Report

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Neuronal Modulations in Visual Cortex Are Associated with Only One of Multiple Components of Attention

Highlights

- A commonly used attention paradigm conflates two distinct components of attention
- We dissociated these components using a specifically designed task
- Neuronal signals in visual cortex correspond to one component, but not the other
- The results suggest that separate brain areas underlie distinct mechanisms of attention

Authors

Thomas Zhihao Luo, John H.R. Maunsell

Correspondence

thomas.zhihao.luo@gmail.com

In Brief

Luo and Maunsell show that the neuronal modulations in visual cortex correspond to only one of multiple components of attention. This result suggests that different brain structures underlie separate mechanisms of attention and that attention is not a unitary process.

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Report

Neuronal Modulations in Visual Cortex Are Associated with Only One of Multiple Components of Attention

Thomas Zhihao Luo[1,2,*] and John H.R. Maunsell[1]
[1]Department of Neurobiology, The University of Chicago, Chicago, IL 60637, USA
[2]Program in Neuroscience, Harvard Medical School, Boston, MA 02115, USA
*Correspondence: thomas.zhihao.luo@gmail.com
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SUMMARY

Neuronal signals related to visual attention are found in widespread brain regions, and these signals are generally assumed to participate in a common mechanism of attention. However, the behavioral effects of attention in detection can be separated into two distinct components: spatially selective shifts in either the criterion or sensitivity of the subject. Here we show that a paradigm used by many single-neuron studies of attention conflates behavioral changes in the subject's criterion and sensitivity. Then, using a task designed to dissociate these two components, we found that multiple aspects of attention-related neuronal modulations in area V4 of monkey visual cortex corresponded to behavioral shifts in sensitivity, but not criterion. This result suggests that separate components of attention are associated with signals in different brain regions and that attention is not a unitary process in the brain, but instead consists of distinct neurobiological mechanisms.

INTRODUCTION

Attending to a location in a visual scene enhances behavioral performance there even when the gaze is directed elsewhere (Posner et al., 1980; Carrasco, 2011). At the attended location, subjects detect target stimuli more readily and respond with shorter delays. These improvements in detection could depend on either of two components: a more lenient criterion for detecting targets or higher sensitivity at discriminating targets from nontargets. Lowering the criterion for the visual location where a target is expected results in more targets being detected at that location. Enhancing the sensitivity of discrimination between targets and nontargets at a location also increases the frequency of target detection at that location.

Many psychophysical studies have used signal detection theory (Green and Swets, 1966), a statistical model of perceptual decisions, to measure how a subject's criterion and sensitivity differ between the attended and unattended locations (Bashinski and Bacharach, 1980; Müller and Findlay, 1987; Downing, 1988; Hawkins et al., 1990; Müller and Humphreys, 1991; Kinchla, 1992; Wyart et al., 2012). These studies found that subjects can shift either their criterion or sensitivity at the attended location relative to the unattended location. When it is adaptive to do so, subjects often modulate both to improve their performance. Therefore, spatially selective changes in both criterion and sensitivity contribute to the behavioral enhancement in detection associated with attention. Moreover, like sensitivity shifts, criterion changes could also depend on perceptual mechanisms (White et al., 2012; Ferrera et al., 2009). Therefore, here we refer to spatially specific shifts in criterion and sensitivity as components of attention.

Neuronal signals related to visual attention have been found in many brain regions, including the cerebral cortex, thalamus, and brainstem (Desimone and Duncan, 1995). These widespread signals are generally thought to participate in a unitary mechanism of attention. However, attention is associated with distinguishable perceptual and behavioral phenomena (Carrasco, 2011), and it has not been investigated whether the attention-related signals in any of these brain structures reflect the same or distinct components of attention. In particular, it is unknown how behavioral changes in criterion and sensitivity are related to neuronal signals associated with attention.

Many single-neuron studies of attention use a paradigm introduced by Posner et al. (1980). Variants of this paradigm have been used to investigate attention in visual cortex (Reynolds et al., 2000; Cohen and Maunsell, 2009), parietal cortex (Herrington and Assad, 2010), prefrontal cortex (Armstrong et al., 2009), superior colliculus (Robinson and Kertzman, 1995), and thalamus (Petersen et al., 1985) as well as the relationship between the attention-related signals in different structures (Gregoriou et al., 2009; Zénon and Krauzlis, 2012). In this paradigm, the subject has to detect a target that appears at one of two locations (Figure 1A). More attention is directed to the location where the target appears more frequently or is rewarded more highly. Appropriate allocation of attention is often ascertained by a higher target detection rate (hit rate) at the attended location (Figure 1B). However, any improvements in the hit rate could depend on a change in only criterion, only sensitivity, or both. This ambiguity is apparent when behavior is analyzed using signal detection theory (Figures 1C and 1D; criterion and sensitivity are indexed as *criterion location* [*c*] and *d'*, respectively). Because of the ambiguity in the behavior,

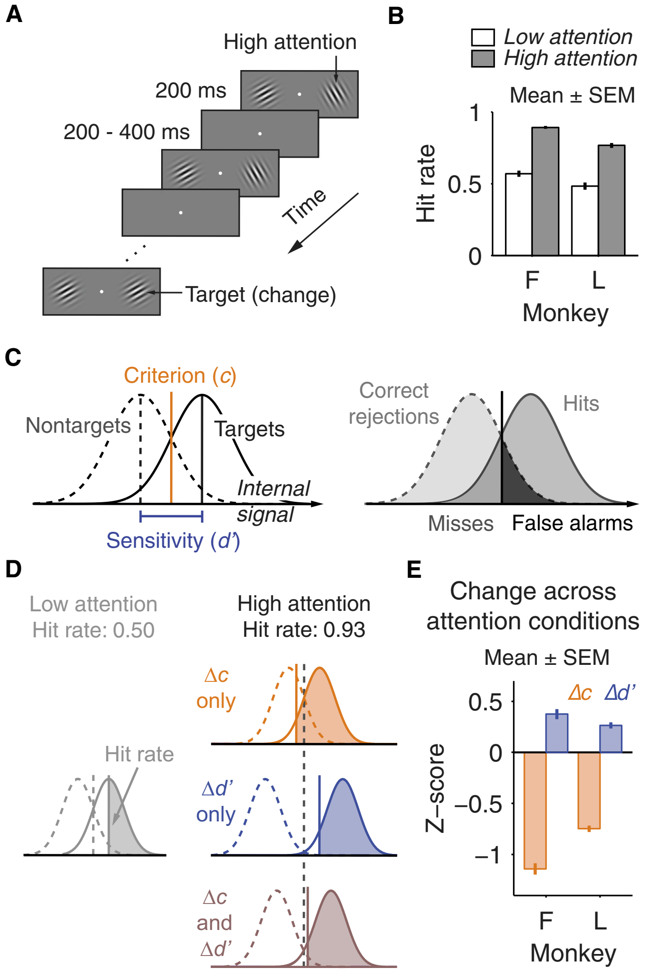

Figure 1. Behavioral Improvement in a Typical Attention Task Conflates Changes in Criterion and Sensitivity

(A) Standard attention task. The subject had to detect a target (orientation change) that occurred at either of two stimulus locations. In alternating blocks of trials, the subject directed more attention to one of two locations.

(B) Monkeys detected targets more frequently at the high attention location. Monkey F, n = 65 sessions; monkey L, n = 50 sessions.

(C) In the signal detection model, each stimulus evokes a noisy internal signal. If the signal is stronger than *c*, the stimulus is reported as a target. The distributions of signals evoked by the target and by the nontarget overlap, and the separation between these two distributions is indexed as *d'*. The response to each stimulus is categorized as a hit, miss, false alarm, or correct rejection, and these responses are used to calculate *c* and *d'*.

(D) Any improvement in the hit rate could be due to changes in only criterion (Δ*c*), only sensitivity (Δ*d'*), or both (Δ*c* and Δ*d'*).

(E) Monkeys changed both criterion and sensitivity between attention conditions. Monkey F, n = 65 sessions; monkey L, n = 50 sessions.

the neuronal modulations attributed to attention in these studies could reflect shifts in the subject's criterion or sensitivity. Therefore, it is uncertain whether the neuronal signals associated with attention in any brain area correspond to changes in one or both components of attention.

The presence of attention-related signals in widespread brain structures and the heterogeneity of the behavioral changes associated with attention suggest that each of these brain structures mediates a distinct component of attention. Investigating this possibility would provide insights into whether attention is a monolithic brain process or depends on distinguishable neurobiological mechanisms. Here we examine whether the neuronal mechanisms of attention in visual cortex are associated with behavioral changes in criterion or sensitivity. We focused on area V4, a region with reliable attention-related signals (e.g., Cohen and Maunsell, 2009) as well as modulation by visual target selection (Chelazzi et al., 2001) and contextual modulation unrelated to the neuron's sensory selectivity (Ferrera et al., 1994). The extrasensory signals in V4 suggest that the attention-related modulation observed previously may be related to behavioral shifts in either criterion, sensitivity, or both.

