

## COGNITIVE NEUROSCIENCE

# Effects of attention and distractor contrast on the responses of middle temporal area neurons to transient motion direction changes

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## Abstract

The ability of primates to detect transient changes in a visual scene can be influenced by the allocation of attention, as well as by the presence of distractors. We investigated the neural substrates of these effects by recording the responses of neurons in the middle temporal area (MT) of two monkeys while they detected a transient motion direction change in a moving target. We found that positioning a distractor near the target impaired the change-detection performance of the animals. This impairment monotonically decreased as the distractor's contrast decreased. A neural correlate of this effect was a decrease in the ability of MT neurons to signal the direction change (detection sensitivity or DS) when a distractor was near the target, both located inside the neuron's receptive field. Moreover, decreasing distractor contrast increased neuronal DS. On the other hand, directing attention away from the target decreased neuronal DS. At the level of individual neurons, we found a negative correlation between the degree of response normalization and the DS. Finally, the intensity of a neuron's response to the change was predictive of the animal's reaction time, suggesting that the activity of our recorded neurons was linked to the animal's detection performance. Our results suggest that the ability of an MT neuron to signal a transient direction change is regulated by the degree of inhibitory drive into the cell. The presence of distractors, their contrast and the allocation of attention influence such inhibitory drive, therefore modulating the ability of the neurons to signal transient changes in stimulus features and consequently behavioral performance.

## Introduction

Detecting changes in a visual scene is an important function of the primate visual system (e.g. detecting transient changes in the direction of a moving object to avoid a collision). Behavioral studies have shown that change-detection performances of humans can be influenced by intrinsic variables, such as the allocation of attention (Pinilla *et al.*, 2001), as well as by extrinsic variables, such as the presence of distractors (Allard & Cavanagh, 2011). One issue that remains poorly investigated is how these factors interact and impact the ability of single neurons in primate visual cortical areas to signal changes in visual features.

In primate middle temporal area (MT), neurons reliably encode motion attributes (e.g. direction and speed), and their sensitivity to detect motion changes correlates with behavioral performance (Britten *et al.*, 1996; Thiele *et al.*, 1999; Cook & Maunsell, 2002; Liu & Newsome, 2005; Purushothaman & Bradley, 2005; Cohen & Newsome, 2009; Price & Born, 2010; Bosking & Maunsell, 2011; Smith *et al.*, 2011). However, most previous studies measured neuronal responses to a single stimulus that changes motion attributes when presented inside the receptive fields (RFs) of neurons. How MT

neurons signal such changes in the presence of a nearby distractor remains unclear. This is not a trivial question given that the responses of MT neurons to a moving stimulus can be strongly modulated by the presence of a second stimulus inside the RF (Treue & Maunsell, 1996).

Interestingly, when two stimuli are positioned within a visual neuron's RF, but one is attended and the other ignored, the contribution of the former to the response is enhanced while the contribution of the latter is suppressed (Moran & Desimone, 1985; Reynolds *et al.*, 1999; Treue & Martinez-Trujillo, 1999; Khayat *et al.*, 2010; Lee & Maunsell, 2010). However, because these effects have mainly been reported during task periods in which stimuli do not change, they cannot be extrapolated to change-detection tasks. Responses to transient changes involve processes such as exogenous/bottom-up attention, which may interact with endogenous/top-down attention, and thus further shape such responses (Hopfinger & West, 2006). In fact, a recent study reported that endogenously directing attention to a single stimulus, positioned inside the RF of MT neurons, shortens response latency to a transient speed change (Galashan *et al.*, 2013). Unfortunately, despite the aforementioned study, such latency effects have otherwise scarcely been reported in single cell studies of endogenous attention.

Here, we trained two macaque monkeys to detect changes in the direction of a moving target. First, we investigated whether

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distractors, located near the target and within the same RF, interfere with an animal's ability to detect transient changes in the target direction. Second, we recorded the responses of MT neurons to transient direction changes in the target both when it was presented alone inside the RF of the cells and when it shared the RF with a distractor. We found that both the change-detection performances of the subjects and the responses of single MT neurons were affected by attention and by the presence of nearby distractors.

## Materials and methods

### Animals

Two adult male macaque monkeys (6 and 7 kg), *Macaca mulatta*, participated in the experiments. All procedures complied with the Canadian Council of Animal Care guidelines and were pre-approved by the McGill Faculty of Medicine's animal care committee.

