased only in the context of the detection task and not during passive fixation (Monkey 1: $p = 0.14$; Monkey 2: $p = 0.05$). **d,k**, Correlated variability decreased with both attention (Monkey 1: $p < 10^{-8}$; Monkey 2: $p < 10^{-8}$) and learning (Monkey 1: $p < 10^{-4}$; Monkey 2: $p < 10^{-5}$). **g,n**, Correlated variability did not change during passive fixation (Monkey 1: $p = 0.47$; Monkey 2: $p = 0.47$).

80 We addressed the importance of attention- and perceptual learning-related changes in
81 response variability by investigating their relationship to behavior. One strong prediction of the
82 hypothesis that response variability limits task performance is that changes in response
83 variability should always be associated with changes in psychophysical performance, regardless
84 of whether the changes in variability came about from attention, learning, or some other factor.

85 Consistent with this prediction, we found that there is a single, robust relationship
86 between correlated variability and perceptual performance, whether changes in perceptual
87 performance happen quickly (attention) or slowly (learning; **Fig. 3a,b**). This relationship does
88 not simply reflect the long-term changes in correlated variability and performance due to
89 perceptual learning or the changes caused on a faster timescale by attention. It also reflects
90 factors outside experimental control: the relationship between correlated variability and detection
91 sensitivity was robust even when we examined the residuals of each measure after removing the
92 variability captured by the exponential fits in **Fig. 2 (Fig. 3c,d)**. These results show that
93 correlated variability in visual cortex is a reliable indicator of performance in this task.

94 We used two additional, complementary measures of population activity to further
95 investigate the hypothesis that the attention- and perceptual learning-related decreases in
96 response variability were responsible for the behavioral improvements we observed. First, we
97 calculated the ability of an optimal, cross-validated linear decoder to detect changes in the
98 orientation of the stimuli we presented. In small neuronal populations, decreases in correlated
99 variability would be expected to reduce redundancy and increase the information encoded by the
100 population if the neurons responded similarly to the stimulus change^{6,30}. In fact, in our data set,
101 the vast majority of the units fired more strongly in response to the orientation change (93% of
102 units; presumably because of a release from adaptation).

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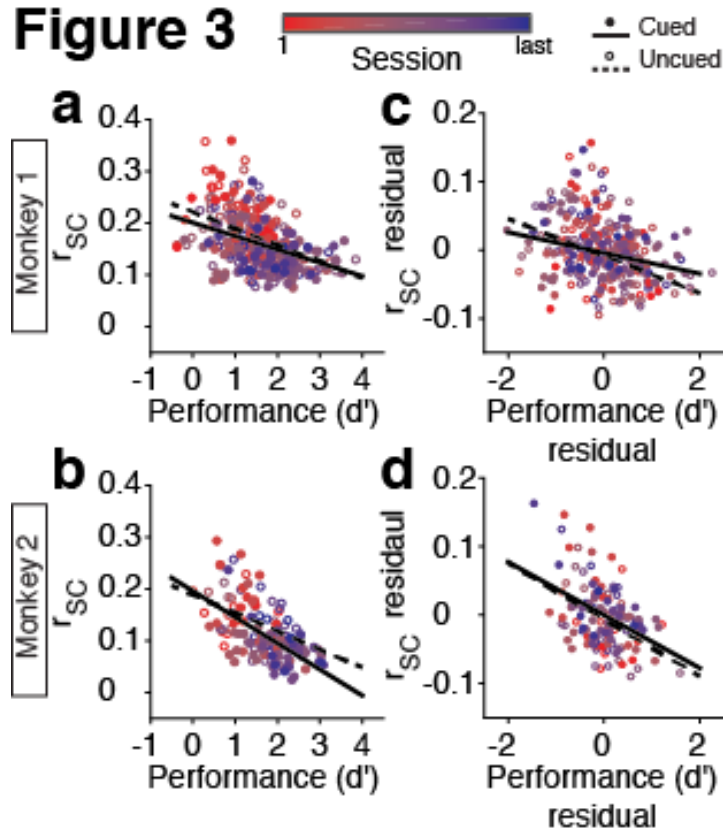


Figure 3 The relationship between correlated variability and performance is the same for attention and perceptual learning. **a,b**, Mean r_{SC} and d' were significantly correlated for both animals and the relationship between the two was indistinguishable for the two attention conditions. **a**, Monkey 1: Pearson correlation coefficients: cued: $R = -0.40$, $p < 10^{-7}$; uncued: $R = -0.48$, $p < 10^{-9}$; the cued and uncued correlation coefficients were indistinguishable (ZPF test: $zpf = -0.92$, $p = 0.36$). **b**, Same for Monkey 2. Cued: $R = -0.59$, $p < 10^{-9}$; uncued: $R = -0.45$, $p < 10^{-4}$; $zpf = 1.12$, $p = 0.26$. In both animals, the relationship between Fano factor and d' was weaker (data not illustrated). Monkey 1 cued: $R = -0.15$, $p = 0.08$; uncued: $R = -0.30$, $p < 10^{-4}$. Monkey 2 cued: $R = -0.56$, $p < 10^{-7}$; uncued: $R = -0.28$, $p = 0.06$. **c,d**, The relationship between r_{SC} and d' persisted even when we looked only at the residuals after removing the effects of attention and learning (exponential fits in **Fig. 2**). **c**, Monkey 1: r_{SC} residual vs. d' residual. Cued: $R = -0.26$, $p < 10^{-3}$; uncued: $R = -0.40$, $p < 10^{-7}$; $zpf = 1.5$, $p = 0.12$. **d**, Same for Monkey 2. Cued: $R = -0.45$, $p < 10^{-5}$; uncued: $R = -0.44$, $p < 10^{-3}$; $zpf = 0.04$, $p = 0.97$. Number of sessions: Monkey 1: $n = 150$, Monkey 2: $n = 78$. To test whether the residuals contained attention- or learning-related trends not captured by the exponential fits, we ran an ANOVA per monkey to test the effects of session number and attention condition on the d' residual, and an ANOVA per monkey to test the effects of those same two variables on the r_{SC} residual: we did not find any significant main effects or interactions for either monkey ($p > 0.40$).