RESULTS

In a preliminary experiment, we examined how two monkeys (F and L) changed their criterion and sensitivity in a task of the sort commonly used in neurophysiological studies of attention ("standard attention task"; Figure 1A). Both monkeys performed with a lower criterion and higher sensitivity at the attended location relative to the unattended location (Figure 1E). Criterion and sensitivity both changed regardless of whether attention was directed using a higher target probability, larger reward size, or both (Figure S1). Criterion changes accounted for most of the behavioral improvement (Figure S2). These results indicate that, although attention-related modulations in neuronal activity in visual cortex are frequently described as related to behavioral changes in sensitivity (e.g., Reynolds et al., 2000; Cohen and Maunsell, 2009), the omission to examine shifts in criterion or sensitivity means that the neuronal modulations might have reflected either. This uncertainty exists not only for tasks like the one used here, where targets occur at the unattended location (e.g., Cohen and Maunsell, 2009), but also for tasks where animals are trained never to respond to targets at the unattended location (e.g., Reynolds et al., 2000; Zénon and Krauzlis, 2012).

To more accurately characterize the neuronal signals associated with attention, we designed a task to dissociate changes in criterion and sensitivity ("dissociation task"; Figure 2A). In each trial, two stimuli ("samples") appeared concurrently for a brief time. After a short delay, a single stimulus ("test") appeared at one of the two sample locations, selected at random. The monkey had to saccade to the test stimulus if it differed in orientation from the sample at the same location. If not, the monkey had to wait and saccade to a second test stimulus that always differed from the sample. The response to the first test stimulus in each trial was categorized as a hit, miss, false alarm, or correct rejection, and these responses were used to compute *c* and *d'*.

As in other neurophysiological experiments, we controlled attention by manipulating reward contingencies, but here with additional refinements to control the subject's criterion and sensitivity (Figure 2B; Figure S3A; Experimental Procedures). The relative reward between hits and correct rejections was manipulated independently at each stimulus location to control the criterion for that location. The relative overall reward between the two locations was used to control the difference in sensitivity between locations. These reward parameters were varied

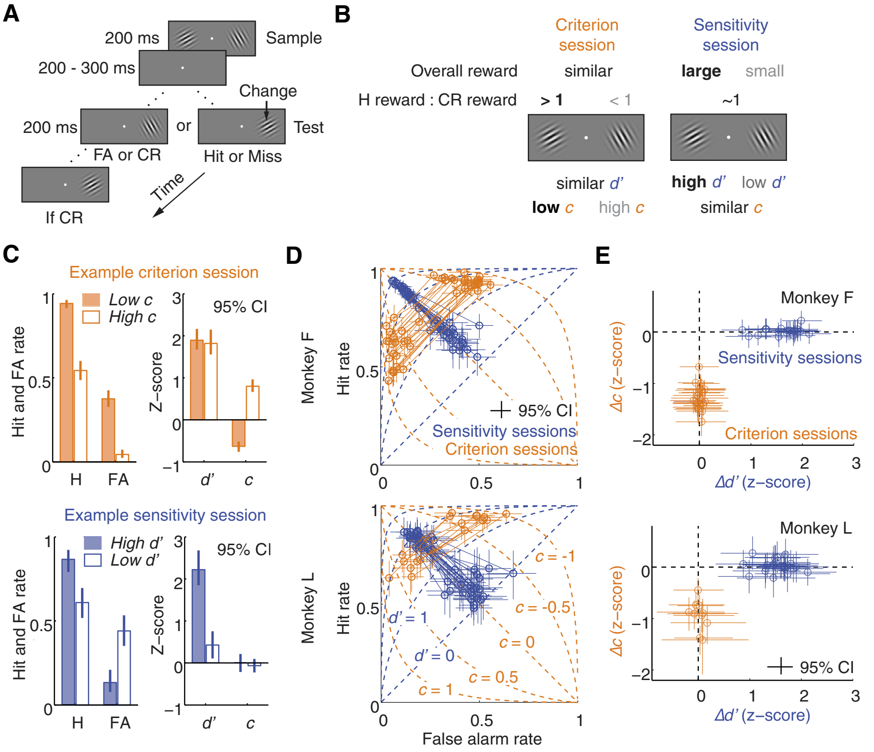

Figure 2. Dissociation Task

(A) Monkeys detected a target (orientation change) that occurred on either the first or the second test stimulus. Behavioral responses to the first test stimulus were categorized as hits (H), misses (M), correct rejections (CR), or false alarms (FA).

(B) Reward manipulations to isolate spatially selective changes in c and d'.

(C) A criterion session of monkey F and a sensitivity session of monkey L. Error bars represent 95% confidence intervals (CIs).

(D) All sessions. Each circle is the behavior in one task condition from one daily session, and a solid line connects the two conditions of each session. Dashed lines are isocriterion and isosensitivity lines. Error bars represent 95% CIs. Monkey F, 22 criterion and 22 sensitivity sessions; monkey L, 10 criterion and 25 sensitivity sessions.

(E) Differences in criterion and sensitivity between the two task conditions of each session (same data as in D). Error bars represent 95% CIs. Monkey F, 22 criterion and 22 sensitivity sessions; monkey L, 10 criterion and 25 sensitivity sessions.

between two task conditions of each daily session to isolate a change in either criterion (in “criterion sessions”) or sensitivity (in “sensitivity sessions”) (Figure 2C). These isolated behavioral changes were spatially selective and unrelated to the global changes because of arousal.

We trained the same two monkeys on this task and achieved precise behavioral dissociation in more than 90% of sessions (Figures 2D and 2E; Figures S3B and S3C). To our knowledge, this is the first demonstration of a consistent, precise separation of spatially specific changes in criterion and sensitivity. We then implanted an array of microelectrodes in each animal’s V4 area and measured how neuronal responses are modulated as the animal shifted either its criterion or sensitivity.

Because criterion changes accounted for most of the behavioral improvements in the standard attention task (Figure S2), we expected attention-related modulations in V4 to be primarily associated with shifts in criterion. But when we isolated changes in criterion and sensitivity, we found that attention-related changes corresponded to changes in sensitivity and not criterion (Figure 3; Figure S4). In sensitivity sessions, neuronal responses were stronger in the high d' condition than in the low d' condition, but in criterion sessions, responses were similar between low c and high c conditions despite large behavioral changes in criterion. To quantify the difference in neuronal responses between the two task conditions of each session, we calculated a modulation index using responses to the sample stimulus (firing rates 60–260 ms after sample onset; Supplemental Experimental Procedures). Modulation indices differed significantly from zero in sensitivity sessions but not in criterion sessions, and modulation indices from sensitivity sessions were significantly larger than indices from criterion sessions (Table 1).

We also analyzed the firing rates during the delay period between the sample and the first test stimulus (60–260 ms after sample offset). Similar to responses to the sample stimulus, firing rates during the delay were stronger in conditions of higher d', and there was no detectable modulation by criterion changes (Table 1). We also found that the modulation by sensitivity was stronger during the delay than during the sample stimulus period (91% and 290% larger and $p < 10^{-6}$ and $p < 10^{-10}$, t test, for monkeys F and L, respectively). Despite the stronger firing rate modulation associated with sensitivity changes during the delay epoch, there was no detectable modulation associated with criterion changes.

We next examined two other neuronal correlates of attention in visual cortex. Attention is associated with a modest decrease in the trial-to-trial variability in the responses of individual neurons, measured as the Fano factor (Mitchell et al., 2007), and a large reduction in the correlated variability in pairs of neurons, measured as noise correlation (Cohen and Maunsell, 2009; Mitchell et al., 2009). The Fano factor and noise correlation were calculated using the sample period. Reduction in both the Fano factor and noise correlation corresponded to enhancement in sensitivity but not shifts in criterion (Figure 3B; Table 1). Taken together with the observations on firing rates, these results indicate that multiple aspects of attention-related modulation of V4 neuronal activity all correspond to shifts in sensitivity but not criterion.

DISCUSSION

Accurate detection of a signal requires proper spatial distribution of criterion and sensitivity. For example, a radar operator needs to adjust his or her criterion for where a signal is expected and where a successful detection is more important than a correct