### Behavioral task and visual stimuli

The animals performed a motion direction change-detection task. On each trial, the animals were presented with two configurations of moving random dot patterns (RDPs), located on opposite hemifields relative to a central fixation spot (FS; Fig. 1A). Each configuration consisted of a high-contrast RDP moving in the neuron's anti-preferred direction (AP-pattern, 180° away from the direction giving the maximal response), that was either presented alone or paired with a second neighboring RDP moving in the neuron's preferred direction (distractor RDP). From trial-to-trial, the distractor RDP could have one of seven contrast levels relative to the contrast of the AP-pattern (0.02, 0.1, 0.3, 0.7, 1.5, 14 or 100%). A trial began once the monkey pressed a button and steadily fixated within a square window of 1.5° centered on the FS (0.1°; Fig. 1B). After an interval of 470 ms, the RDPs appeared on the screen; one of the stimulus pairs was located inside the RF of the recorded MT neuron, and the second outside in the opposite hemifield. Three-hundred and fifty milliseconds after stimulus onset, a small line (1° length) appeared next to the FS and pointed towards one of the AP-patterns (inside or outside the RF), cueing the monkey to covertly attend to that pattern (target). The monkey had to report a brief motion direction change (30° for 118 ms) in the cued AP-pattern (the change occurred at a variable delay of 660–2900 ms from cue onset; flat hazard function) by releasing the button within 150–500 ms after the change in order to receive a juice reward (responses faster than 150 ms were considered as anticipated responses).

In half of the trials, the uncued AP-pattern located in the opposite visual hemifield changed motion direction. The monkey had to ignore this event (occurring randomly between 660 and 1400 ms from cue onset) and wait until the target changed. Importantly, the target change always occurred at least 550 ms after the uncued change. In addition, we presented the animals with trials in which the two AP-patterns were presented alone. The different trial types were presented in random sequence, and only correct trials were analysed (except for the behavioral analyses). Trials were aborted without reward if the monkey: (i) responded before the target event; or (ii) responded to the uncued AP-pattern direction change; or (iii) broke fixation before releasing the button.

In this motion direction change-detection task, either AP-pattern was a potential target across trials. However, in a given trial, only one pattern could be the target. The direction change occurred inside the RF when the AP-pattern at that location was attended (target inside the RF, as shown in the example in Fig. 1B), or when it was

ignored (target outside the RF). Importantly, during these conditions, the other patterns were behaviorally irrelevant (contrast-distractors; Fig. 1A). By manipulating the contrast of the distractor, while attention was on the AP-pattern, we could modulate the sensory responses of MT neurons within a dynamic range of firing rates. This manipulation potentially provides variable excitatory and/or inhibitory inputs into a recorded neuron. The response to the stimulus pair could range from very low (when the distractor had low contrast and moved in the preferred direction) to approximately 70–80% of the maximum response evoked by the preferred direction alone (when the distractor had high contrast; Martinez-Trujillo & Treue, 2002; Khayat *et al.*, 2010).

Visual stimuli were back-projected using a video projector (NEC WT610, 1024 × 768 pixels resolution at 85 Hz) on a flat screen positioned 57 cm away from the monkey's eyes. The RDPs were generated by plotting white dots (dot size = 0.01 degree<sup>2</sup>, luminance = 2.4 cd/m<sup>2</sup>) at a density of 4 dots per degree<sup>2</sup> within a circular stationary virtual aperture on a dark background (luminance = 0.02 cd/m<sup>2</sup>). Dots moved with 100% coherence at the preferred speed of the neurons. When they crossed the aperture's border they were re-plotted at the opposite side. The size of the RDPs (1.3–3° diameter) was chosen so that they could fit within the classical RF excitatory boundaries. Generally, the distractor was positioned below the target; however, the exact position of the stimuli varied depending on the RF position and extension.

The contrast of the RDP was quantified as  $\text{contrast} = \frac{\sum [p(i) \times (L(i) - L_m)^2]}{\sum [p(i) \times L(i)]}$ , where  $p(i)$  is the proportion of pixels with luminance  $L(i)$  and  $L_m = \sum [p(i) \times L(i)]$  (Moulden *et al.*, 1990; Martinez-Trujillo & Treue, 2002).