104 Both attention and perceptual learning improved the performance of the optimal stimulus
105 decoder (**Fig. 4a-d**). The attention- and learning-related differences in decoder performance
106 tended to increase with increasing number of units (the lines in **Fig. 4a-d** diverge), suggesting
107 that changes in the relationships between multiple units, rather than changes in the means or
108 variability of the responses of single neurons, were responsible for the improvement in decoder
109 performance. Consistent with this idea, the relationship between correlated variability and the
110 amount of information encoded by the neuronal population was the same for attention and
111 learning (**Fig. 4e-f**).

112 Although it is tempting to infer from the results in **Fig. 4** that attention and perceptual
113 learning improve the amount of visual information encoded in V4, the neuronal populations we
114 recorded are small subsets of the neurons that encode task-relevant visual information, and it is
115 possible that changes in correlated variability do not affect the amount of visual information
116 encoded in larger populations. However, the robust relationship between correlated variability,
117 the amount of information encoded by small populations, and behavior suggests that correlated
118 variability is at least a byproduct of the process causally responsible for improving performance.

119 We reasoned that we could examine the relationship between correlated variability and
120 performance more directly by looking at the relationship between population activity and the
121 animal's behavior on a trial-by-trial basis. For example, finding that correlated variability can
122 predict errors would imply a close relationship between spike count correlations and decisions.
123 However, comparing variability to individual choices requires a measure of correlated variability
124 on a single trial, and spike count correlations (and Fano factor) are only defined over many trials.
125 We therefore used principal component analysis (PCA) on population responses to repeated
126 presentations of the same visual stimulus (the stimuli before the orientation change; the same