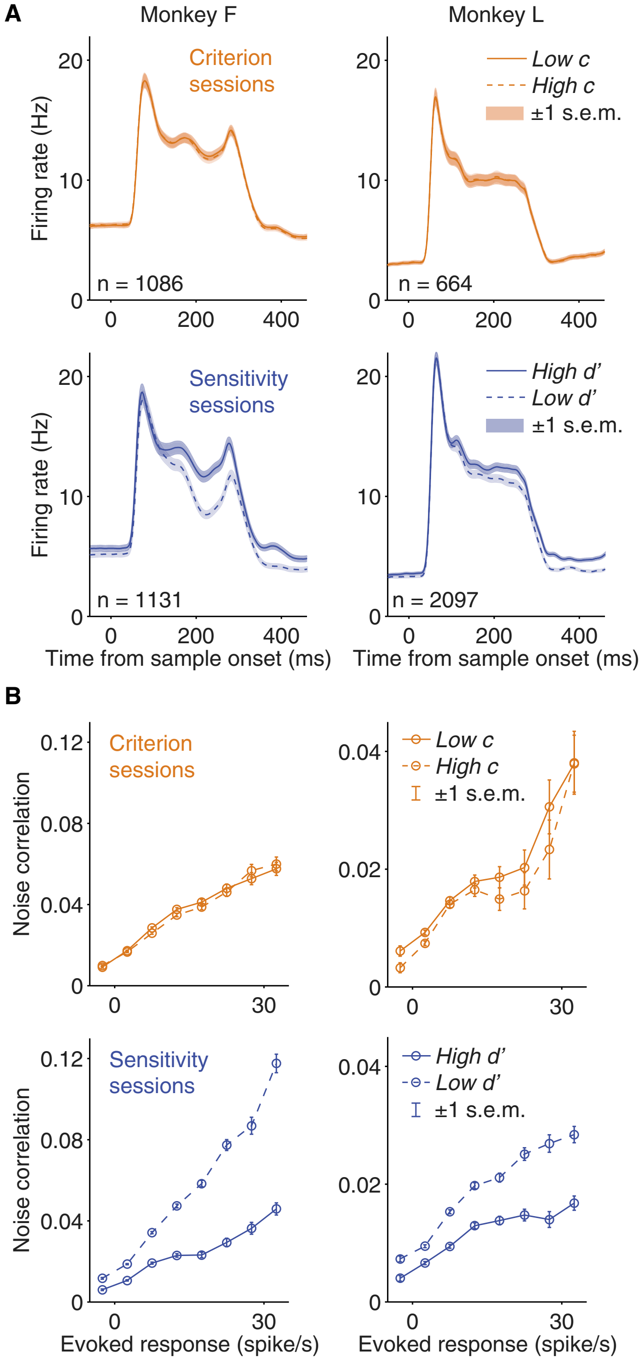

Figure 3. Neuronal Modulations in V4 Correspond to Changes in Sensitivity, but Not Criterion

Data are from the same sessions in Figures 3D and 3E and Table 1.

(A) Peristimulus histograms showing the population response to the sample stimuli. Histograms used 1-ms bins and were smoothed with a Gaussian filter (σ = 5 ms). Responses were modulated by changes in sensitivity but not in criterion.

(B) Noise correlations between pairs of simultaneously recorded neurons binned by the geometric mean of their evoked responses. Noise correlations were reduced when behavioral sensitivity increased but were unaffected by shifts in criterion. The y axis scaling differs for monkeys F and L.

rejection. Sensitivity needs to be focused to where successful detections and rejections have the greatest overall importance. Failure to optimize either criterion or sensitivity undermines performance.

Here we show that these two distinct components of attention are conflated in a paradigm used by many single-neuron studies of attention. Using a task designed to dissociate these two components, we found that the neuronal mechanisms of attention in area V4 of visual cortex corresponded to shifts in sensitivity but not criterion. This result shows that spatially selective criterion changes must be mediated by brain structures separate from V4 and, perhaps, outside of visual cortex. Furthermore, this result indicates that separate brain regions support distinct components of attention and suggests that attention depends on multiple neurobiological mechanisms.

Task Difficulty

Because the magnitude of attention-related modulation of firing rates in V4 is larger for tasks of greater difficulty (Boudreau et al., 2006), the modulations related to sensitivity shifts would likely be larger in a more difficult task. A more challenging task might also reveal modulation associated with criterion changes, which we did not detect here. But even if criterion-related modulation were found in a more difficult task, it is likely to be much smaller than the sensitivity-related modulation in the same task, and, therefore, V4 modulations would still be dominated by behavioral changes in sensitivity and not criterion. In the task used here, the firing rate modulation related to criterion changes was 10-fold smaller than the modulation related to sensitivity changes (Table 1). Even if V4 modulation related to criterion shifts were revealed in a more difficult task, it is unlikely that V4 contributes substantially to the animal's changes in criterion.

Neural Mechanisms of Criterion and Sensitivity

Although criterion is generally formulated as a post-perceptual process in signal detection theory (Green and Swets, 1966; Macmillan and Creelman, 2004), a subject's criterion can depend on perceptual as well as decisional and motor processes. For example, neuronal signals related to whether a visual stimulus is a target or nontarget are observed in V4 and other areas of the ventral visual pathway (Chelazzi et al., 2001; Pagan et al., 2013). A simple perceptual mechanism of criterion shifts could be to selectively control the gain of these signals for different spatial locations. However, the results here suggest that such signals in V4 are unlikely to support behavioral shifts in criterion.

Spatial shifts of sensitivity are likely to be mediated by sensory regions of the cerebral cortex, but the structures mediating criterion changes are less clear. It is possible that criterion shifts are associated with subcortical structures, such as the superior colliculus. If so, this dichotomy would explain a puzzling result from pharmacological inhibition of the superior colliculus (Zénon and Krauzlis, 2012). During collicular inactivation, monkeys showed behavioral deficits in attention, but neuronal modulations related to attention were intact in visual cortex. This result was unexpected because the behavioral deficits from collicular inactivation were thought to arise from the perturbation of cortical modulations. But this result would be expected if the cortex

Table 1. Modulation Indices of Attention-Related Neuronal Changes

	Criterion Sessions (Δc)		Sensitivity Sessions ($\Delta d'$)		Criterion Sessions versus Sensitivity Sessions	
Modulation index	monkey F (n = 22)	monkey L (n = 10)	monkey F (n = 22)	monkey L (n = 25)	monkey F	monkey L
Firing rate (sample stimulus)	0.006 ± 0.005	0.002 ± 0.007	0.060 ± 0.004	0.028 ± 0.003	$p < 10^{-8}$	$p < 10^{-3}$
	$p < 0.31$	$p < 0.78$	$p < 10^{-11}$	$p < 10^{-8}$		
Firing rate (delay period)	0.009 ± 0.005	0.004 ± 0.012	0.109 ± 0.006	0.078 ± 0.005	$p < 10^{-14}$	$p < 10^{-7}$
	$p < 0.09$	$p < 0.75$	$p < 10^{-13}$	$p < 10^{-13}$		
Noise correlation	0.040 ± 0.026	0.057 ± 0.056	−0.295 ± 0.020	−0.198 ± 0.030	$p < 10^{-12}$	$p < 10^{-3}$
	$p < 0.13$	$p < 0.34$	$p < 10^{-11}$	$p < 10^{-6}$		
Fano factor	0.002 ± 0.004	0.007 ± 0.014	−0.043 ± 0.010	−0.019 ± 0.004	$p < 10^{-3}$	$p < 0.02$
	$p < 0.68$	$p < 0.62$	$p < 10^{-3}$	$p < 10^{-4}$		

Each of the four columns to the left reports the mean ± SEM across sessions and the probability that the indices have a mean 0 (t test). The remaining two columns indicate the probability that the modulation indices from the two types of sessions have the same mean (paired t test). A single modulation index was computed for each session. A positive index for a sensitivity session indicates a higher measure (e.g., firing rates) under the high *d'* task condition, and a positive index for a criterion session reflects a higher measure in the low *c* condition. Indices were computed using both correct and error trials, but the results were highly similar when only correct trials were used.

and colliculus contribute to distinct components of attention. In that case, the behavioral impairment because of collicular inhibition could be explained by a perturbation of the animal's criterion. A different study has shown that inactivation of the colliculus within a given attention condition changed the monkeys' criterion but not sensitivity (McPeek and Keller, 2004). These observations make it possible that shifts in criterion are associated with neuronal modulations in the colliculus.

Attention as an Aggregate Process

Attention is associated with a broad range of perceptual and behavioral phenomena. These include increased perceived contrast and spatial resolution even when these effects are irrelevant or impair behavioral performance (Carrasco et al., 2004; Yeshurun and Carrasco, 1998). Psychophysical studies show that sensitivity enhancement can be separated further into multiple component mechanisms (Lu and Dosher, 2000). In many studies, visual attention is defined not as the orienting of resources as here (Posner et al., 1980) but as the detection process itself (Juan et al., 2004; Buschman and Miller, 2007). In addition, attention is tightly entwined with saccade target selection, and covert attention and saccade selection may be mediated by highly overlapping circuits (Rizzolatti, 1983). Therefore, criterion and sensitivity shifts are only a subset of the many mechanisms of selective processing associated with the term attention. Given its heterogeneity, future investigations into attention would be most fruitful when focusing the specific mechanism of selective processing rather than relying solely on the umbrella term attention.

An alternative view would be to limit the term attention to sensitivity changes and exclude criterion shifts and other processes. Although that approach could be taken, it would exclude many phenomena commonly attributed to attention, including not only selection of external stimuli but also selection of internal representations in memory, task rules, and motor responses (Chun et al., 2011). Moreover, the current definitions of attention, which ascribe selective processing as a central property, can aptly describe mechanisms other than behavioral sensitivity (Carrasco, 2011). In particular, spatially specific shifts in criterion, which selectively improve performance at a visual location, are entirely consistent with these definitions.

Finally, it is likely that complex brain processes such as attention all consist of disparate neurobiological mechanisms. Memory, another complex process, is composed of different sub-processes that depend on separate brain structures (Squire, 2004). Other cognitive functions, such as decision-making, may also comprise distinct mechanisms. Experiments that can dissociate the components of such processes are likely to be needed to elaborate the circuits that mediate higher behaviors.