### Electrophysiological recordings

Before the experiment, each animal underwent a surgical procedure under general anesthesia during which it was implanted with a titanium head post and a recording chamber (20 mm diameter; Crist Instruments, Hagerstown, MD, USA). The chamber was positioned over a craniotomy of the parietal bone providing access to area MT (Khayat *et al.*, 2010). During recording sessions, transdural penetrations were made with a guide tube that contained an electrode attached to a microdrive (NaN; Plexon, Dallas, TX, USA). Extracellular single-cell activity was recorded using tungsten electrodes (1–2 MΩ at 1 kHz; FHC, ME, USA) and a Plexon data acquisition system (Plexon). Signals were amplified, filtered between 250 Hz and 8 kHz, and digitized at 40 kHz. All single units were sorted offline using the Plexon spike sorter (Plexon). An interactive stimulus presentation program was used to qualitatively assess the location and size of each neuron's RF, as well as its preferred direction and speed. Cells were determined as belonging to area MT according to their response properties (i.e. direction selectivity as well as RF position and size) and to the position of the electrode relative to the superior temporal sulcus. Electrode position was determined through magnetic resonance imaging scans (Khayat *et al.*, 2010). During the recordings, an infrared eye-tracking device (EyeLink, ON, Canada) was used to monitor eye position at a sampling frequency of 200 Hz.

### Data analysis

Spike times in the different conditions (attended and ignored) were aligned relative to the onset of the direction change, which occurred at a random time between 660 and 2900 ms across trials. For each cell and condition, we computed the spike density function (SDF);