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Figure 4

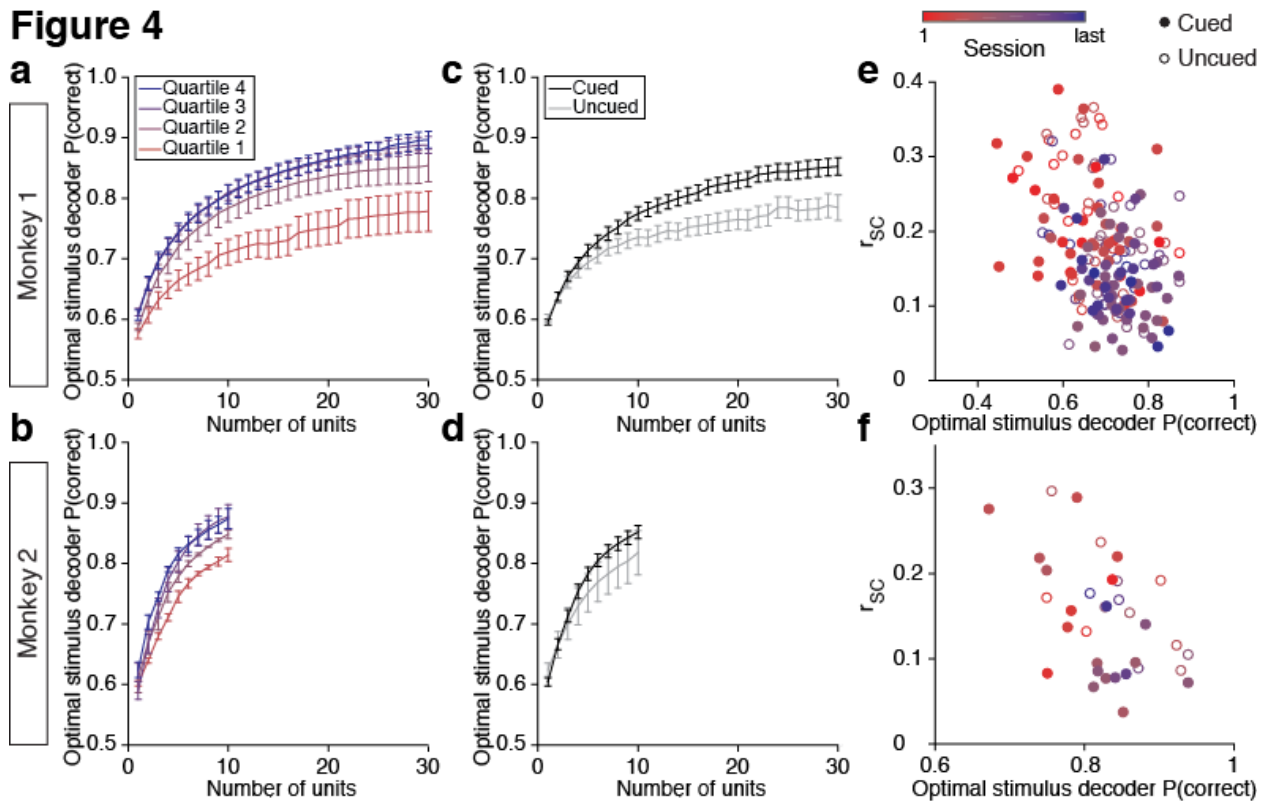


Figure 4 The ability of an optimal, linear, cross-validated decoder to detect changes in the visual stimulus improves with perceptual learning and attention in a way that is predicted by changes in correlated variability. **a**, Optimal stimulus decoder performance improves throughout learning over a long time period (see **Fig. 1c** for learning quartile illustration) for Monkey 1, **b**, and Monkey 2, **c**, as well as with attention within each day for Monkey 1, **d**, and Monkey 2. Error bars are S.E.M. Number of days: Monkey 1: $n = 37$, Monkey 2: $n = 10$. **e**, The relationship between correlated variability (r_{SC}) and optimal stimulus decoder performance is the same for attention and learning for Monkey 1: Pearson correlation coefficients: cued: $R = -0.41$, $p < 10^{-5}$; uncued: $R = -0.37$, $p < 10^{-3}$; ZPF test: $zpf = 0.30$, $p = 0.77$, **f**, and Monkey 2: cued: $R = -0.56$, $p = 0.01$; uncued: $R = -0.66$, $p = 0.01$; $zpf = -0.44$, $p = 0.66$. The relationship between Fano factor and decoder performance was weaker (Monkey 1 cued: $R = -0.19$, $p = 0.06$; uncued: $R = -0.18$, $p = 0.15$. Monkey 2 cued: $R = -0.53$, $p = 0.02$; uncued: $R = -0.42$, $p = 0.14$). Number of sessions/days (days separated into sessions when possible): Monkey 1: $n = 101$, Monkey 2: $n = 20$.

128 stimuli used to compute spike count correlations in **Fig. 2-3**) to identify the axis in population
129 space that accounts for the most correlated variability. To do so, we plotted the responses of the
130 population in a population space where each dimension represents the firing rate of one unit, and
131 performed PCA on the result (**Fig. 5a**). Because this cluster of points consisted of population
132 responses to repeated presentations of the same visual stimulus, the first PC represents the
133 dimension that accounts for the most shared trial-to-trial variability across the population (dashed
134 line in **Fig. 5a**). Consistent with the recent observation that correlated variability is typically low
135 dimensional³¹⁻³⁴, we found that the variance explained by the first PC accounted for the majority
136 of the session-to-session variability in spike count correlations, even when we accounted for the
137 changes caused by attention and perceptual learning (**Fig. 5b,c** and **Supplementary Fig. 5**).

138 These analyses show that, to a first approximation, variability along the first PC accounts
139 for pairwise spike count correlations. This puts us in a position to assess the importance of
140 correlated variability to the monkey by determining whether population activity along this first
141 PC can predict the monkey's choices on a trial-by-trial basis.

142 We found that activity along this first PC (and therefore correlated variability) has a
143 much stronger relationship with the monkey's behavior than its influence on the performance of
144 the stimulus decoder. A linear, cross-validated choice decoder (**Fig. 5a**) could detect differences
145 in hit- vs. miss-trial responses to the changed stimulus as well from population activity along the
146 first PC alone as it could maximally differentiate hit- vs. miss-trial responses with larger
147 numbers of PCs (green lines; **Fig. 5d,e**). In contrast, the stimulus decoder (**Fig. 5a**) was much
148 worse at detecting differences in responses to the previous stimulus (the stimulus prior to the
149 change) vs. the changed stimulus based on the first PC alone as compared to its maximum
150 performance with larger numbers of PCs (black lines; **Fig. 5d,e**).