EXPERIMENTAL PROCEDURES

Criterion and Sensitivity

Criterion and sensitivity were measured using signal detection theory (Green and Swets, 1966; Macmillan and Creelman, 2004). Criterion was indexed as *criterion location* (*c*),

$$c = -\frac{1}{2}\left[\Phi^{-1}(\textit{hit rate}) + \Phi^{-1}(\textit{false alarm rate})\right].$$

In this equation, Φ^{-1} is the inverse normal cumulative distribution function. When $c = 0$, the subject shows no bias toward reporting either targets or nontargets. In the signal detection model (Figure 1C), this is the x value where the two Gaussian distributions intersect. When $c < 0$, the subject exhibits a bias toward reporting targets and when $c > 0$, a bias toward nontargets.

Sensitivity was indexed as *d'*,

$$d' = \Phi^{-1}(\textit{hit rate}) - \Phi^{-1}(\textit{false alarm rate}).$$

In the signal detection model, *d'* is the horizontal offset between the two Gaussian distributions. A larger *d'* indicates better sensitivity. The index *d'* characteristically ranges from zero to infinity, although negative *d'* values can result from sampling errors.

The results here generalize for other indices in signal detection theory, such the likelihood ratio (β) and area under the receiver operating characteristic (ROC). The indices used here have the advantages that *c* is well defined for $d' = 0$ and that *c* and *d'* have the same units to simplify comparison.

Behavioral Tasks and Neuronal Recording

Two rhesus monkeys, F and L (*Macaca mulatta*, adult males, 9 and 10 kg), were first trained to perform a standard attention task and then, for the main experiment, a dissociation task. The standard attention task is described in the

Supplemental Experimental Procedures, and the dissociation task is described below. Before training, each animal was implanted with a head post. Eye movements were tracked using a video system (EyeLink 1000, 500 Hz). After training in the dissociation task, we implanted a 10 × 10 array of microelectrodes (Blackrock Microsystems) in area V4 to record simultaneously from dozens of neurons in each daily session (median 66 units, 4 single units, 62 multiunits). Neurophysiological recording and analyses are described in the Supplemental Experimental Procedures.

All procedures were approved by the Institutional Animal Care and Use Committee of Harvard Medical School and complied with the United States Public Health Policy on the humane use and care of laboratory animals.

Dissociation Task

The monkey began each trial by fixating for 400–600 ms within a 1.5° window on a video display (57 cm away, 100-Hz frame rate). Two sample stimuli (full-contrast Gabors) appeared on opposite sides of the fixation point for 200 ms. After a delay of 200–300 ms, a single test stimulus appeared at one of the two sample locations for 200 ms. The monkey had to decide whether the test had a different orientation from the sample that had appeared at the same location. The location of the test was selected randomly, and the probability that the test was different was 0.5. If the test differed from the sample, the monkey had to saccade to it within 100–500 ms to receive a juice reward. If the test was the same as the sample, the monkey had to wait to saccade to a second test stimulus that appeared at the same location as the first test stimulus. The second test always differed from the sample, and it was used to ensure that the monkey was engaged during correct rejection trials. The monkey rarely failed to respond to the second test stimulus (< 1%), and these failures were not included in analyses.

Each trial was categorized as a hit, miss, false alarm, or correct rejection based on the response to the first test stimulus. A target trial was a hit if the monkey responded to the changed test stimulus and a miss otherwise. A nontarget trial was a false alarm if the monkey responded incorrectly to the unchanged first test stimulus, and it was a correct rejection if the monkey waited to respond to the changed second test stimulus.

Session Types

Each daily recording session was either a sensitivity session or a criterion session.

In a sensitivity session, we maximized the behavioral difference in *d'* while minimizing the difference in *c*. On other days, in criterion sessions, we maximized the behavioral difference in *c* while minimizing the difference in *d'*.

Each daily session had two different task conditions. In a sensitivity session, throughout one task condition, the animal performed at high *d'* for one stimulus location and at low *d'* for the other location. Under the other task condition, performance was reversed for the two locations. For both conditions, the criterion was controlled to be unbiased ($c = 0$ or, equivalently, $\beta = 1$).

On a separate day, in a criterion session, the animal performed at low *c* for one location and high *c* for another location and switched performance for the two locations between task conditions. Sensitivity was similar across task conditions for each location.

The animal alternated between two task conditions in blocks of 240–360 trials. Each task condition was termed high *d',* low *d'*, low *c*, or high *c* according to the animal's performance at the stimulus location represented by the recorded neurons.

Reward Manipulations

To control criterion and sensitivity, we adjusted the reward sizes for hits and correct rejections for each stimulus location (average reward, ~150 μl). At each location, the criterion was controlled primarily by the ratio of the reward given for hits and correct rejections (H:CR reward ratio) at that location. The difference in sensitivity between the two locations was controlled primarily by the relative difference in the overall reward size (across H and CR) between locations.

In criterion sessions, the H:CR reward ratio was >1 at the low *c* location (on average 1.5) and <1 at the high *c* location (on average 0.5). The overall reward at each location (across H and CR) was adjusted to maintain a similar *d'* across task conditions. The overall reward at the low *c* location averaged 90% of the overall reward at the high *c* location.

In sensitivity sessions, the reward at the high *d'* location was set to be two to six times larger than the reward at the low *d'* location (on average five times larger). The H:CR reward ratio was adjusted independently for each location to control the criterion to be unbiased at that location. The H:CR reward ratio averaged 0.7 at the high *d'* location and 1.1 at the low *d'* location.

To achieve clear behavioral dissociation within each session, reward values were titrated throughout the session, and priming trials, which were excluded from analysis, were used at the beginning of each block to stabilize behavior (Supplemental Experimental Procedures).

SUPPLEMENTAL INFORMATION

Supplemental Information includes four figures and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.neuron.2015.05.007.

AUTHOR CONTRIBUTIONS

T.Z.L. and J.H.R.M. designed the experiments, performed the surgeries, and wrote the paper. T.Z.L. performed the experiments and analyzed the data.

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Neuron

Supplemental Information

Neuronal Modulations in the Visual Cortex Are Associated with Only One of Multiple Components of Attention

Thomas Zhihao Luo and John H.R. Maunsell

SUPPLEMENTAL INFORMATION

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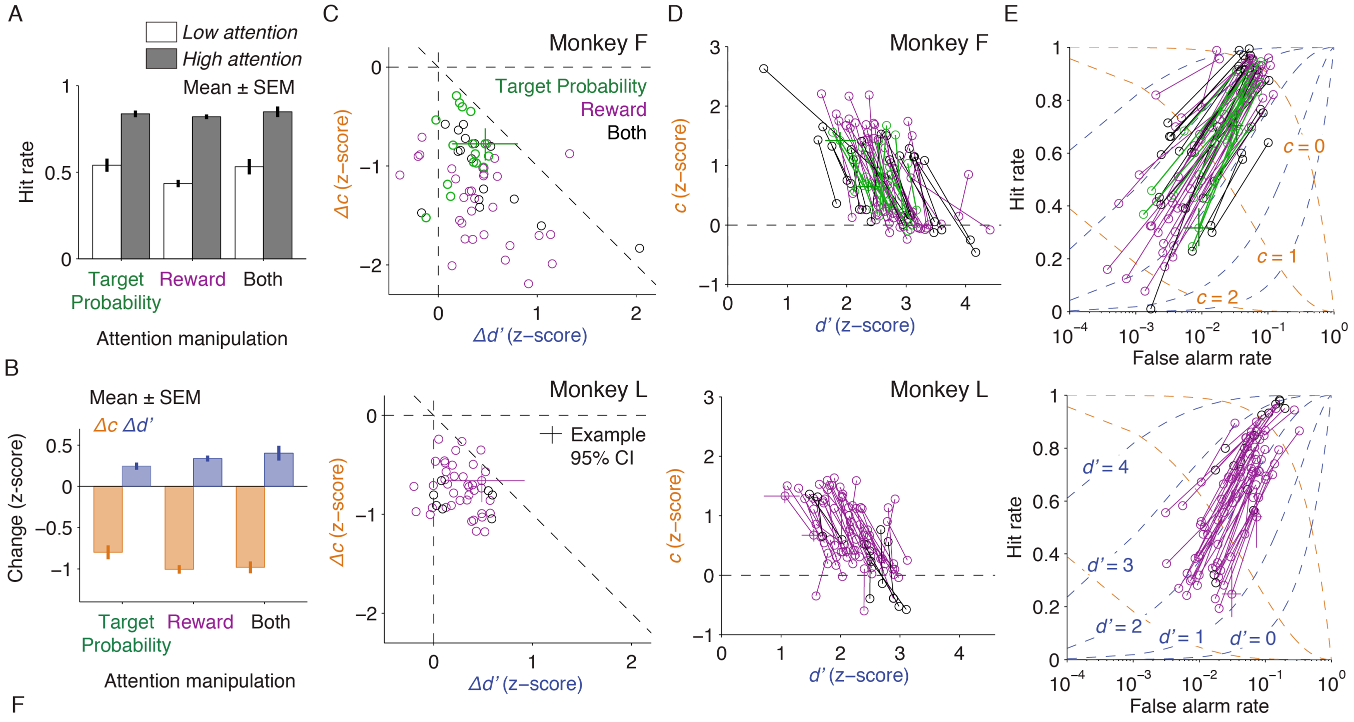
SUPPLEMENTAL DATA



F

Median values of behavioral measurements across sessions.