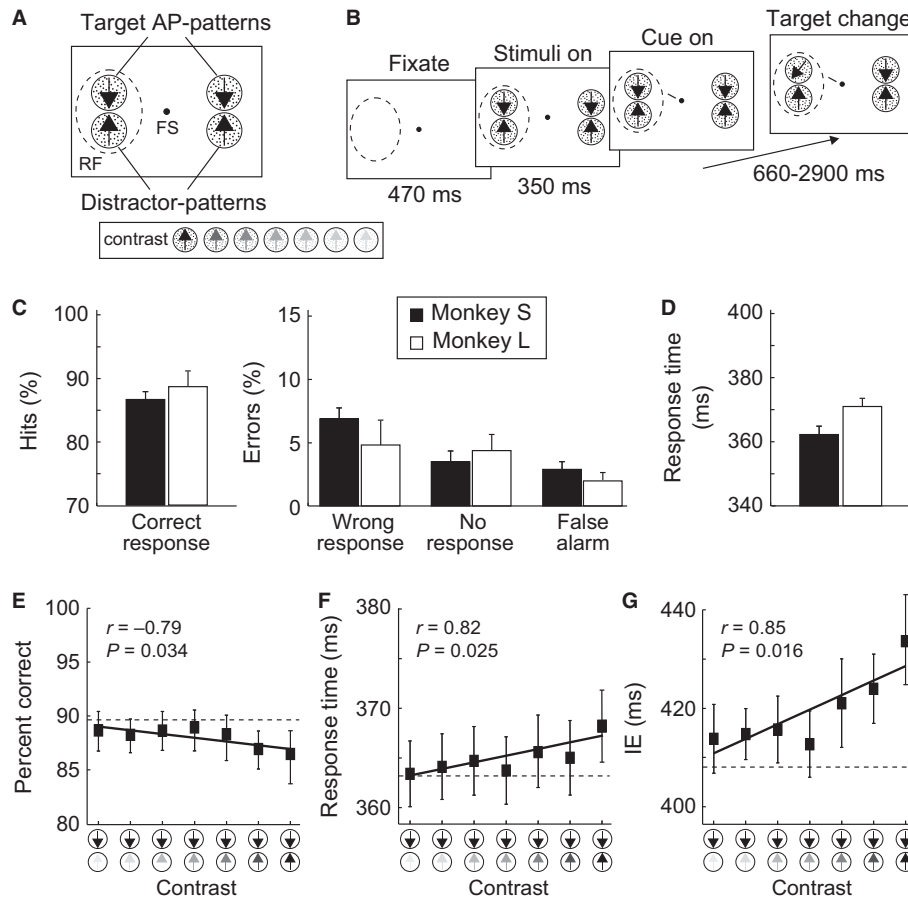


FIG. 1. Detection task and performance. (A) Illustration of the visual display and stimulus configurations. Two pairs of random dot patterns (RDPs) were displayed on each side of the fixation spot (FS), one inside and the other outside the recorded neuron's receptive field (RF; dashed circle). The target RDP moved in the neuron's anti-preferred direction (AP-pattern; downward arrow), and was paired with a distractor RDP moving in the preferred direction (represented by the upward arrow), but that had different contrast levels from trial-to-trial relative to the target's contrast (see sketches on the bottom). (B) Sequence of events when the target was inside the neuron's RF. (C) Overall percentage of hits and errors, and (D) mean response times (RTs) for monkey S (black bars) and monkey L (white bars). (E) Percent correct hits, and (F) RTs averaged across monkeys and sessions ( $n = 70$ ) during the different trial types. Solid line, linear regression slope fitted to the data. The horizontal dashed line represents the data during target-alone trials. Error bars denote the 95% bootstrap confidence intervals in (C, E), and SEM in (D, F). (G) Inverse efficiency (IE) scores for each stimulus combination. Same conventions as in (F).

1 ms resolution, Gaussian kernel with  $\sigma = 20$  ms). A total of 82 units were recorded, but cells were only included in the analyses if: (i) at least five correctly performed trials per stimulus combination were available; and (ii) the neuronal response after the direction change (i.e.  $30^\circ$  away from anti-preferred), during trials in which the target was presented alone inside the RF, was not suppressed relative to the response before the change. The rationale behind the latter criterion was to ensure that neuronal responses to the direction change fell on the ascending slope of the direction-tuning curve. These selection procedures resulted in the inclusion of 70 units (43 in monkey S and 27 in monkey L) in the attended condition, and 62 units (39 in monkey S and 23 in monkey L) in the attend-outside (ignored) condition.

The response latency evoked by the direction change was estimated by fitting a function  $f(t)$  to the response (Khayat *et al.*, 2006, 2009; Roelfsema *et al.*, 2007; Moro *et al.*, 2010). Other, more common procedures that take, for example, the first of a number of time bins that satisfy a significance criterion to determine the latency are sensitive to the amount of collected data and may thus yield biased estimates. On the other hand, our method has the advantage of providing a reliable estimate of the response latency that is relatively independent of the number of trials (Khayat *et al.*, 2006, 2009).

The shape of  $f(t)$  was derived from the following two assumptions: (i) the onset of response follows a Gaussian distribution; and (ii) a fraction of it dissipates exponentially. These assumptions yield the following two differential equations:  $\partial m_1(t)/\partial t = -\alpha m_1(t) + g(t, \mu, \sigma)$  for the dissipating response, and  $\partial m_2(t)/\partial t = g(t, \mu, \sigma)$  for the non-dissipating response. The total response is  $m_1(t) + m_2(t) = f(t)$ ,  $g(t, \mu, \sigma)$  is a Gaussian density with mean  $\mu$ , standard deviation  $\sigma$  and dissipation time constant  $\alpha$ . The solution to these equations is the sum of an ex-Gaussian (Luce, 1986) and a cumulative Gaussian, which was fitted to the response:  $f(t) = d \cdot \text{Exp}(\mu\alpha + 0.5\sigma^2\alpha^2 - \alpha t) \cdot G(t, \mu + \sigma^2\alpha, \sigma) + c \cdot G(t, \mu, \sigma)$ .

Thus,  $f(t)$  is described by five parameters,  $\mu$ ,  $\sigma$ ,  $\alpha$ ,  $c$  and  $d$ ;  $G(t, \mu, \sigma)$  is a cumulative Gaussian, and  $c$  and  $d$  are the contributions of the non-dissipating and dissipating response, respectively. The latency of the direction change-evoked response was defined as the point in time that the fitted function reached 33% of its maximum. The latency estimate obtained with different criteria gave rise to qualitatively similar results. For each neuron, we fitted this function to the response evoked by the AP-pattern presented alone in the RF, in both attended and ignored conditions. Cells for which we obtained reliable fits ( $r^2 > 0.5$ ) in both conditions were included in the analyses (42 out of 62 cells).