Figure 5

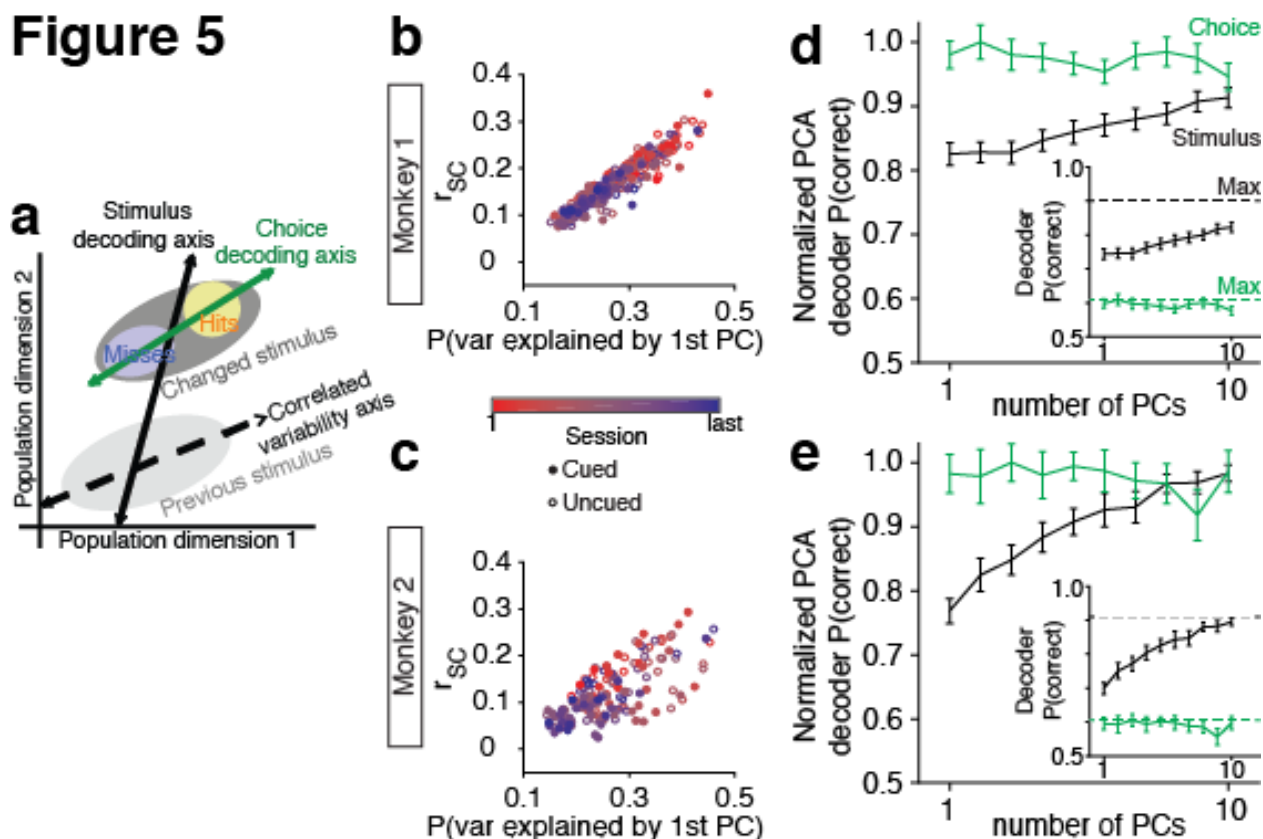


Figure 5 Correlated variability affects the monkey's behavior more than it affects the optimal stimulus decoder. **a**, Decoder schematic. Responses to the stimulus before the change (previous stimulus, *light gray ellipse*) and to the changed stimulus (*dark gray ellipse*) are plotted in a subset of a high dimensional space in which each dimension represents the responses of one unit. The axis that explains the most variability in responses to the previous stimulus (*dashed line*) is by definition the axis that explains the most correlated variability. The choice decoder (*green line*) decodes differences in responses between detected (hits) and missed stimulus changes (*yellow and blue ellipses*). The stimulus decoder detects differences between the neuronal responses to the previous and changed stimuli. **b**, The mean r_{SC} is highly correlated with the proportion of variance explained by the first PC (*dashed line* in **a**). Monkey 1: Pearson correlation coefficients: cued: $R = 0.94$, $p < 10^{-68}$; uncued: $R = 0.94$, $p < 10^{-68}$. The relationship remains for the residuals of the exponential fits for r_{SC} vs. variance explained by PC 1. Cued: $R = 0.92$, $p < 10^{-60}$; uncued: $R = 0.92$, $p < 10^{-61}$. **c**, Same for Monkey 2. Cued: $R = 0.67$, $p < 10^{-11}$; uncued: $R = 0.67$, $p < 10^{-11}$. Residuals: cued: $R = 0.62$, $p < 10^{-9}$; uncued: $R = 0.67$, $p < 10^{-11}$. Number of sessions: Monkey 1: $n = 150$, Monkey 2: $n = 78$. **d**, PCA choice decoder and PCA stimulus decoder performance per number of PCs, normalized to the respective decoder's maximum performance (each decoder was run with all testable numbers of PCs, from 1 to a maximum of 42). Inset shows raw decoder performance. For Monkey 1, the PCA choice decoder could distinguish hit from miss trials as well from population activity along the first PC only (*leftmost point of the green line*) as it could maximally distinguish with larger numbers of PCs ($p = 0.44$). The stimulus decoder could not distinguish the previous from the changed stimuli as well based on the first PC (*leftmost point of the black line*) as it could maximally distinguish with larger numbers of PCs ($p < 10^{-3}$). Error bars are S.E.M. **e**, Same format as **d**, for Monkey 2. Choice decoder paired t-test: $p = 0.93$. Stimulus decoder paired t-test: $p < 10^{-6}$. Number of days: Monkey 1: $n = 37$, Monkey 2: $n = 10$.

152 Unsurprisingly for a population of neurons in visual cortex, a linear decoder could detect
153 the stimulus change from the neuronal population responses (black lines; **Fig. 5d,e** insets) much
154 better than it could detect the animal's choices from those same responses (green lines; **Fig. 5d,e**
155 insets). However, the relative influence of the first PC was much stronger for the choice decoder
156 than for the stimulus decoder. We normalized the performance of each PCA decoder per number
157 of PCs to its own maximum performance to highlight the very different slopes (**Fig. 5d,e**). The
158 choice-predictive activity was essentially completely explained by variability along the first PC,
159 while the stimulus-predictive signals along the first PC were much lower than their peak. The
160 choice decoder uses the monkey's choices to infer the most important subspace of population
161 activity for the monkey's decisions, and this subspace was highly influenced by correlated
162 variability.

