Title: Simultaneous multi-area recordings suggest a novel hypothesis about how attention improves performance

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Abstract – Visual attention dramatically improves subjects' ability to see and also modulates the responses of neurons in every known visual and oculomotor area, but whether those modulations can account for perceptual improvements remains unclear. We measured the relationship between populations of visual neurons, oculomotor neurons, and behavior, and found that neither of the two prominent hypothesized neuronal mechanisms underlying attention (which concern changes in information coding and the way sensory information is read out) accounted for the observed behavioral improvements. Instead, our results are more consistent with the novel hypothesis that attention reshapes the representation of attended stimuli to more effectively influence behavior. Our results suggest a path toward understanding the neural underpinnings of perception and cognition in health and disease by analyzing neuronal responses in ways that are constrained by behavior and interactions between brain areas.

Keywords – *attention, decoding, population analyses*

Introduction –

Each of the huge number of psychophysical and physiological studies of visual attention show that attention profoundly affects subjects' perceptual abilities and also modulates the responses of populations of neurons at every stage of visual and oculomotor processing[1-4], Despite these oft replicated observations, whether any of the observed neuronal modulations can account for the improvements in psychophysical performance remains unknown. Two, non-mutually exclusive, hypotheses have dominated the literature (Figure 1A): that attention 1) improves visual information coding[5-7], or 2) improves the efficiency with which visual information is read out by the premotor neurons involved in decision-making [8-11].

The studies used to support these hypotheses were limited by available data and analysis methods, which primarily involved the responses of single neurons or pairs of simultaneously recorded neurons in the same brain area. We evaluated these hypotheses using the responses of groups of simultaneously recorded neurons in multiple stages of visuomotor processing, psychophysics, and data analysis methods that leverage that unique combination. We recorded simultaneously from groups of neurons in area MT, which encodes motion information[12,13] and the superior colliculus (SC), where neuronal responses are either visual, oculomotor, or intermediate[14-16] and have been hypothesized to be involved in computing perceptual decisions[17-19]. When we analyzed the responses of single neurons or pairs of neurons, we replicated previous observations. However, constraining our analyses by the animals' behavior and the simultaneous recordings from both areas made it clear that neither prior hypothesis constituted a satisfying account of the observed attention-related improvements in performance.

Our results suggest that at least in the context of a change detection task that is often used to study attention[5,9,20-22] and on the long (hundreds of ms) timescale of perceptual decision-making[23], attention does not act primarily by improving information coding or by changing the way visual information is read out. Instead, the long-observed attention-related changes in the responses of visual cortical neurons account for perceptual improvements, but they do so by reshaping the representation of attended stimuli such that they more effectively drive downstream neurons and guide behavior (Figure 1B). Our study provides a framework for leveraging multi-neuron, multi-area recordings and controlled psychophysics to study how neuronal networks mediate flexible behavior in many systems, timescales, and tasks.

Results –

We compared evidence for and against two hypothesized attention mechanisms using neuronal responses collected while two rhesus monkeys performed the widely studied motion direction change-detection task in Figure 1C[5,9,20-22]. The animals' performance was greatly affected (Figure 1D) by a cue instructing them to shift spatial attention between a stimulus within the same or opposite hemifield as the joint receptive fields of several dozen neurons that were recorded on multielectrode probes in MT (Figure 1E, red points) and the SC (blue points). MT and the SC represent different stages of perceptual decision-making and therefore provide the opportunity to evaluate each hypothesized attention mechanism. MT contributes to motion perception[12,13]. The SC is thought to play many roles in visually guided tasks[14-16], decision-making[17-19] and attention[4].