For each neuron and stimulation condition, we determined the mean spike count over trials in two different time periods. The first covered a 100-ms response period immediately prior to the direction change onset (pre-event period); this period served as a response reference for each stimulus combination. The second period extended from 100 to 200 ms after the event (post-event window), thereby capturing the changes in firing rates triggered by the transient direction change. A 100-ms window produced high enough spike counts that allowed us to compute meaningful metrics of neuronal activity and therefore perform reliable statistics. The magnitude of change in each cell's response relative to the event was determined by computing a firing rate index,  $FRI = (FR_{post} - FR_{pre}) / (FR_{post} + FR_{pre})$ , where  $FR_{post}$  and  $FR_{pre}$  are the mean firing rates during the post- and pre-event periods, respectively. Population responses, for each trial type, were obtained by averaging the FRI across neurons. Normalizing each neuron's response, prior to averaging, yielded similar results.

In order to measure how reliable an MT neuron signaled a direction change that took place inside its RF, we determined the cell's detection sensitivity (DS) by applying a receiver-operating characteristic (ROC) analysis and calculating the standard area under the curve (Thompson *et al.*, 1996; Niebergall *et al.*, 2011; Smith *et al.*, 2011). For each neuron, the DS compares the distribution of the mean spike counts in the pre-event period across trials to the distribution of mean spike counts in the post-event period. Values of 0.5 indicate that firing rates in the post-event period are not reliably different from the pre-event activity and correspond to chance performance. Values higher than 0.5 indicate that firing rates were reliably enhanced relative to the pre-event activity. The statistical significance of DS values for individual neurons was assessed using a permutation test. Pre- and post-event firing rates were shuffled and reassigned into two distributions for over 1000 repetitions, and the DS was computed for each repetition. From the generated distribution of DS values, we then calculated the mean and standard deviation to set the 95% confidence intervals.

## Results

### Behavioral performance

Two monkeys were trained to detect a transient motion direction change in a target stimulus. During the task, two identical pairs of moving RDPs were presented in opposite hemifields, one inside and the other outside the recorded neuron RF (Fig. 1A). Each pair consisted of a potential target and a behaviorally irrelevant distractor. The potential target was a high-contrast RDP moving in the neuron's AP-pattern, while the nearby distractor RDP moved in the preferred direction but could have, from trial-to-trial, one of seven different contrast levels (see sketches in Fig. 1A). Early in the trial, one of the AP-patterns (i.e. the target) was cued (Fig. 1B). The animal had to covertly detect a brief 30° change in the motion direction of the target that occurred at a random time from cue onset by releasing the button. In a subset of trials, the AP-patterns were presented alone (target-alone trials). To ensure that the animals attended the cued AP-pattern, in 50% of the trials the other, uncued AP-pattern located in the opposite visual hemifield changed motion direction. The animals had to ignore this event and wait until the target changed motion direction before responding.

In order to examine the detection performances of the animals, we measured their accuracy and response time (RT). All in all, monkey S and monkey L performed similarly on the task – they responded accurately on 86.7 and 88.8% of trials (Fig. 1C, left

panel; Wilcoxon rank-sum test,  $Z = -1.63$ ,  $P = 0.1$ ) and had an average RT of 362 and 371 ms (Fig. 1D;  $Z = -1.12$ ,  $P = 0.26$ ), respectively. In error trials (Fig. 1C, right panel), the animals made a mistake by either responding to the uncued AP-pattern direction change (6.9 and 4.8% of trials for monkey S and monkey L, respectively;  $Z = 2.88$ ,  $P = 0.004$ ), not responding at all to the target event (3.5 and 4.4%,  $Z = -0.89$ ,  $P = 0.37$ ), or responding independently of any direction change (false alarm, 2.9 and 2%,  $Z = 1.78$ ,  $P = 0.08$ ).

The detection performance (hit rate and RT) was also similar between monkeys for each trial type of a given stimulus combination ( $P > 0.05$ , Wilcoxon rank-sum test). Figure 1E and F displays the percentage of correct responses and the RTs to the target direction change when paired with each contrast-distractor, averaged across monkeys and recording sessions ( $n = 70$ ). The average detection performance during target-alone trials (correct hit = 89%; RT = 363 ms) is also shown in each panel (dashed horizontal line). Both detection accuracy (Fig. 1E) and response speed (Fig. 1F) were influenced by the distractor contrast. Accuracy deteriorated with increasing distractor contrast (Fig. 1E, black line; regression slope  $\pm$  95% confidence interval =  $-0.35 \pm 0.24$ ,  $r = -0.79$ ,  $P = 0.034$ ), and was also associated with a corresponding increase in RTs (Fig. 1F; slope =  $0.63 \pm 0.39$ ,  $r = 0.82$ ,  $P = 0.025$ ).