163 It is difficult to determine from extracellular recording data whether choice-predictive
164 signals come from a bottom-up, causal relationship between sensory responses and decisions or
165 from trial-to-trial variability from cognitive factors or post-decision signals^{35,36}, and a recent
166 study identifying the directionality of choice-predictive signals in mouse sensory cortex found
167 that they are both bottom-up and top-down in origin³⁷.

168 To determine whether the choice-predictive activity in the populations of neurons we
169 recorded is well positioned to causally affect decisions, we examined the time course of the
170 choice-predictive activity. Neuronal responses to the changed stimulus were calculated based on
171 each neuron's initial response to the changed stimulus (60-130 ms after stimulus onset, which
172 corresponds to the first 70 ms of the evoked response after the response latency of V4 neurons)
173 to avoid artifacts from behavioral responses (the monkeys began eye movement responses to the
174 changed stimulus an average of 210 ms after stimulus onset; as a note, all changed and previous

175 stimulus responses were taken from this same time frame for all decoder analyses). We
176 compared the choice-predictive activity in the first half of this time frame (60-95 ms) to that of
177 the second half (96-130 ms) and found that the choice-predictive activity was as strong during
178 the first spikes of the stimulus response (Monkey 1: mean of 61% correct decoder performance;
179 Monkey 2: mean of 60%) as it was later in the response (Monkey 1: mean of 60%, paired t-test:
180 $p = 0.43$; Monkey 2: mean of 57%, $p = 0.25$). That the choice-predictive activity described here
181 is present early in the evoked response suggests that it does not reflect post-decision feedback.
182 Therefore, while we cannot determine whether the choice-predictive signals come from sensory
183 or cognitive factors, they are present during the full decision-making period.

184 The results from **Fig. 5** are consistent with the idea that correlated variability influenced
185 the monkeys' performance. This would mean that the monkeys are suboptimal in a very
186 particular way, such that correlated variability strongly influences performance. To investigate
187 whether the monkeys' choices were influenced by activity along the first PC (and thus, spike
188 count correlations; **Fig. 5b,c**) in a complementary way, we compared projections of population
189 responses to the stimuli before the orientation change onto the first PC with weighted sums of
190 population activity using a method described by Haefner and colleagues⁹ to infer the weights the
191 monkeys used to make decisions (based on the correlation structure and the neuronal responses
192 to the changed stimulus on hit vs. miss trials). We found that the projections onto the first PC
193 were correlated with the weighted sums predicted by this decoding method for both monkeys
194 (Monkey 1: median Pearson correlation coefficient across days: $R = 0.69$; two-tailed Wilcoxon
195 signed rank test of the Pearson correlation coefficient across days: $p < 10^{-8}$; Monkey 2: $R = 0.48$,
196 $p < 10^{-6}$). Together, these results suggest that while an optimal decoder may in theory be able to

197 discount correlated variability, the monkey's choices can be predicted by the very dimension that
198 is most influenced by correlated variability.

199 **Discussion**

200 We showed that attention and perceptual learning have the same effects on populations of
201 neurons in visual cortex, and that changes in spike count correlations might underlie behavioral
202 improvements. Correlated variability covaries with performance in ways that are
203 indistinguishable for attention, learning, and factors outside experimental control (based on
204 comparisons of residuals that exclude attention and learning effects in **Fig. 3c,d**), and population
205 activity along the dimension that explains most correlated variability is strongly associated with
206 the animal's choices on a trial-by-trial basis.

207 The notable perceptual learning-related changes in spike count correlations we observed
208 are in contrast to the often modest effects of learning on the activity of single neurons that we
209 and others observed. Most prior electrophysiological studies of perceptual learning that focused
210 on the trial-averaged activity of single neurons found, as did we, minimal to no effects of
211 learning on evoked firing rates in visual cortex^{21,23-27}. A study of pairs of simultaneously
212 recorded units found that spike count correlations varied across subjects based on training
213 experience, but did not find a relationship between this shared variability and population coding
214 efficiency⁵, while other studies suggest that learning shapes neuronal population measures^{38,39}.
215 These results are consistent with the idea that correlated variability might affect decision-making
216 through means other than the information that can be gleaned by an optimal decoder. Our
217 approach allowed us to study perceptual learning in two ways: measuring its effects on neuronal
218 populations and comparing it to visual attention in the same neurons and trials. This approach
219 revealed that attention and learning have similar effects on visual cortex, including
220 indistinguishable effects on spike count correlations that are well positioned to affect
221 performance.

222 An alternative hypothesis is that the monkeys were learning to attend throughout the
223 recording period, and that the behavioral and neurophysiological effects of attention and
224 perceptual learning were similar because perceptual learning acts through attention^{18-20,23,25,26,40}.
225 However, the effects of attention did not change throughout the perceptual learning period, as the
226 behavioral and neuronal signatures of attention did not change across sessions (**Supplementary**
227 **Fig. 4**).

228 The robustness of the relationship between correlated variability and perceptual
229 performance, whether detection sensitivity changes on a moment-by-moment basis due to shifts
230 in attention or gradually over long periods through perceptual learning, suggests that while the
231 mechanisms of attention and learning act on different time frames, these processes share a
232 common computation in terms of their effects on the information encoded in visual cortex. Some
233 characteristics of this computation are informed by recent studies showing that a low rank
234 modulator whose strength is affected by attention could simultaneously account for the attention-
235 related changes in rate, Fano factor, and correlated variability in populations of V4 neurons³³⁻³⁴.
236 An intriguing possibility proposed by a recent theoretical study³² is that attention and perceptual
237 learning decrease the strength of such a modulator by changing the balance of inhibition and
238 excitation in V4. Such a mechanism might improve performance through some combination of
239 improving the amount of visual information encoded in populations of neurons and improving
240 the fidelity with which that information is communicated to the downstream areas involved in
241 forming perceptual decisions^{12,41}. Studying how very different processes such as attention and
242 learning affect perception in common ways provides a new framework for understanding the
243 relationship between neuronal population activity and perception.