Figure 1

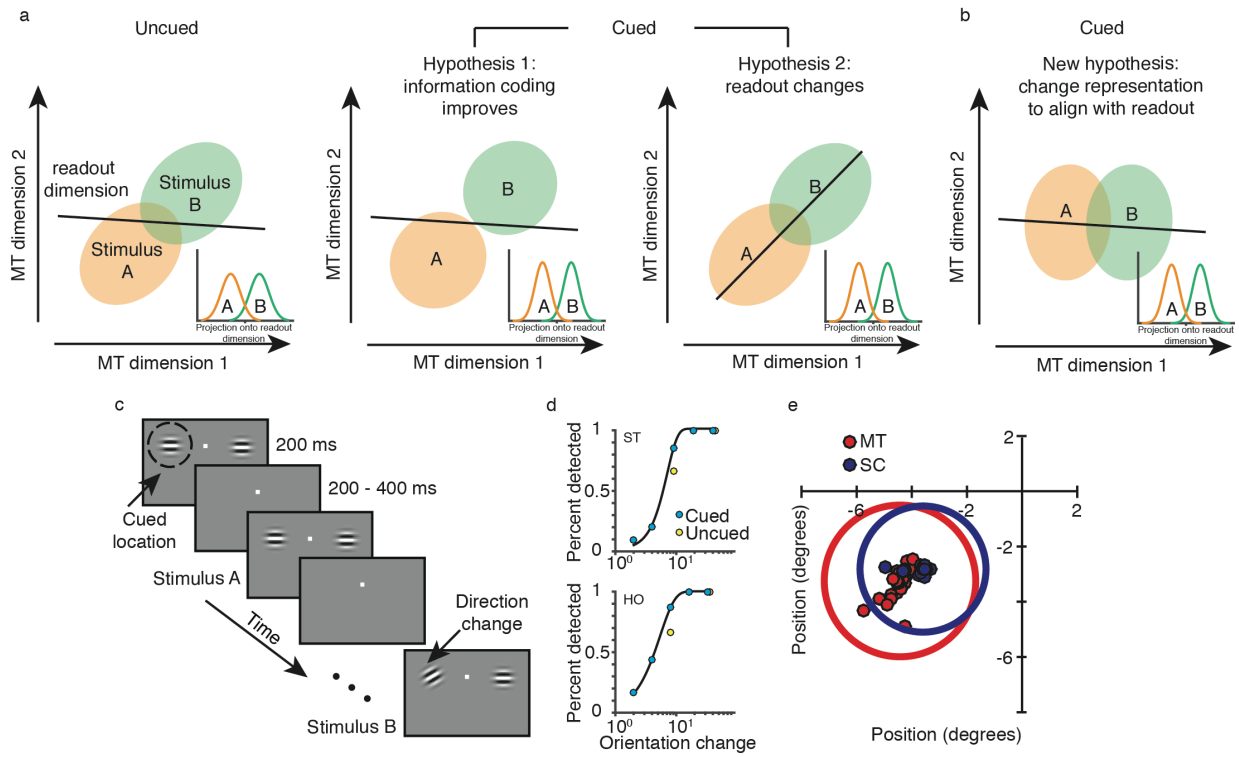

Figure 1. Hypotheses and methods. (A) Schematics describing predominant hypotheses about links between attention, visual cortical activity, and behavior. The left plot depicts MT population responses to two visual stimuli plotted along two dimensions in population response space (e.g. the first two principal components; see Methods) and a readout dimension which represents the visual information that is communicated to neuronal populations involved in planning behavior during the uncued condition. The insets depict projections of the population responses onto the readout dimension. Hypothesis 1 is that the MT representations of the two stimuli become more easily distinguishable (e.g. by separating the distributions of responses to the two stimuli). In this scenario, the distributions of projections along even a suboptimal readout axis may also be more separable. Hypothesis 2 suggests that attention changes the way visual information is read out from MT such that projections of MT population responses to the two stimuli onto the readout dimension are more separable. (B) Our new hypothesis: attention reshapes population responses so they are better aligned with relatively static readout dimensions. This alignment could be a direct result of widely observed attention-related changes in firing rates and response variability. (C) Direction change-detection task with cued attention. The drifting Gabor stimuli before the change were identical on every trial within an experimental session and can be thought of as stimulus A, while the changed stimulus can be thought of as stimulus B in the schematics in (A). (D) Psychometric curves from two example sessions (monkey ST, top, monkey HO, bottom) with best-fitting Weibull functions. Attention improved detection of median difficulty trials by 25% on average across all experiments (cued 76.5% detected across sessions, uncued 51.8% detected; Wilcoxon signed-rank test, p<.001). (E) Receptive field (RF) centers of recorded units from the same example session as in the top plot in (D). Dots represent the RF center (red, MT; blue, SC). The circle represents the size and location of the median RF from each area.

Population recordings replicate previously observed effects of attention

The two predominant attention hypotheses make different predictions about how attention should affect MT and the SC in our task. The first (information coding) hypothesis predicts that attention improves the motion direction information encoded in MT. The second (readout) hypothesis posits that attention changes the way that stimulus information is read out of MT to influence SC responses and ultimately behavior. Our strategy was to show that our data are consistent with those in past studies by replicating the past results that have been used as evidence to support each hypothesis and then to evaluate each hypothesis using analyses that are constrained by the subjects' behavior and leverage our simultaneous multi-neuron, multi-area recordings.

Past studies have evaluated these hypotheses by analyzing the responses of individual neurons or pairs of neurons, which typically lack the statistical power to reveal a strong link to behavior. Using our data set, we replicated the observations that have been used as evidence in favor of each hypothesis. Consistent with previous studies evaluating the information coding hypothesis [2,3,24], we found that attention increased the trial-averaged responses of neurons in both MT and the SC (Supplementary Figure 1A and B) and that attention decreased the extent to which the trial to trial fluctuations in neuronal responses to repeated presentations of the same stimulus are shared between pairs of MT neurons[5,7,21] (quantified as the average spike count or noise correlation, or r_{SC}[25]; Supplementary Figure 1C). Consistent with studies evaluating the readout hypothesis, attention increases correlated variability between the two areas[9,10,26] (Supplementary Figure 1C). This increase between areas suggests that attention-related effects are not simply due to global reductions in slow fluctuations, which has recently been hypothesized to explain