	Monkey F						Monkey L				Both monkeys All manipulations (n = 115)	
	Target Probability (n = 17)		Reward (n = 32)		Both (n = 16)		Reward (n = 43)		Both (n = 7)			
H	0.86	0.52	0.91	0.41	0.91	0.46	0.77	0.39	0.94	0.74	0.86	0.44
FA	0.05	0.01	0.06	0.004	0.05	0.005	0.07	0.02	0.13	0.03	0.06	0.01
c	0.28	1.10	0.08	1.48	0.13	1.28	0.31	1.25	−0.27	0.58	0.19	1.28
d'	2.68	2.44	2.91	2.46	2.99	2.54	2.26	1.94	2.75	2.48	2.68	2.33
Δc	−0.79		−1.29		−0.89		−0.73		−0.80		−0.90	
Δd'	0.24		0.41		0.35		0.29		0.21		0.34	

The first column (dark) is the *high attention* condition, and the second column (gray) is the *low attention* condition. Hit rates (H) and false alarm rates (FA) are unit-less. The unit for *c*, *d'*, *Δc*, and *Δd'* is z-score.

Figure S1 [related to Figure 1]. Different attention manipulations in the standard attention task (preliminary experiment) all changed criterion and sensitivity between attention conditions.

Data are from the same sessions shown in Figure 1B, E and Figure S2. (A) In some sessions, attention was controlled by setting the target probability to be 2 to 4 times higher at the attended location (n = 17). In different sessions, the reward size was 2 to 4 times larger at the attended location (n = 75). In the remaining sessions, we changed both target probability and reward size (n = 23). All three manipulations increased the subject's hit rate between attention conditions. (B) Both criterion (*c*) and sensitivity (*d'*) changed between task conditions for all three manipulations. (C-E) Top: monkey F; bottom: monkey L. The bootstrapped 95% confidence interval is shown for a representative session for each monkey. (C) Changes in criterion (*Δc*) and sensitivity (*Δd'*) between attention conditions in each session. (D) Criterion (*c*) and sensitivity (*d'*) for each attention condition of each session. Each circle represents the behavior in one attention condition of each session, and each line connects the two attention conditions of each session. (E) Plots of the hit rate and false alarm rate of each attention condition of each session. Each circle represents the behavior in one attention condition of each session. Each solid line connects the two attention conditions of each session. Dashed lines indicate isosensitivity and isocriterion lines. Because the overall false alarm rates were low (~10% or less), the x-axis is plotted in logarithmic scale. (F) Median values of behavioral measurements across sessions.

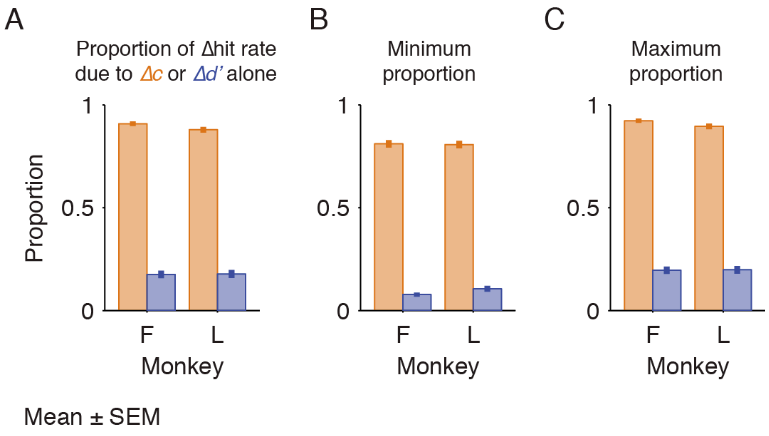
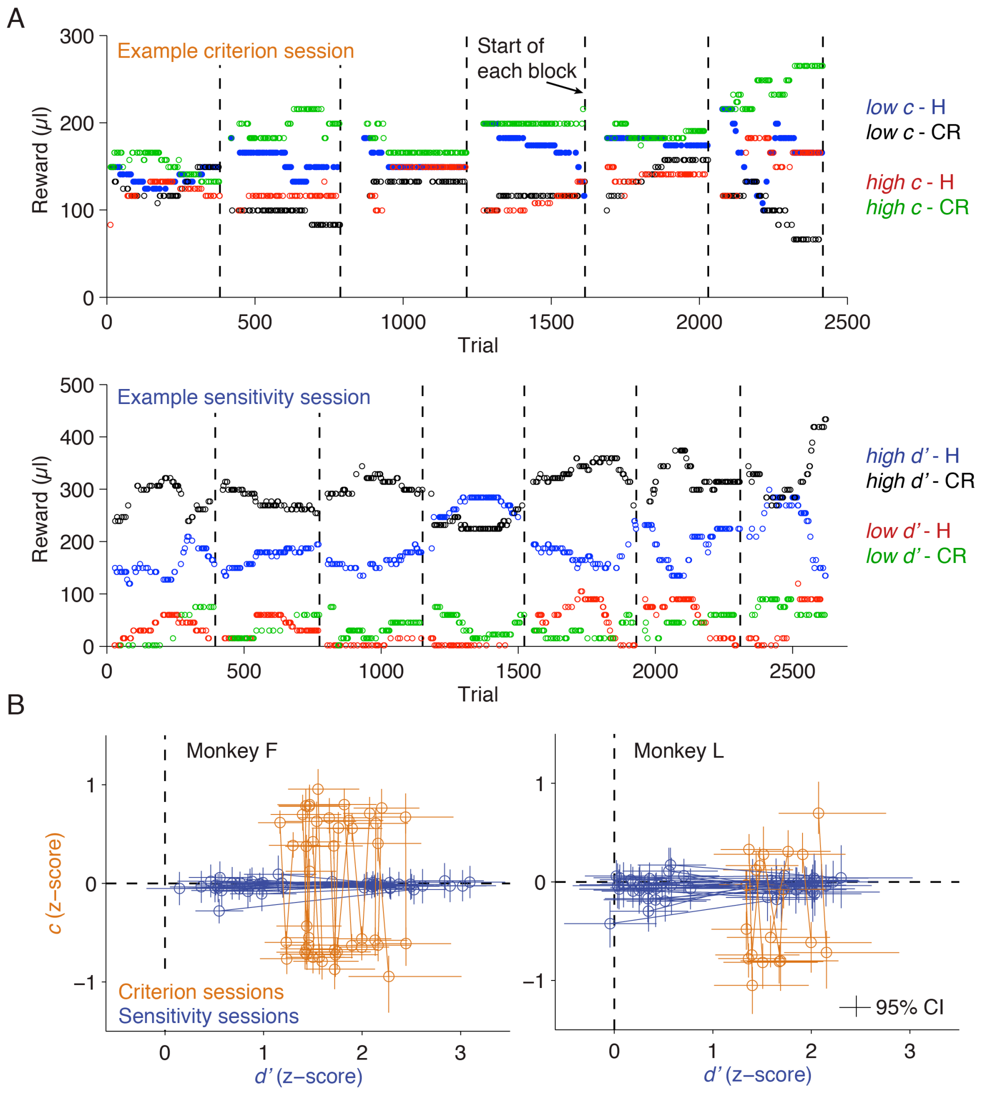


Figure S2 [related to Results]. Criterion changes accounted for most of the improvement in hit rate in the standard attention task (preliminary experiment). Same sessions as in Figure 1B, E and Figure S1. Monkey F, n = 65 sessions; monkey L, n = 50. (A) Because changes in both criterion and sensitivity contribute to the changes in hit rate, for each session we computed the proportion of the change in hit rate (ΔH) separately due to the change in criterion (Δc) or the change in sensitivity ($\Delta d'$). (B) Because Δc and $\Delta d'$ interact nonlinearly to determine the change in hit rate, we also computed the theoretically minimum proportions of the observed change in hit rate separately due to the observed Δc and $\Delta d'$. (C) The theoretically maximum proportions. All measures indicate that criterion changes accounted for most of the changes in hit rate in the standard attention task.



C

Median values of behavioral measurements across sessions.

	Monkey F				Monkey L			
	Criterion sessions (n = 22)		Sensitivity sessions (n = 22)		Criterion sessions (n = 10)		Sensitivity sessions (n = 25)	
	Low c	*High c*	***High d'***	*Low d'*	***Low c***	*High c*	***High d'***	*Low d'*
H	0.94	0.62	0.88	0.67	0.94	0.72	0.84	0.58
FA	0.44	0.07	0.14	0.37	0.49	0.17	0.18	0.47
c	–0.67	0.63	–0.02	–0.03	–0.76	0.22	–0.03	–0.04
d'	1.66	1.61	2.28	0.76	1.55	1.49	1.87	0.34
Δc	–1.34		0.02		–0.90		0.02	
Δd'	–0.001		1.72		0.03		1.60	

Hit rates (H) and false alarm rates (FA) are unit-less. The unit for *c*, *d'*, *Δc*, and *Δd'* is z-score.