244 Spike count correlations have been a subject of many studies in part because they provide

245 a tempting explanation for why performance on sensory tasks is worse than the amount of
246 information encoded by neuronal populations with independent neurons¹⁴. Spike count
247 correlations are flexible and change depending on the behavioral task in ways that seem
248 consistent with the hypothesis that they limit performance on psychophysical tasks²⁻⁷. However,
249 the relationship between correlated variability and population coding is complicated because it
250 depends strongly on population size, and determining whether spike count correlations could
251 change the information encoded by large populations would require simultaneous recordings
252 from an experimentally unfeasible number of neurons over an even more impossible number of
253 behavioral trials^{10,14}.

254 We approached this question using behavior as our anchor, and found two lines of
255 evidence suggesting that spike count correlations affect psychophysical performance. First, there
256 is a robust, consistent relationship between correlated variability and performance, which is
257 identical for attention and perceptual learning. Second, correlated variability is associated with
258 the animals' choices on a trial-by-trial basis: variability along the axis in population space that
259 was most closely associated with spike count correlations accounted for essentially all of the
260 choice-predictive activity in our recorded population of neurons.

261 These results suggest that 1) if the change in correlated variability does not cause the
262 improvements in performance associated with attention and perceptual learning, it is a byproduct
263 of the neuronal mechanism that does and 2) the decision-making mechanism is suboptimal in a
264 way that emphasizes the impact of correlated variability. This might arise because some
265 biological mechanism (perhaps related to the aspects of population activity that are
266 communicated to the downstream neurons involved in perceptual decision making⁴¹) causes
267 correlated variability to affect the readout of neuronal populations more strongly than predicted

268 by an optimal decoder. It is difficult to dissociate whether the monkeys are acting optimally with
269 less information or suboptimally: in the future, inactivation experiments may help make this
270 distinction^{11,42}. Our results suggest that correlated variability is well posed to limit performance
271 on visually guided tasks.

272 **Methods**

273 The subjects were two adult male rhesus monkeys (*Macaca mulatta*, 8 and 10 kg). All
274 animal procedures were approved by the Institutional Animal Care and Use Committees of the
275 University of Pittsburgh and Carnegie Mellon University.

276 **Behavioral task**

277 Before recording, we trained each monkey on the basic orientation change-detection task
278 (**Fig. 1a**) and the meaning of the attention cue. Attention was cued to the left stimulus in one
279 block of 125 trials, and to the right stimulus in a second block, with the two blocks making up a
280 single session. In each session, 20% of trials (all at the middle or largest orientation change) were
281 invalidly cued². We began recording once the monkey's behavior was stable enough to produce
282 reliable fits of the Weibull function to the psychometric data. The size, location, and spatial
283 frequency of the Gabor stimuli were fixed throughout learning. The orientation of all stimuli
284 before the orientation change was consistent throughout each recording session but changed by
285 15° between days.

286 **Recordings**

287 We recorded extracellularly from single units and sorted multiunit clusters (the term
288 “unit” refers to either; 19-42 units per session, mean 34 for Monkey 1; 6-25 units per session,
289 mean 15 for Monkey 2) in V4 of the left hemisphere using 96-channel microelectrode arrays
290 (Blackrock Microsystems) as previously described². We presented visual stimuli and tracked eye
291 position as previously described⁶.

292 The data presented are from 42 d of recording for Monkey 1 and 28 d of recording for
293 Monkey 2. Each day consisted of 1-7 sessions (mean of 3.6/d for Monkey 1; 2.9/d for Monkey
294 2), for a total of 150 sessions for Monkey 1 and 78 sessions for Monkey 2. Data were collected

295 during passive fixation on 35 d for Monkey 1 and 22 d for Monkey 2.

296 **Data analysis**

297 We based most neuronal analyses on spike count responses between 60-260 ms after
298 stimulus onset. All analyses used correct and miss trials only (i.e., trials in which an orientation
299 change occurred). To minimize the impact of adaptation on our results, we did not analyze the
300 first stimulus presentation in each trial.

301 We only analyzed a recorded unit if its stimulus-driven firing rate was significantly
302 higher than baseline (Wilcoxon signed rank test; $p < 10^{-10}$). We only included complete sessions,
303 and excluded sessions from analyses if average baseline activity across included units was less
304 than 20 Hz, and outlier sessions were excluded from analyses based on the Tukey method.

305 We fit sets of data across all sessions with the following exponential equations. For
306 exponential decay of increasing form:

$$y = a(1 - e^{-bx}) + c$$

307 For exponential decay of decreasing form:

$$y = ae^{-bx} + c$$

308 We compared the correlation between two variables in the cued attention condition to the
309 correlation between the same two variables in the uncued attention condition using the ZPF test
310 for dependent but non-overlapping Pearson's correlation coefficients⁴³.