112 attention-related correlation decreases within a single brain area[27] (Supplementary Figure 2 and
113 Supplementary Text). Further, this attention-related increase was weakly dependent on the visual
114 responsivity of SC neurons (Supplementary Figure 3).
115
116 *Neuronal population decoding methods fail to support the information coding or readout*
117 *hypotheses*
118 We reasoned that analyzing the relationship between populations of simultaneously recorded
119 neurons in multiple brain areas with the animals' behavior would provide insight into the relative
120 importance of each hypothesized mechanism. To this end, we determined whether attention
121 affects the amount of stimulus information that can be decoded from the population of MT
122 neurons using linear decoders that are optimized to a) dissociate between the original and
123 changed stimuli (Stimulus decoder in Figure 2), b) predict the animals' choices (whether or not
124 they made an eye movement; Choice decoder), or c) predict the activity of the population of SC
125 neurons we recorded (SC decoder). These decoders were always constructed using data from
126 trials with the intermediate change amount (see Figure 1D).

Figure 2

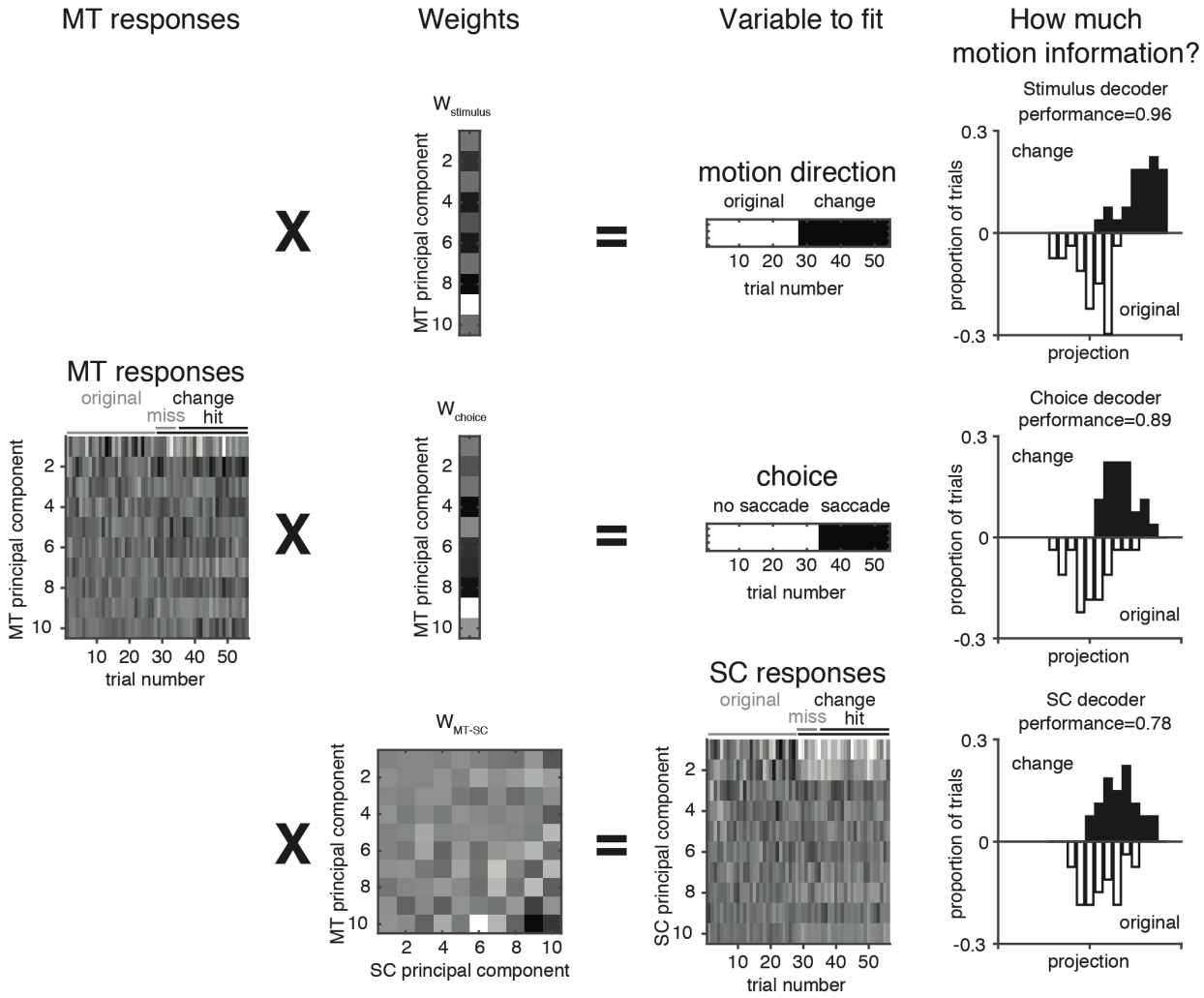

Figure 2 – Schematic of our decoding procedure. We used linear regression to find the weights (second column) that best relate the first ten principal components of the MT population's response (left) to the visual stimulus (Stimulus decoder; top row), the animal's choice (Choice decoder; middle row), or the projections of the responses of the population of simultaneously recorded SC neurons (SC decoder; bottom row). We assessed the performance of each decoder by decoding stimulus information from MT responses on a separate set of trials using each set of weights (right column). See methods for detailed decoding and cross validation procedures.