These effects illustrate a linear correlation between response speed and correct detection ( $r = -0.78$ ,  $P = 0.03$ ). To better appreciate this relationship, we computed the inverse efficiency (IE) scores (Townsend & Ashby, 1983) for each session and trial type. The IE scores are calculated as the ratio of mean RT to the proportion of correct responses; they provide an index of the detection efficiency, with higher values indicating worse performance. As anticipated, the best performance was observed during target-alone trials (Fig. 1G, dashed horizontal line). The presence of the distractor had a negative impact on detection efficiency, and this effect increased with increasing contrast (slope =  $2.99 \pm 1.67$ ,  $r = 0.85$ ,  $P = 0.016$ ).

### Effects of attention and nearby distractors on neuronal responses to the transient motion direction change

Next, we examined if the responses of MT neurons evoked by the transient change in motion direction (30° away from AP-pattern) were influenced by the allocation of attention and/or by the distractor contrast. We thus compared neuronal responses during trials in which the attended AP-pattern was located inside (see example in Fig. 1B) vs. outside the RF. Importantly, when the attended AP-pattern was outside the RF, in half of the trials, a motion direction change occurred earlier in the ignored AP-pattern inside the RF, but this had to be ignored; this allowed us to measure the responses to the direction change when attention was away, in the opposite hemifield. When the attended AP-pattern was inside the RF, the direction change could occur either without a preceding change in the AP-pattern outside (target-event first trials), or after (target-event second trials). In the latter case, presumably bottom-up attention could have, to a certain degree, transiently shifted to the first irrelevant direction change (Busse *et al.*, 2008). However, the direction changes were always separated by at least 550 ms, allowing the animals to re-allocate attention to the relevant target. Because neuronal responses evoked by the attended direction change in the RF did not differ between target-event first and second trials (paired *t*-test,  $t_{69} = 1.11$ ,  $P = 0.27$ ), or did the RTs of the animals (see below), we pooled the data from these trials.

Figure 2A illustrates the time course of the population responses ( $n = 62$ ) aligned to the direction change event, during trials in

which the event within the RF was attended (left panel) or ignored (right panel). In both behavioral conditions, a distractor with one out of seven different contrast levels was presented near the target AP-pattern (see stimulus sketches on the right of each response trace). Moreover, in some trials, the AP-patterns were presented in isolation without a distractor (dashed traces). Before the occurrence of the direction change event (i.e. pre-event window, gray area), the neuronal response reflected the cell's sensitivity for the contrast of the distractor; responses tended to increase with increasing contrast (Fig. 2A). Neuronal responses were also modulated by attention (compare the pre-event sustained responses between corresponding traces in the left and right panels of Fig. 2A). For the combinations of AP-pattern and nearby distractors, the pre-event activity was weaker overall when the AP-pattern inside the RF was attended vs. ignored, indicating that attention suppressed responses when it was directed to the neuron's anti-preferred stimulus inside the RF. These attentional effects were previously described in detail elsewhere (Khayat *et al.*, 2010) and will not be considered here.

Interestingly, MT neurons differentially responded to the same AP-pattern direction change (i.e. transient 30° change towards the preferred direction) depending on the nearby distractor's contrast, and on whether it was attended or ignored. The neuron's post-event response significantly deviated from the mean pre-event activity only when the nearby distractor's contrast was low/intermediate (see thick marks over the response traces of Fig. 2A;  $P < 0.05$ , paired  $t$ -test). In addition, the intensity of this effect appeared stronger when the direction change was attended compared with when it was ignored. The largest response change occurred during AP-pattern-alone trials, in the absence of a nearby distractor.