311 **Decoder**

312 The optimal stimulus decoder was a linear classifier with leave-one-out cross validation
313 that was trained to discriminate the stimulus before the change from the changed stimulus. We
314 measured decoder performance as a function of population size. The maximum number of units
315 per monkey was based on classifier constraints on the pooled covariance matrix (Monkey 1: 30

316 units; Monkey 2: 10 units). We randomly selected subsets of units without replacement 1000
317 times for each population size. To maximize the number of behavioral trials, we analyzed all
318 trials in a given day together (with the exception of the comparisons to spike count correlations
319 and Fano factor in **Fig. 4e,f**, for which days were divided into sessions when possible), focusing
320 only on trials that presented the middle orientation change amount, for which we had cued and
321 uncued changes. Because the middle orientation change amount varied across recording days, we
322 matched the distributions of orientation change amounts across learning in all analyses. For
323 comparisons to spike count correlations and Fano factor (**Fig. 4e,f**), spike count correlations and
324 Fano factor were calculated for the same stimuli used for the decoder.

325 To avoid artifacts in neuronal firing rates due to eye movements in response to the
326 changed stimulus, we performed decoder analysis on the changed and previous stimulus
327 responses with an abbreviated time window: spike count stimulus responses were measured
328 between 60-130 ms after stimulus onset.

329 The PCA stimulus decoder differed from the optimal stimulus decoder only in that we
330 decoded activity in the first n PCs instead of in the responses of subsets of n neurons. The PCs
331 were based on responses to the stimulus before the orientation change as described in the text.
332 All neuronal responses used for the decoder (responses to the stimulus before the change and
333 responses to the changed stimulus) were projected onto those PCs. The PCA choice decoder
334 (*Choice decoding axis*; **Fig. 5a**) classified population responses to the changed stimulus on hit
335 vs. miss trials projected onto the PCs from the stimulus before the change.

336 **Methods References**

337 43. Raghunathan, T. E., Rosenthal, R. & Rubin, D. B. Comparing correlated but nonoverlapping
338 correlations. *Psychol Methods* **1**, 178-183 (1996).

339 **References**

- 340 1. Cohen, M. R. & Kohn, A. Measuring and interpreting neuronal correlations. *Nat Neurosci*
341 **14**, 811-819 (2011).
- 342 2. Cohen, M. R. & Maunsell, J. H. R. Attention improves performance primarily by reducing
343 interneuronal correlations. *Nat Neurosci* **12**, 1594-1600 (2009).
- 344 3. Cohen, M. R. & Maunsell, J. H. R. Using neuronal populations to study the mechanisms
345 underlying spatial and feature attention. *Neuron* **70**, 1192-1204 (2011).
- 346 4. Mitchell, J. F., Sundberg, K. A. & Reynolds, J. H. Spatial attention decorrelates intrinsic
347 activity fluctuations in macaque area V4. *Neuron* **63**, 879-888 (2009).
- 348 5. Gu, Y. *et al.* Perceptual learning reduces interneuronal correlations in macaque visual cortex.
349 *Neuron* **71**, 750-761 (2011).
- 350 6. Ruff, D. A. & Cohen, M. R. Attention can either increase or decrease spike count
351 correlations in visual cortex. *Nat Neurosci* **17**, 1591-1597 (2014).
- 352 7. Ruff, D. A. & Cohen, M. R. Global cognitive factors modulate correlated response variability
353 between V4 neurons. *J Neurosci* **34**, 16408-16416 (2014).
- 354 8. Ecker, A. S., Berens, P., Tolias, A. S. & Bethge, M. The effect of noise correlations in
355 populations of diversely tuned neurons. *J Neurosci* **31**, 14272-14283 (2011).
- 356 9. Haefner, R. M., Gerwinn, S., Macke, J. H. & Bethge, M. Inferring decoding strategies from
357 choice probabilities in the presence of correlated variability. *Nat Neurosci* **16**, 235-242
358 (2013).
- 359 10. Moreno-Bote, R. *et al.* Information-limiting correlations. *Nat Neurosci* **17**, 1410-1417
360 (2014).

- 361 11. Pitkow, X., Liu, S., Angelaki, D. E., DeAngelis, G. C. & Pouget, A. How can single sensory
362 neurons predict behavior? *Neuron* **87**, 411-423 (2015).
- 363 12. Ruff, D. A. & Cohen, M. R. Attention increases spike count correlations between visual
364 cortical areas. *J Neurosci* **36**, 7523-7534 (2016).
- 365 13. Clery, S., Cumming, B. G. & Nienborg, H. Decision-related activity in macaque V2 for fine
366 disparity discrimination is not compatible with optimal linear readout. *J Neurosci* **37**, 715-
367 725 (2017).
- 368 14. Kohn, A., Coen-Cagli, R., Kanitscheider, I. & Pouget, A. Correlations and neuronal
369 population information. *Annu Rev Neurosci* **39**, 237-256 (2016).
- 370 15. Anton-Erxleben, K. & Carrasco, M. Attentional enhancement of spatial resolution: linking
371 behavioural and neurophysiological evidence. *Nat Rev Neurosci* **14**, 188-200 (2013).
- 372 16. Krauzlis, R. J., Lovejoy, L. P. & Zenon, A. Superior colliculus and visual spatial attention.
373 *Annu Rev Neurosci* **36**, 165-182 (2013).
- 374 17. Maunsell, J. H. R. Neuronal mechanisms of visual attention. *Annu Rev Vis Sci* **1**, 373-391
375 (2015).
- 376 18. Sasaki, Y., Nanez, J. E. & Watanabe, T. Advances in visual perceptual learning and
377 plasticity. *Nat Rev Neurosci* **11**, 53-60 (2010).
- 378 19. Sagi, D. Perceptual learning in Vision Research. *Vision Res* **51**, 1552-1566 (2011).
- 379 20. Watanabe, T. & Sasaki, Y. Perceptual learning: toward a comprehensive theory. *Annu Rev*
380 *Psychol* **66**, 197-221 (2015).
- 381 21. Schoups, A., Vogels, R., Qian, N. & Orban, G. Practising orientation identification improves
382 orientation coding in V1 neurons. *Nature* **412**, 549-553 (2001).