The information coding hypothesis posits that attention improves the stimulus information that could be gleaned by an optimal Stimulus decoder, but our data provided only weak support for this idea. Attention did not significantly affect the performance of an optimal decoder in our data set, even when we used a decoder optimized separately for each attention condition (Figure 3A,

left bars). We repeated this analysis on a large dataset recorded from visual area V4 during an identical attention task and found a small, but significant, effect of attention (Supplementary Figure 4A[5]). Recent theoretical work suggests that the effects of attention on the stimulus information that can be decoded from small neuronal populations like the ones we recorded are likely to be even more minimal for larger populations[28-30], making it seem unlikely that attention-related improvements in information coding account for the robust improvements in behavioral performance that we observed.

The readout hypothesis posits that attention changes the importance of the attended stimulus in guiding behavior by changing the way its representation is read out by the neurons involved in computing decisions. Therefore, this hypothesis posits that attention should change the weights relating MT responses to either behavior or SC responses. We found that attention had larger effects on the stimulus information that is related to the animals' choices on individual trials (Figure 3A, middle bars) or that is shared with the SC (Figure 3A, right bars) than it did on the Stimulus decoder ($p<.05$). This was also true for the Choice decoder in the V4 dataset (Supplementary Figure 4A; $p<.05$). However, this difference could arise from either a weight change (Figure 1A) or a change within MT that results in more visual information being projected onto a static readout dimension (Figure 1B).

Figure 3

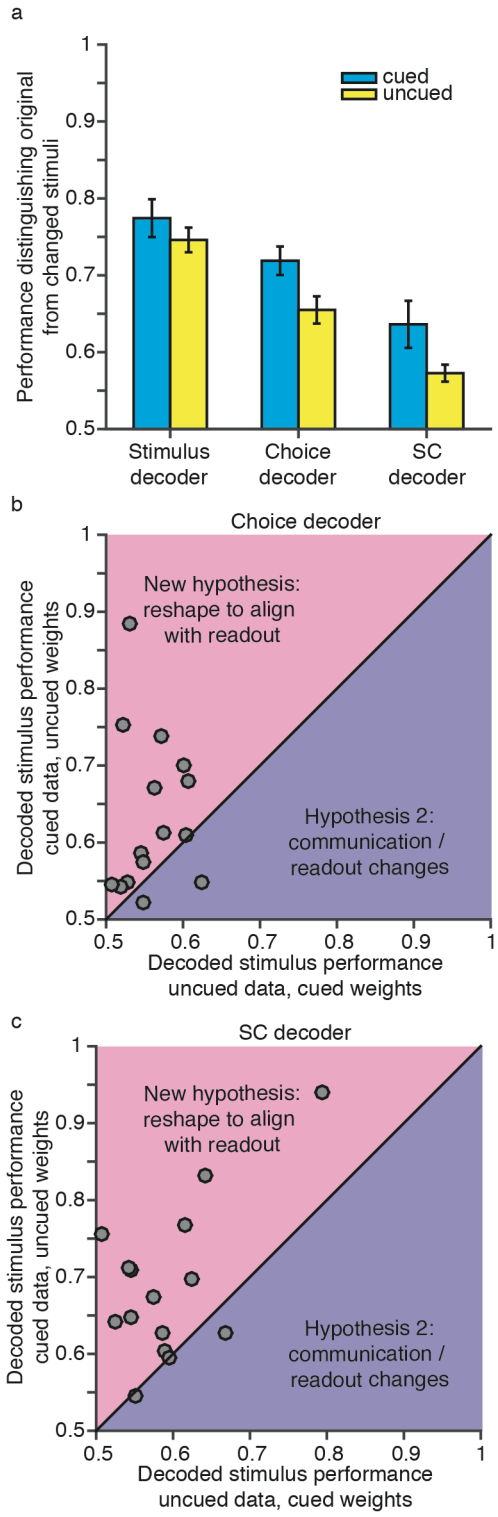

Figure 3. Effects of attention on the stimulus information that can be decoded from small populations of MT neurons. (A) Ability of a cross-validated linear decoder to distinguish the original from changed stimuli (intermediate change amount) for each decoder. Error bars represent SEM. The effect of attention was significant for the Choice and SC decoders (paired t-tests, p<.05) but not for the Stimulus decoder (p=0.28). The effects of attention on the Choice and SC decoders were greater than for the Stimulus decoder (paired t-tests, p<.05), but not significantly different from each other (p=0.21). (B) Weight swapping analysis demonstrates that decoding performance was typically better using the MT responses from the cued condition and the Choice decoder weights from the uncued condition (y-axis) than using the MT responses from the uncued condition and the Choice decoder weights from the cued condition (x-axis; paired t-test, p<.05). (C) Same, using the weights from the SC decoder (paired t-test, p<.05).