Figure S3 [related to Figure 2]. Control of sensitivity and criterion in the dissociation task. (A) Reward time course for an example criterion session and example sensitivity session. (B) Criterion (*c*) and sensitivity (*d'*) of all sessions. Each circle plots the behavior of each task condition, and each line connects the two task conditions of each session. Error bars indicate 95% bootstrapped confidence intervals. (C) Median values of behavioral measurements across sessions. (B-C) Data are from the same sessions shown in Figure 2, Figure 3, Figure S4C, and Table 1.

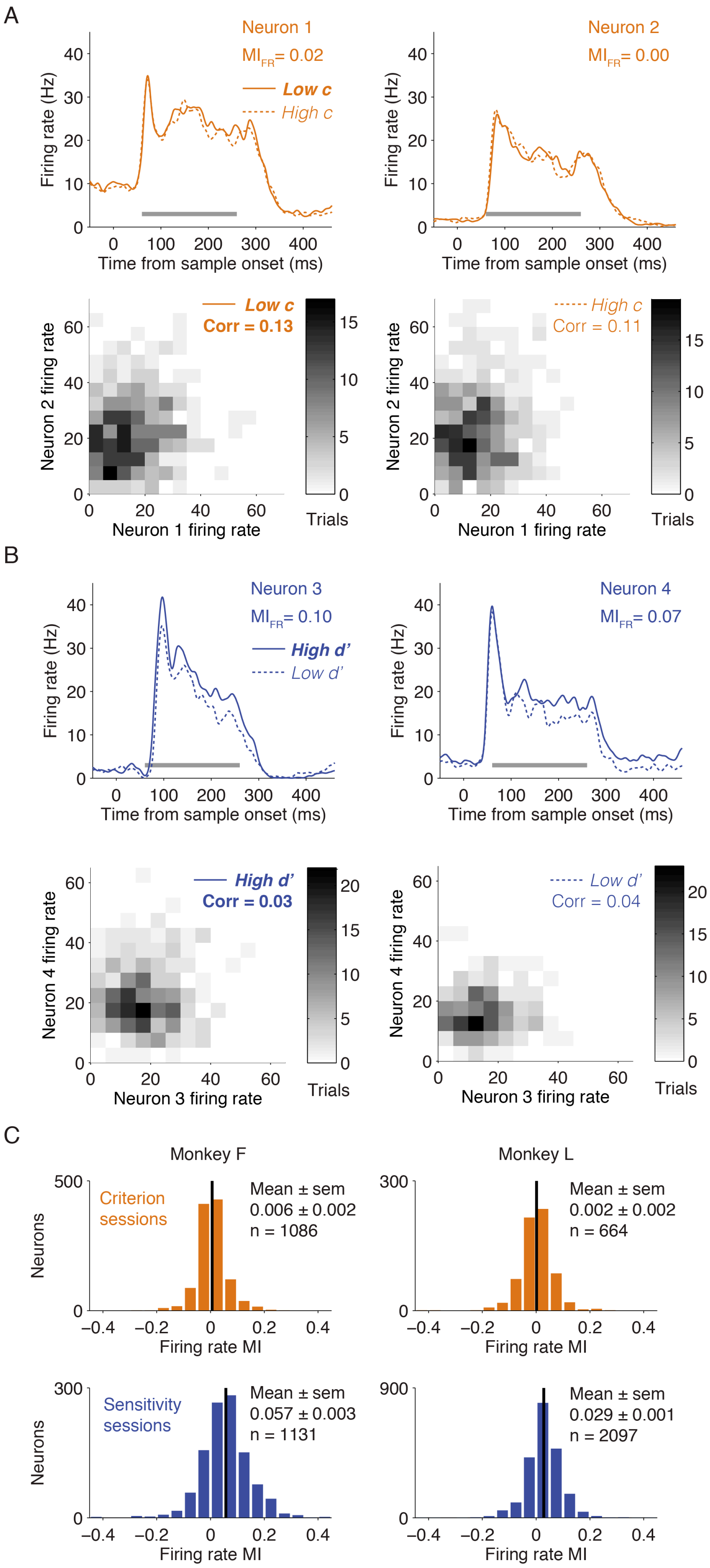


Figure S4 [related to Figure 3]. Changes in neuronal firing rate and pairwise correlations.

(A) Two example neurons from a criterion session. Each of the top panels shows the trial-averaged PSTH of one neuron in the *low c* and *high c* task conditions. Gray bar indicates the trial epoch used to compute noise correlation (sample period; 60 ms to 260 ms after sample onset). Each of the bottom panels shows the noise correlation between the two neurons in one task condition (*low c* or *high c*). The color map for the correlations plots the numbers of trials for a given spike count pairing.

(B) Two example neurons from a sensitivity session and their noise correlation. Although large changes in pairwise correlations were evident for the population of neurons (Figure 3B), the data from individual neurons were noisy.

(C) The distribution of modulation indices of firing rate during the sample period (60 ms to 260 ms after sample onset) for all responsive neurons in all criterion sessions and in all sensitivity sessions.

SUPPLEMENTAL EXPERIMENTAL PROCEDURES

Neurophysiological Recording

Neuronal activity was recorded while the animal performed the dissociation task as part of the main experiment. Only behavior was recorded for the standard attention task as part of the preliminary experiment.

At the beginning of each recording session, we presented a variety of Gabor stimuli to characterize the receptive fields of the neurons recorded by the array, and then we optimized stimulus parameters in the dissociation task to drive as many neurons as possible. The stimulus inside the receptive fields of the recorded neurons was set to an orientation 90° from the orientation of stimulus in the opposite hemifield to minimize effects of feature attention. The receptive fields were in the lower hemifield and had eccentricities 2-4° for monkey F and 5-7° for monkey L.

Action potential waveforms were sorted offline using spike-sorting software (Plexon) that computes principal component analysis scores for each spike. Waveforms were classified as a single unit if the waveforms formed a cluster that was separate from other waveforms.

Neuronal Analyses

Neuronal Analyses – Inclusion of Neurons and Trials

A neuronal unit was classified as visually responsive if its firing rate in the sample period (60 ms to 260 ms after the onset of the sample stimulus) was on average greater than its firing rate during the fixation period (200 ms to 0 ms before sample onset), and if its responses in the two periods were significantly different ($p < 0.01$, *t*-test). The median number of responsive units per session was 50 units (88% of all recorded units) for monkey F and 80 units (93%) for monkey L. Only responsive neurons were included in the PSTH in Figure 3A and in analyses of firing rate and Fano factor. All neurons regardless of responsiveness were considered for computing pairwise noise correlation, but the results were almost identical if only responsive neurons were used.

Single units and multiunits were combined for analyses. Separate analyses for the two populations showed highly similar results, corresponding to previous findings (Cohen and Maunsell, 2009).

Both correct (H and CR) and incorrect (M and FA) trials were used for neuronal analyses, but we excluded trials with premature fixation breaks and priming trials. The results were highly similar if only correct trials were used instead of both correct and incorrect trials. We included both correct and incorrect trials in the analyses because that would allow us to use the same set of trials to calculate behavioral and neuronal changes.

Neuronal Analyses – Noise Correlation and Fano factor

Noise correlation between each pair of simultaneously recorded neurons was computed as the Pearson's correlation coefficient of their firing rates across all trials.

$$\rho\left(FR_i, FR_j\right) = \frac{Cov\left(FR_i, FR_j\right)}{\sigma_i\ \sigma_j}$$

The noise correlation of the i^{th} neuron and j^{th} neuron, denoted $\rho\left(FR_i, FR_j\right)$, is the covariance of the firing rates of the two neurons across trials divided by the product of the standard deviations of each neuron's firing rates.

In Figure 3B, the noise correlation of each pair of neurons is binned according to the geometric mean of the evoked response of the two neurons. The evoked response of each neuron was calculated as the firing rate during the sample period (60 ms to 260 ms after sample stimulus onset), averaged across trials, minus the firing rate in the fixation period (200 ms to 0 ms before sample onset), also averaged across trials. The bin less than 0 spikes/s includes all pairs of neurons whose geometric mean evoked response is less than 0 spikes/s, and the bin greater than 30 spikes/s includes all pairs of neurons whose mean evoked response is greater than 30 spikes/s.

A single value of Fano factor was computed for each task condition of each session. For each task condition, the spike count variance of each responsive unit was plotted against its spike count mean, and we then fitted a line that was constrained to pass through zero. The slope of the regression line was then taken as the Fano factor. Similar results were found if we instead computed a single Fano factor for each responsive neuron in each task condition and then average across neurons to compute the Fano factor for that task condition.

Neuronal Analyses – Modulation Index

Modulation indices of firing rate were defined as the difference in mean firing rate between the two task conditions divided by the sum. In sensitivity sessions, the modulation index was defined such that a positive index indicates higher firing rates in the *high d'* condition.

$$MI_{FR}^{\Delta d'} = \frac{\left(FR_{high\,d'} - FR_{low\,d'}\right)}{\left(FR_{high\,d'} + FR_{low\,d'}\right)}$$

In criterion sessions, a positive index indicates higher firing rates in the *low c* condition (the task condition with the higher hit rate).

$$MI_{FR}^{\Delta c} = \frac{\left(FR_{low\,c} - FR_{high\,c}\right)}{\left(FR_{low\,c} + FR_{high\,c}\right)}$$

Modulation indices for noise correlation and Fano factor were similarly defined: a positive index indicates a higher value in the *high d'* condition in sensitivity sessions and a higher value in the *low c* condition in criterion sessions.