- 383 22. Ni, A. M. & Maunsell, J. H. R. Microstimulation reveals limits in detecting different signals
384 from a local cortical region. *Curr Biol* **20**, 824-828 (2010).
- 385 23. Crist, R. E., Li, W. & Gilbert, C. D. Learning to see: experience and attention in primary
386 visual cortex. *Nat Neurosci* **4**, 519-525 (2001).
- 387 24. Ghose, G. M., Yang, T. & Maunsell, J. H. R. Physiological correlates of perceptual learning
388 in monkey V1 and V2. *J Neurophysiol* **87**, 1867-1888 (2002).
- 389 25. Raiguel, S., Vogels, R., Mysore, S. G. & Orban, G. A. Learning to see the difference
390 specifically alters the most informative V4 neurons. *J Neurosci* **26**, 6589-6602 (2006).
- 391 26. Law, C. T. & Gold, J. I. Neural correlates of perceptual learning in a sensory-motor, but not a
392 sensory, cortical area. *Nat Neurosci* **11**, 505-513 (2008).
- 393 27. Yang, T. & Maunsell, J. H. The effect of perceptual learning on neuronal responses in
394 monkey visual area V4. *J Neurosci* **24**, 1617-1626 (2004).
- 395 28. Series, P., Latham, P. E. & Pouget, A. Tuning curve sharpening for orientation selectivity:
396 coding efficiency and the impact of correlations. *Nat Neurosci* **7**, 1129-1135 (2004).
- 397 29. Shamir, M. & Sompolinsky, H. Implications of neuronal diversity on population coding.
398 *Neural Comput* **18**, 1951-1986 (2006).
- 399 30. Averbeck, B. B., Latham, P. E. & Pouget, A. Neural correlations, population coding and
400 computation. *Nat Rev Neurosci* **7**, 358-366 (2006).
- 401 31. Goris, R. L., Movshon, J. A. & Simoncelli, E. P. Partitioning neuronal variability. *Nat*
402 *Neurosci* **17**, 858-865 (2014).
- 403 32. Wiese, T., Cohen, M. R. & Doiron, B. Modeling attention-induced drop of noise correlations
404 by inhibitory feedback. *Cosyne Abstracts 2014*, 160-161 (2014).

- 405 33. Rabinowitz, N. C., Goris, R. L., Cohen, M. & Simoncelli, E. P. Attention stabilizes the
406 shared gain of V4 populations. *Elife* **4**, e08998 (2015).
- 407 34. Ecker, A. S., Denfield, G. H., Bethge, M. & Tolias, A. S. On the structure of neuronal
408 population activity under fluctuations in attentional state. *J Neurosci* **36**, 1775-1789 (2016).
- 409 35. Nienborg, H. & Cumming, B. G. Decision-related activity in sensory neurons reflects more
410 than a neuron's causal effect. *Nature* **459**, 89-92 (2009).
- 411 36. Cumming, B. G. & Nienborg, H. Feedforward and feedback sources of choice probability in
412 neural population responses. *Curr Opin Neurobiol* **37**, 126-132 (2016).
- 413 37. Kwon, S. E., Yang, H., Minamisawa, G. & O'Connor, D. H. Sensory and decision-related
414 activity propagate in a cortical feedback loop during touch perception. *Nat Neurosci* **19**,
415 1243-1249 (2016).
- 416 38. Jeanne, J. M., Sharpee, T. O. & Gentner, T. Q. Associative learning enhances population
417 coding by inverting interneuronal correlation patterns. *Neuron* **78**, 352-363 (2013).
- 418 39. Yan, Y. *et al.* Perceptual training continuously refines neuronal population codes in primary
419 visual cortex. *Nat Neurosci* **17**, 1380-1387 (2014).
- 420 40. Li, W., Piech, V. & Gilbert, C. D. Learning to link visual contours. *Neuron* **57**, 442-451
421 (2008).
- 422 41. Huang, C., Ruff, D. A., Cohen, M. R. & Doiron, B. Modeling within and across area
423 neuronal variability in the visual system. *Cosyne Abstracts 2017*, 123-124 (2017).
- 424 42. Lakshminarasimhan, K. J., Pouget, A., DeAngelis, G. C., Angelaki, D. E. & Pitkow, X.
425 Inferring decoding strategies for multiple correlated neural populations. *bioRxiv*, doi:
426 10.1101/108019 (2017).

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435 A.M.N., D.A.R., and M.R.C. designed the experiments, A.M.N., D.A.R., J.J.A., and J.S.
436 collected the data, A.M.N. performed the analyses, and A.M.N. and M.R.C. wrote the paper.

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