A new hypothesis: attention reshapes sensory activity so that it more effectively guides decisions

Our data do not support the hypothesis that attention changes weights relating MT responses to SC responses or behavior. Both the Choice and SC decoders gleaned more stimulus information from MT responses in the attended than unattended condition, even when we used the weights computed in the opposite attention condition for which they were calculated (Figures 3B and 3C). Together, these neuronal population analyses that use the animals' behavior and the activity of downstream neurons to assess the hypothesized attention mechanisms reveal that neither the information

192 coding nor readout hypothesis provide a satisfactory account of the large observed attention-
193 related behavioral improvement.
194
195 Our data support the hypothesis that attention reshapes the representation of attended stimuli to
196 more effectively guide behavior (Figure 1B). In this scenario, the critical changes are in visual
197 cortex. However, this does not result in a large improvement in the stimulus information that can
198 be gleaned by an optimal Stimulus decoder. Instead, the modulated neuronal activity in MT
199 better aligns with the readout dimensions using relatively static weights.
200
201 How could a reshaping of the representation of an attended stimulus be implemented? The
202 simplest mechanism would make use of the signatures of attention that have been observed for
203 many years such as changes in firing rate gain[2,3,24] or noise correlations[5-7,9,20-22,31-37]. We
204 investigated the possibility that these simple response changes can account for the attention-
205 related improvement in the stimulus information decoded using the Choice decoder in two
206 stages. First, to verify the prediction of the weight-swapping analyses (Figures 3B and 3C), we
207 constructed a single Choice decoder for both attention conditions (Figure 4A) and determined
208 that it captured the attention-related improvement in decoded stimulus information (compare the
209 blue and yellow bars in Figure 4B). Second, we used those same weights to decode stimulus
210 information from population responses constructed using the mean rates from the uncued
211 condition and the residuals from the cued condition. We found that simply using residuals
212 (which incorporate both response variability that is private to each neuron and that which is
213 shared between neurons) from the cued condition was enough to completely account for the
214 attention-related improvement in decoded stimulus information (Figure 4B).

Figure 4

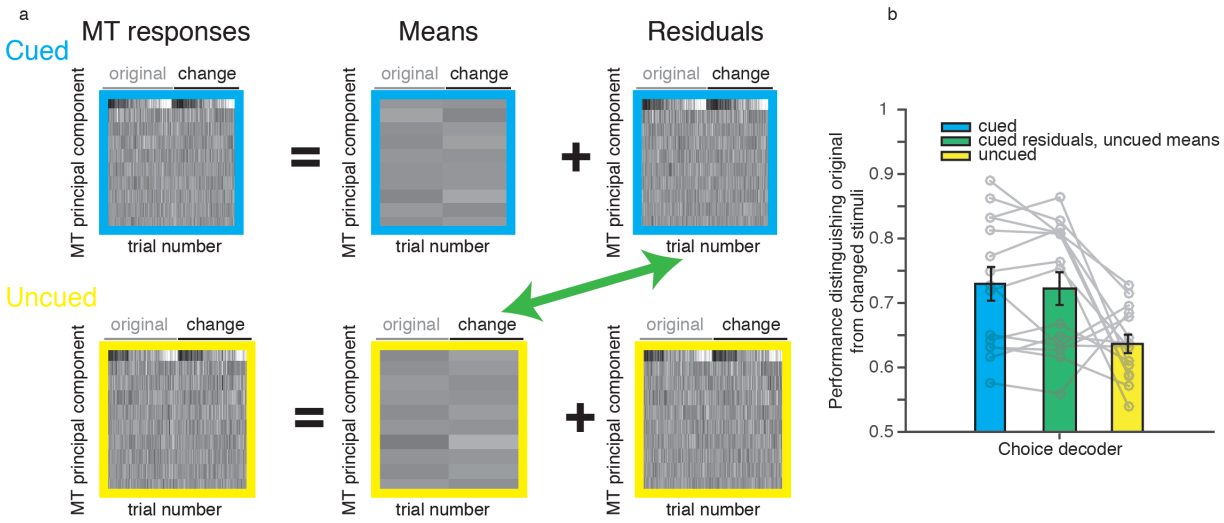

Figure 4. Effects of attention on the stimulus information that can be decoded from small populations of MT neurons is explained by changes in response variability. (A) Schematic of our procedure to understand which attention-related changes could account for the improvement in the amount of stimulus information that could be gleaned using the Choice decoder. We separated the first ten principal components of the MT population response (left) to the original and changed stimulus in both attention conditions into mean responses (scale adjusted to account for smaller value range) and residuals. We assessed the extent to which decoder performance was affected by attention-related changes in means and residuals by decoding stimulus information from MT responses on a separate set of trials in each attention condition and also using the residuals from the cued condition and the mean responses from the uncued condition (green double-sided arrow). See methods for detailed decoding and cross validation procedures. (B) Using the procedure described in (A), we found that the reshaping of the MT representation of the attended stimulus can be accomplished as a result of attention-related changes in response variability (e.g. noise correlations). The amount of stimulus information that can be decoded using a single Choice decoder whose weights are determined from data from both attention conditions is indistinguishable for the cued data and data constructed using the mean responses from the uncued condition and the residuals from the cued condition (paired t-test, p=0.84).