For firing rates, a modulation index was computed for each neuron and then averaged across the visually responsive neurons recorded in each session to provide a single modulation index for that session. Highly similar results were found if we pool spikes across visually responsive neurons to compute a population firing rate and calculate a modulation index of the population firing rate.

Noise correlation was first averaged across all pairs of simultaneously recorded neurons for each task condition. The noise correlation of the two task conditions of a daily session was then used to compute the modulation index for that session.

Fano factor was computed for each task condition as a single value (as described above), and the modulation index was calculated using the Fano factor of each condition.

In each session, the sample stimuli had one of two different orientations: the base or the base plus change (e.g. 40° and 60° in a session in which the orientation change was 20°). Modulation indices were computed separately for each orientation and then averaged between the two orientations to provide a single index for each session.

Standard Attention Task

The standard attention task was part of the preliminary experiment. Video display and visual stimuli were the same as those in the dissociation task of the main experiment. The standard attention task was a variant of the Posner attention paradigm frequently used in single-neuron studies of attention. In each trial, monkeys fixated within a 1.5° window in the center of a video display. Two Gabor stimuli flashed on for 200 ms and off for 200-400 ms, one in each visual hemifield. At an unexpected time, a target stimulus appeared in one of the two locations. The monkey had to look at the target to receive a juice reward. The target was a change in the stimulus: an orientation change for monkey L and a small white spot in the center of the Gabor for monkey F. When the target appeared, the monkey had to saccade to it within 100-500 ms to receive a juice reward. The target could appear on the third through seventh stimulus presentation (selected from a uniform distribution to discourage guessing at the beginning of trials). No target appeared in 5% of the trials, and the monkey received a reward if it maintained fixation past the seventh stimulus appearance.

Monkeys alternated between blocks of 100-200 trials in which attention was directed to one of two locations. Attention was controlled by setting the target probability to be 2 to 4 times higher at the attended location, or in different sessions, the reward size to be 2 to 4 times larger at the attended location. In the remaining sessions, we changed both target probability and reward size.

To compute *c* and *d'*, each stimulus presentation in which a target could occur (third to seventh) was categorized as a hit (H), miss (M), false alarm (FA), or correct rejection (CR). Stimulus presentations with no target were classified as either correct rejections or false alarms, and presentations with a target were categorized as hits or misses. Each presentation that was categorized as a correct rejection was scored for both stimulus locations, and each presentation that was classified as a hit, false alarm, or miss was scored only for the stimulus location where the target occurred or the saccade was directed. For presentations that were hits, false alarms, or misses, it was equally valid to score a correct rejection for other stimulus location or not to do so. We tried both methods of scoring, and the results were highly similar because of the large number of correct rejections. We chose not to score a correct rejection for the other stimulus location for presentations that were hits, misses, or false alarms.

Dissociation Task

Dissociation Task – Reward Titration

At the beginning of each session, reward parameters were set to values that were expected to approximately isolate the behavioral difference appropriate for that session. As described in the Experimental Procedures, a difference between the H:CR reward ratio at each stimulus location results in a criterion difference between locations, and a difference between the overall reward size of the two locations results in a sensitivity difference between locations. However, the animal's criterion and sensitivity at each stimulus location fluctuates over the course of a session. If reward contingencies were kept constant throughout the session, we would not be able to maintain reliable behavioral isolation during the session. To achieve reliable isolation within each session, we adjusted the reward sizes by a small amount (typically 10%) to control for the animal's fluctuating criterion and sensitivity (reward time courses of two example sessions are shown in Figure S3A).

In criterion sessions, reward was titrated after every 10-20 trials. If the animal's *d'* fluctuates to be higher at one location than the other, the overall reward size for the location with higher *d'* would be decreased by a small amount, and reward at the location with lower *d'* would be increased by the same amount. The overall reward at the *low c* location averaged 90% of the reward at the *high c* location. The H:CR ratios were adjusted to keep the criterion at the *low c location* near c = -0.5 and at the *high c* location at c = 0.5. We found these values to produce the largest criterion difference while providing statistically reliable measures of c and *d'* given the number of trials an animal typically worked in a day.

In sensitivity sessions, after each miss trial at either location, the hit reward at that location would be increased by a small amount (typically 10%) and the CR reward at that location would be decreased by the same amount. After each FA trial, the CR reward would be increased by a small amount and the hit reward would be decreased by the same amount at the location of the error. The ratio in overall reward size between the *high d'* and *low d'* locations averaged 5:1, and this ratio was adjusted after every 10-20 trials. This difference in reward size between locations was adjusted to maximize *d'* difference while at the same time keeping the animal motivated to respond to the *low d'* location so that we could obtain accurate behavioral measures at that location.

Dissociation Task – Priming Trials

At the beginning of each task condition (one block of 240-360 trials), 10-80 priming trials were presented to habituate the monkey to the reward contingencies of that task condition. In priming trials, the test stimulus occurred at only one stimulus location, rather than appearing at a random one of the two locations. Priming trials were presented as a continuous sequence and never interleaved with non-priming trials and not used in behavioral or neuronal analyses.

Priming trials were important for producing large, isolated differences in criterion or sensitivity. Repeatedly testing the same location helped the animal to recognize the reward contingencies at that location and stabilized its behavior. Typically, priming trials were presented to test a single location until the monkey's behavior stabilized for that location, and then priming trials were presented to test the other location until behavior also stabilizes there. Occasionally, a continuous sequence of 5-20 priming trials was presented in the middle of a block to stabilize the animal's behavior. On average, priming trials made up 8% of all trials in a session for monkey F and 10% of all trials for monkey L.

Dissociation task – Choice of Reward Parameters

We chose to manipulate reward size and not target probability (probability of an orientation change) because the animals adjusted their behavior more quickly to changes in reward size than to changes in target probability. This was expected, as changes in reward size are apparent within a single trial, whereas changes in target probability can only be assessed over many trials. We could achieve much finer control over the animal's behavior using reward size. Additionally, for a given number of trials, more reliable statistics of behavioral performance are obtained when target probability is 0.5.

Either reward size or target probability would likely elicit the same neuronal signal, because neuronal modulations associated with larger reward size and with higher target probability have similar magnitude and timing, and these two types of neuronal modulations are also strongly correlated among neurons in visual cortex (Stanisor et al., 2013).

One potential concern is that because the behavioral changes in *d'* are induced by differences in relative reward, it is plausible that corresponding neuronal changes are more closely associated with spatial differences in relative reward than with *d'* changes. But there is good reason to believe that the V4 neuronal changes are more closely associated with behavioral *d'* than with relative reward. Task difficulty modulates V4 responses in much the same ways as does attention (Spitzer et al. 1988; Boudreau et al., 2006; Ruff and Cohen, 2014), even though changes in task difficulty do not involve any change in relative reward. But, like higher relative reward, higher task difficulty increases behavioral *d'*. Because higher relative reward and higher task difficulty are two separate experimental manipulations that increase both the subject's *d'* and neuronal responses, we view the V4 modulations that we observed in this study to be more closely related to changes in *d'* than to changes in relative reward.

Dissociation Task – Sessions

On each day, the monkey performed only a criterion session or only a sensitivity session. We focused on isolating a single behavioral change each day to maximize the number of trials, which maximized the statistical reliability of the behavioral measurements of criterion and sensitivity.

Only two orientations were used for the sample and test stimuli at each location in each session. On each trial, either orientation was equally likely to be selected to be the sample, and the orientation was independently selected at each location. The difference between the two orientations specified the task difficulty for that session, and it was selected to keep the animal challenged.

Task difficulty was similar between criterion and sensitivity sessions for each monkey. For monkey F, the orientation change averaged 20° (16° to 23°) in criterion sessions and 18° (14° to 25°) in sensitivity sessions. For monkey L, the change was 90° for both criterion and sensitivity sessions.

The session type was alternated every six to eight days for monkey F. For monkey L, we alternated after 31 days, but neuronal signals from the array degraded after 41 days of recording. For each monkey and each session type, the results from the first half of the sessions were highly similar to the results to the second half.

Dissociation Task – Inclusion of Sessions

A session was excluded from analysis if the magnitude of the behavioral measure we sought to keep constant (*c* or *d'*) had a z-score greater than 0.3 (resulting median 0.04) or if that measure was greater than 1/3 of the behavioral measure we sought to vary (resulting median ratio 1/34). We excluded 1 of 45 sessions for monkey F and 6 of 41 sessions for monkey L. Including these sessions in the analyses did not affect the conclusions.

Dissociation task – Confidence intervals

We calculated binomial confidence intervals for the hit rate and false alarm rate in each task condition (Figure 3C-D, Figure S1E). Confidence intervals for *c* and *d'* in each task condition (Figure S3B) were computed through a bootstrapping method assuming binomial error around the observed hit rate and false alarm rate. Confidence intervals were similarly calculated for the difference in *c* and *d'* between the two task conditions of each session (Figure 3E).