Discussion –

We used multi-neuron, multi-area recordings and psychophysics to test two previous hypotheses and one novel hypothesis about the relationship between attention-related changes in perception and in neuronal responses on the timescale of perceptual decisions. In contrast with the hypotheses motivating most of the extensive literature concerning the neuronal basis of attention, our data are most consistent with the novel hypothesis that attention reshapes population activity

so that information about the attended stimulus is read out to guide behavior. Our conclusions are based on comparing the visual information that can be gleaned from decoders optimized for the stimulus, the animals' choices, and the activity of groups of neurons in the superior colliculus. These results support the idea that behavioral flexibility may be mediated by reshaping the representation of visual stimuli rather than improvements in information coding (which may be impossible given the immense amount of sensory information encoded in the brains of even anesthetized animals[30] or in the responses of single neurons[13]) or by changing read out, which may involve synaptic plasticity that takes longer than the ~150 ms timescale on which subjects can shift attention[38-40].

The idea of realigning sensory information to align with static read out mechanisms seems like it would require much more exotic mechanisms than the other hypothesized attentional mechanisms. However, we showed that commonly observed effects of attention on neuronal response variability were sufficient to reshape the representation of attended stimuli so that they more effectively influence behavior (Figure 4B). Changing covariability may require a simpler mechanism than changing information coding or synaptic weights: we showed recently in a model that the covariability of a population of neurons can be readily changed by altering the balance of inhibition to excitation[41].

The idea that changing correlated variability better aligns sensory responses to a fixed readout is also consistent with our recent observation that in this task, monkeys' choices are well-aligned with the axis in population space that explains the most correlated noise[21]. One exciting possibility is that the correlated variability axis represents the fixed readout dimension, perhaps

because it is well-positioned to decode the motion direction of the broad set of stimuli that animals encounter outside the limited environment of most laboratory tasks[24]. If so, reducing noise correlations and increasing firing rate gains would improve the stimulus information projected along that readout axis (following the intuitions in[42]).

Our conclusions rest on data using one psychophysical task and recordings from two visual cortical areas. It is possible that the mechanisms underlying change detection, which is an important component of natural vision, are different than other tasks or that the mechanisms differ by brain areas. Even if we happened upon a special, albeit common, scenario, it is remarkable to observe a situation in which the large attention-related change in behavioral performance can be accomplished without changing information coding or weights between areas. In contrast, theoretical models and machine learning techniques accomplish flexibility in computation almost solely by changing weights [43-46]. Our results constitute an existence proof: an example of a situation in which flexibility can be mediated by simple changes within sensory cortex.

In the future, it will be interesting to use the same approach to determine whether similar mechanisms can account for behavioral changes associated with other cognitive processes (e.g. task switching) that might seem more likely to change the weights relating stimulus information to downstream neurons or behavior. Further, many neuropsychiatric disorders (including disorders of attention, Autism, and schizophrenia) are thought to involve changes in the same computations thought to underlie attention[47]. An exciting possibility is that these changes might

be identified and potential therapies evaluated in animal models using the combination of behavioral evaluation and multi-neuron, multi-area recordings that we described here.

Online Methods

Methods Summary

The subjects were two adult male rhesus monkeys (*Macaca mulatta*, 8 and 9 kg). All animal procedures were approved by the Institutional Animal Care and Use Committees of the University of Pittsburgh and Carnegie Mellon University. Using linear 24 channel moveable probes (Plexon), we simultaneously recorded extracellular activity from direction-selective neurons in area MT and neurons in the superior colliculus that responded either visually, prior to a saccade, or both. Before beginning the experiment, we searched for neurons in both areas that had overlapping spatial receptive fields (Figure 1E) as determined by mapping with both drifting gratings and a delayed saccade task. The monkeys performed a direction change-detection task that commenced upon fixation of a central spot (Figure 1C). Two drifting Gabor stimuli, whose direction was selected to drive the recorded population of MT neurons well, flashed on and off until the direction of one stimulus changed at a random, unsignaled time. The monkeys signaled detection of the change by making a saccade to the changed stimulus within 450 ms of its onset. The location of the stimulus change was cued using instruction trials prior to each block of trials and the cue was valid 80% of the time. On the other 20% of trials, the change happened at the uncued location. In order to encourage fixation on longer trials, catch trials, where no stimulus changed direction and monkeys were rewarded for maintaining fixation, were intermixed. We analyzed spiking activity in response to all visual stimuli except the first stimulus in each trial.

Materials and Methods

309 The subjects were two adult male rhesus monkeys (*Macaca mulatta*, 8 and 9 kg). All animal
310 procedures were approved by the Institutional Animal Care and Use Committees of the
311 University of Pittsburgh and Carnegie Mellon University.

312 We presented visual stimuli using custom software (written in MATLAB using the
313 Psychophysics Toolbox [48,49] on a CRT monitor (calibrated to linearize intensity; 1024x768
314 pixels; 120 Hz refresh rate) placed 54 cm from the animal. We monitored eye position using an
315 infrared eye tracker (Eyelink 1000; SR Research) and recorded eye position and pupil diameter
316 (1000 samples/s), neuronal responses (30,000 samples/s), and the signal from a photodiode to
317 align neuronal responses to stimulus presentation times (30,000 samples/s) using hardware from
318 Ripple.
319
320 Behavioral Task

321 As previously described[5], a trial began when the monkey fixated a small, central spot within a
322 1.25° per side square fixation window in the center of a video display while two peripheral full
323 contrast, drifting Gabor stimuli (one overlapping the receptive fields of the recorded neurons, the
324 other in the opposite visual hemifield) synchronously flashed on (for 200 ms) and off (for a
325 randomized period between 200-400 ms) until, at a random, unsignaled time, the direction of one
326 of the stimuli changed from that of the preceding stimuli (Figure 1C). The monkey received a
327 liquid reward for making a saccade to the stimulus that changed. Attention was cued in blocks of
328 50-100 trials, and alternated between blocks where attention was cued to either the left or the
329 right stimulus. In each block, the direction change occurred at the cued stimulus on 80% of trials,
330 and at the uncued stimulus in 20% of trials (all uncued changes used either the middle or largest

direction change, Figure 1D). Catch trials, where no stimulus changed direction and the monkey was rewarded for maintaining fixation, were randomly intermixed throughout each block and made up approximately 12% of total trials. Psychometric data were fit with Weibull functions. Before recording commenced, the monkeys were extensively trained to have stable thresholds across a range of spatial locations (3-6 months). Because we recorded from several dozen neurons simultaneously, we could not optimize the stimuli for all neurons. We made sure to position one Gabor stimulus in the joint receptive field of the recorded neurons in both areas and we made an effort to set the properties of the size (approximately 3-6 degrees of visual angle), speed (approximately 3-12 degrees of visual angle per second) and direction of the stimuli so that they drove as many MT units as possible. The direction of all of the stimuli prior to the direction change was constant throughout a recording session and this direction was typically either the median or mode of the distribution of MT preferred directions from that session. The range of direction changes differed from session to session, was selected based on the animals' training history and depended on stimulus properties such as eccentricity and size. A typical range of change amounts for both animals was 1-35 degrees in log-spaced steps.

Electrophysiological Recordings

We simultaneously recorded extracellularly from single units and sorted multiunit clusters (the term "unit" refers to either). The dataset consisted of a total of 306 responsive MT units and 345 responsive SC units total (36-58 units per session, mean 20 in MT, 24 in the SC for Monkey HO; 36-53 units per session, mean 21 in MT, 22 in SC for Monkey ST) in both MT and the SC in the right hemisphere using moveable, linear 24-channel V-probes (Plexon; inter-electrode spacing in MT = 50μm, SC = 100μm). We presented visual stimuli and tracked eye position as previously

354 described[9]. The data presented are from 6 days of recording for Monkey HO and 9 days of
355 recording for Monkey ST. Each day consisted of multiple blocks of the attention task (Figure 1C;
356 mean 1015 of trials for Monkey HO, 745 for Monkey ST) preceded by receptive field mapping
357 using a delayed saccade task and direction tuning during passive fixation.

358 Data Analysis

359 All spike sorting was done offline manually using Offline Sorter (version 3.3.5; Plexon). We
360 based our analyses on both single units and multiunit clusters and use the term "unit" to refer to
361 either. All neuronal analyses prior to Figure 3 used spike count responses between 50-250 ms
362 after stimulus onset to account for visual latencies in the two areas. To remove response
363 contamination from eye movements during change stimuli, data presented in the decoding
364 analyses in Figure 3 and 4 used shorter response windows. Responses to both unchanged and
365 changed stimuli were measured from 50-185 ms after stimulus onset for monkey HO and 50-220
366 ms for monkey ST. These times were selected based on the distribution of each animal's reaction
367 times with the goal of maximizing the number of trials that could be included in the analyses.
368 Trials with reaction times that began during those windows were excluded. To minimize the
369 impact of adaptation on our results, we did not analyze the first stimulus presentation in each
370 trial. We only analyzed a recorded MT unit if its stimulus-driven firing rate was 10% higher than
371 its firing rate as measured in the 100 ms prior to the onset of the first stimulus. We only analyzed
372 a recorded SC unit if its stimulus-driven firing rate was 10% higher than its firing rate as
373 measured in the 100 ms prior to the onset of the first stimulus or if its response during a 100 ms
374 epoch prior to a saccade on correct trials to the contralateral side was 10% larger than that same
375 baseline. Stimulus presentations during which a microsaccade was detected were excluded from
376 analyses[9,50]).