Methods for Figure S2

Figure S2A: Proportion of the change in hit rate *(ΔH)* separately due to criterion change (*Δc)* alone or due to sensitivity change (*Δd')* alone

In most sessions, changes in both criterion and sensitivity contributed to the changes in hit rate between attention conditions in the standard attention task. Figure S2 shows analyses that isolate the proportion of the change in hit rate (ΔH) separately due to the change in criterion (Δc) or the change in sensitivity ($\Delta d'$). The intuition behind these analyses is to recalculate ΔH while keeping either *c* or *d'* to be the same in the *high attention* condition as in the *low attention* condition. The recomputed ΔH is then divided by the observed ΔH to obtain a proportion of the observed ΔH that is due to Δc alone or due to $\Delta d'$ alone.

We first denote the hit rate (*H*) as a function of *c* or *d'*:

$$H = \Phi\left(\frac{d'}{2} - c\right)$$

In this equation, Φ is the normal cumulative distribution function. The hit rate for each attention condition (*high attention* or *low attention*) can be denoted as a function of the *c* and *d'* measured in that condition.

$$H_{high\,attention} = \Phi\left(\frac{d'_{high\ attention}}{2} - c_{high\,attention}\right)$$

$$H_{low\ attention} = \Phi\left(\frac{d'_{low\ attention}}{2} - c_{low\ attention}\right)$$

For each session, the observed change in hit rate (*ΔH*) between the two attention conditions is the difference in hit rate between the *high attention* condition and the hit rate in the *low attention* condition.

$$\Delta H = H_{high\,attention} - H_{low\ attention}$$

$$\Delta H = \Phi\left(\frac{d'_{high\ attention}}{2} - c_{high\,attention}\right) - H_{low\ attention}$$

We first show the calculations for the proportion of *ΔH* due to *Δc* alone. To obtain this proportion, we recalculate *ΔH* as $\Delta H^{\Delta c}$, the change in hit rate solely due to the change in criterion. To compute $\Delta H^{\Delta c}$, we recalculated the hit rate for the *high attention* condition by fixing the *d'* to be the same as the *d'* in the *low attention* condition:

$$\Delta H^{\Delta c} = H^{d'\ equalized}_{high\ attention} - H_{low\ attention}$$

$$\Delta H^{\Delta c} = \Phi\left(\frac{d'_{low\ attention}}{2} - c_{high\,attention}\right) - H_{low\ attention}$$

The expression for $H^{d'\ equalized}_{high\ attention}$ is the expression for $H_{high\,attention}$ except that $d'_{high\,attention}$ is changed to $d'_{low\,attention}$. Finally, to obtain the proportion of *ΔH* solely due to the *Δc*, we divided $\Delta H^{\Delta c}$ by observed *ΔH.*

$$\text{Proportion of } \Delta H \text{ due to } \Delta c \text{ alone } = \frac{\Delta H^{\Delta c}}{\Delta H}$$

We then similarly calculate the proportion of *ΔH* due to *Δd'* alone. To obtain this proportion, we need to calculate $\Delta H^{\Delta d'}$, the change in hit rate solely due to the change in sensitivity.

$$\Delta H^{\Delta d'} = H_{high\ attention}^{c\ equalized} - H_{low\ attention}$$

$$\Delta H^{\Delta d'} = \Phi\left(\frac{d'_{high\ attention}}{2} - c_{low\ attention}\right) - H_{low\ attention}$$

In the second equation, the first term is the expression for $H_{high\,attention}$ except with $c_{high\,attention}$ changed to $c_{low\,attention}$. Finally, to obtain the proportion of *ΔH* solely due to the change in *d'*, we divided $\Delta H^{\Delta d'}$ by the observed *ΔH*.

$$\text{Proportion of } \Delta H \text{ due to } \Delta d' \text{ alone } = \frac{\Delta H^{\Delta d'}}{\Delta H}$$

These proportions are computed for each session and averaged across sessions to provide the plot in Figure S2A.

Figure S2B-C: Minimum and maximum proportions of the change in hit rate *(ΔH)* separately due to criterion change (*Δc)* alone or due to sensitivity change (*Δd')* alone

The analyses shown in Figure S2B and S2C were performed because *Δc* and *Δd'* interact nonlinearly to determine *ΔH*. For each session we computed the theoretically minimum and maximum proportions of the observed *ΔH* separately due to the observed *Δc* and *Δd'*.

We first show computations for the minimum proportion of observed *ΔH* that could be attributed to the observed *Δc*. To obtain this proportion, we needed to calculate $\Delta H_{\min}^{\Delta c}$, the minimum *ΔH* that could be attributed to *Δc*. In calculating $\Delta H_{\min}^{\Delta c}$, criterion values for both attention conditions are not changed from the observed values, while *d'* is a parameter that is varied to minimize the difference in hit rate between attention conditions.

$$\Delta H_{\min}^{\Delta c} = \min_{d'}\left[H_{\textit{high attention}}^{\textit{varying } d'} - H_{\textit{low attention}}^{\textit{varying } d'}\right]$$

$$\Delta H_{\min}^{\Delta c} = \min_{d'}\left[\Phi\left(\frac{d'}{2} - c_{\textit{high attention}}\right) - \Phi\left(\frac{d'}{2} - c_{\textit{low attention}}\right)\right]$$

$$d' \in \left[d'_{\textit{low attention}}, d'_{\textit{high attention}}\right]$$

A single value of *d'* is chosen for both attention conditions to minimize $\Delta H_{\min}^{\Delta c}$. This value of *d'* is selected from the interval delimited by the observed *d'* values in the *low attention* and *high attention* task conditions ($d'_{\textit{low attention}}$ and $d'_{\textit{high attention}}$, respectively). The *d'* that minimizes $\Delta H_{\min}^{\Delta c}$ was obtained using the MATLAB algorithm *fminbnd.* Finally, we obtained the minimum proportion of observed ΔH that could be attributed to the observed Δc:

$$\text{Minimum proportion of } \Delta H \text{ due to } \Delta c = \frac{\Delta H_{\min}^{\Delta c}}{\Delta H}$$

We similarly computed maximum proportion of observed ΔH that could be attributed to the observed Δc:

$$\Delta H_{\max}^{\Delta c} = \max_{d'}\left[H_{\textit{high attention}}^{\textit{varying } d'} - H_{\textit{low attention}}^{\textit{varying } d'}\right]$$

$$\Delta H_{\max}^{\Delta c} = \max_{d'}\left[\Phi\left(\frac{d'}{2} - c_{\textit{high attention}}\right) - \Phi\left(\frac{d'}{2} - c_{\textit{low attention}}\right)\right]$$

$$d' \in \left[d'_{\textit{low attention}}, d'_{\textit{high attention}}\right]$$

$$\text{Maximum proportion of } \Delta H \text{ due to } \Delta c = \frac{\Delta H_{\max}^{\Delta c}}{\Delta H}$$

The minimum and maximum proportions of observed ΔH that could be attributed to the observed $\Delta d'$ were similarly calculated. We first computed $\Delta H_{\min}^{\Delta d'}$ and $\Delta H_{\max}^{\Delta d'}$, the minimum and maximum ΔH that could be attributed to $\Delta d'$. To obtain $\Delta H_{\min}^{\Delta d'}$ and $\Delta H_{\max}^{\Delta d'}$, sensitivity values for both attention conditions are not changed from the observed values, while *c* is a parameter that is varied to minimize or maximize the difference in hit rate between attention conditions.

$$\Delta H_{\min}^{\Delta d'} = \min_{c}\left[H_{high\ attention}^{varying\ c} - H_{low\ attention}^{varying\ c}\right]$$

$$\Delta H_{\min}^{\Delta d'} = \min_{c}\left[\Phi\left(\frac{d'_{high\,attention}}{2} - c\right) - \Phi\left(\frac{d'_{low\,attention}}{2} - c\right)\right]$$

$$c \in \left[c_{high\ attention}, c_{low\ attention}\right]$$

$$\Delta H_{\max}^{\Delta d'} = \max_{c}\left[H_{high\ attention}^{varying\ c} - H_{low\ attention}^{varying\ c}\right]$$

$$\Delta H_{\max}^{\Delta d'} = \max_{c}\left[\Phi\left(\frac{d'_{high\,attention}}{2} - c\right) - \Phi\left(\frac{d'_{low\,attention}}{2} - c\right)\right]$$

$$c \in \left[c_{high\ attention}, c_{low\ attention}\right]$$

A single value of *c* is chosen for both attention conditions to minimize $\Delta H_{\min}^{\Delta d'}$ or maximize $\Delta H_{\max}^{\Delta d'}$, and this value comes from the interval determined by observed *c* values in the *low attention* and *high attention* task conditions ($c_{low\ attention}$ and $c_{high\ attention}$, respectively). Finally, $\Delta H_{\min}^{\Delta d'}$ and $\Delta H_{\max}^{\Delta d'}$ are each divided by *ΔH* to obtain the proportions:

$$\text{Minimum proportion of } \Delta H \text{ due to } \Delta d' = \frac{\Delta H_{\min}^{\Delta d'}}{\Delta H}$$

$$\text{Maximum proportion of } \Delta H \text{ due to } \Delta d' = \frac{\Delta H_{\max}^{\Delta d'}}{\Delta H}$$

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