For firing rate analyses in Supplementary Figure 1A and B, attention indices were calculated using average spike counts on the stimulus presentation prior to correct detections of the intermediate change amount depending on whether attention was directed into or out of the receptive fields of the recorded neurons using the formula $(attend_{in} - attend_{out})/(attend_{in} + attend_{out})$. Significance of individual units was determined by a paired t-test ($p<0.05$).

Noise correlations

We defined the correlated variability of each pair of simultaneously recorded units (quantified as spike count correlation or r_{SC}[25]) as the Pearson correlation coefficient between the responses of the two units to repeated presentations of the same stimulus. This measure of r_{SC} represents noise correlations rather than signal correlations because the responses used in this analysis were always to an identical visual stimulus. For Supplementary Figure 1C, we included responses from stimulus presentations 2 though 10 from trials that ended with either a hit, miss or correct catch trial and that were immediately followed by the maintenance of fixation and continuation of the trial (i.e., stimulus presentations where the behavioral response on the subsequent stimulus presentation was not a saccade). We z-scored responses as a function of the stimulus presentation number in each trial and then pooled data across stimulus presentations before calculating noise correlations. Results did not qualitatively change if we did not perform this z-score procedure. For Supplementary Figure 1D, we included data from all stimulus presentations prior to the change stimulus (except the first) and sorted them depending on what the behavioral outcome was on the subsequent stimulus presentation. Pairs of units that were recorded on the same

electrode were not included in correlation analyses. The data presented in Supplementary Figures 1C consisted of 3,285 MT pairs, 3,948 SC pairs and 6,934 between area pairs.

Decoding

We focused our decoding analyses on trials in which the third largest (middle) direction change occurred, because changes of that magnitude occurred in both attention conditions. We used the decoding strategy schematized in Figure 2. We began by constructing four matrices in each attention condition: 'MT responses' (a # MT neurons by 2*# trials matrix of MT responses to the stimuli before the direction change and the changed stimulus on the relevant trials), 'motion direction' (a 1 by 2*# trials vector of zeros for the stimulus before the change, referred to as 'original', and ones for the changed stimulus, referred to as 'change'), 'choice' (a 1 by 2*# trials vector of zeros for stimulus presentations on which the animal did not make an eye movement, referred to as 'no saccade', and ones when the animal made an eye movement, referred to as 'saccade'), and 'SC responses' (a # SC neurons by 2*# trials matrix of SC responses to the stimuli before the direction change and the changed stimulus on the relevant trials).

We cross validated by holding out the two stimulus presentations (for the original and changed stimuli) from one trial at a time to perform the rest of our analyses. To reduce the number of weights we needed to fit and therefore improve our confidence in the weights we did fit, we performed PCA on the MT and SC responses to find the first 10 PCs in each area. We then performed linear regression to find the weight vectors (for the Stimulus and Choice decoders) or weight matrices (for the SC decoder) that related projections along the first ten MT PCs plus a

vector of ones to ‘motion direction’, ‘choice’, or projections along the first 10 SC PCs in each attention condition.

We assessed the stimulus information in each decoder (Figure 3) by multiplying projections of MT responses to the original and changed stimuli from the held-out trial by the fitted weights and either determining whether those weighted sums correctly classified the stimuli as original or changed (Stimulus and Choice decoders) or whether a linear classifier correctly classified those stimulus presentations on the basis of the predicted SC responses (SC decoder). For the decoding analysis in Figure 4B, we took a similar approach to the previously described Choice decoder, except that we combined data from both the cued and uncued conditions to calculate decoding weights. We then decomposed the responses of the population responses to each stimulus in each attention conditions into mean responses and residuals (R=M+S, where R is the number of neurons by number of trials matrix of spike count responses to one stimulus in one attention condition, M is a matrix of mean responses for each neuron, and S is the matrix of residuals). We tested the hypothesis that attention-related changes in the residuals account for the improvement in stimulus information used to guide behavior by decoding stimulus information from responses created by using the mean responses from the uncued condition and residuals from the cued condition.

The stimulus and choice decoder using the V4 data were set up in an identical manner to the MT data described above (Supplementary Figure 4). This dataset consisted of multineuron recordings from both hemispheres of V4 during 37 experimental sessions in two animals, the details of which are described in [5].

Code availability

Custom Matlab code is available upon reasonable request to the authors.

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Author contributions
Both authors conceived and designed the experiments, analyzed the data and wrote the manuscript. D.A.R. collected the data.

Data availability
The data that support the findings of this study are available from the corresponding author upon reasonable request.

Competing interests
The authors declare no competing interests

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