We quantified these observations by computing the mean firing rate of each neuron during two 100-ms periods relative to the direction change (pre-event and post-event periods; see gray areas in Fig. 2A). Figure 2B shows the firing rate averaged across neurons for these two periods and during the two attention conditions. Clearly, the response increased with increasing distractor contrast. However, the difference in firing rate between pre- and post-event time windows became smaller as distractor contrast increased. To

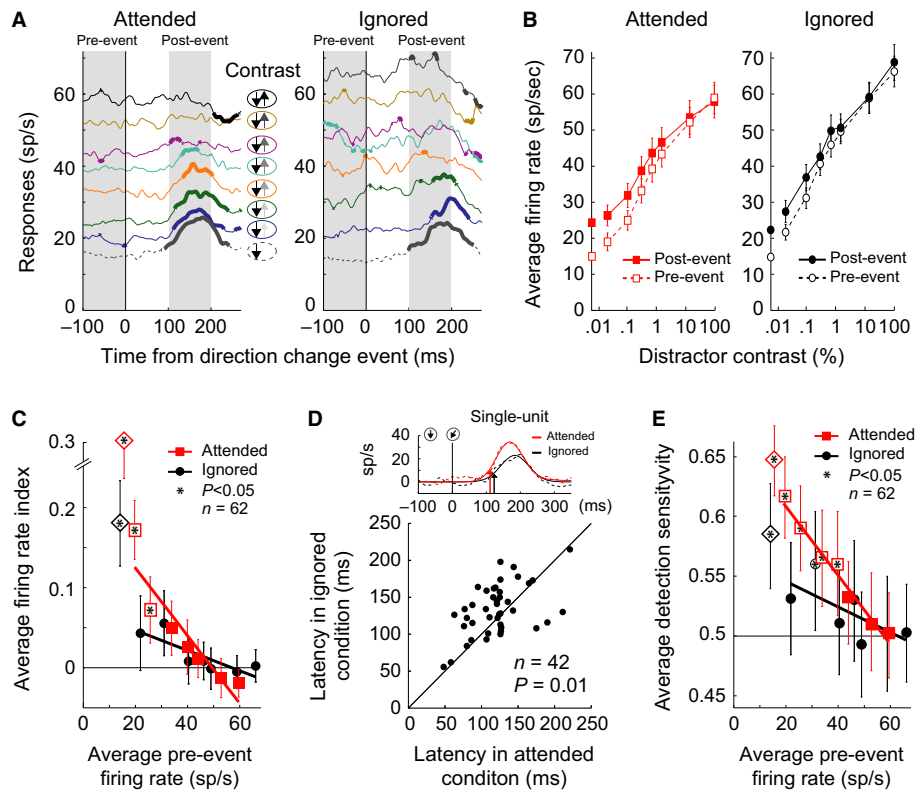


FIG. 2. Influence of attention and distractor's contrast on neuronal responses to the motion direction change. (A) Spike density functions (SDFs) averaged across neurons ( $n = 62$ ) for each stimulus combination. Responses are aligned relative to the motion direction change in the anti-preferred pattern (AP-pattern) within the receptive field (RF) when it was attended (left panel) or ignored (right panel). Each colored trace shows the response to a stimulus combination depicted on the right. The dashed traces show the responses during trials with the AP-pattern presented alone in the RF. Thick marks over each trace denote time bins that are significantly different from the mean pre-event activity. Shaded areas represent the pre- and post-event analyses periods. (B) Firing rates averaged across neurons in each analysis period as a function of the distractor's contrast in the attended (red) and ignored (black) conditions. Data points on the y-axis depict the firing rates during trials with the AP-pattern presented alone. Error bars, SEM. (C) Average firing rate index (FRI) comparing post- vs. pre-event responses as a function of the pre-event firing rates during the different trial types. Squares and circles are indices during trials with contrast-distractors. Diamonds are indices during trials with the AP-pattern presented alone. Asterisk symbols, indices significantly different from 0. Error bars, SEM. Lines, linear regression fits. (D) Latency of the direction change-evoked response in single units ( $n = 42$ ) during attended and ignored trials with the AP-pattern presented alone. Insert on the top shows the response of an example single unit to the direction change in the AP-pattern presented alone in the RF (see stimulus sketched). Red and black dotted traces illustrate responses in the attended and ignored conditions, respectively. The latency was determined by fitting a function to the responses (solid curves), and was equal to 111 and 123 ms in the attended and ignored conditions, respectively. (E) Average neuronal detection sensitivity (DS;  $n = 62$ ) in both conditions, comparing the firing rate distribution between pre- and post-event periods during contrast-distractor trials, as a function of the corresponding average pre-event firing rates. Diamond symbols, data during trials with the AP-pattern alone in the RF. Lines, linear regression fits. Asterisk symbols, DS significantly different from the 0.5 chance level. Error bars, 95% bootstrap confidence intervals.

compare the magnitude of the response change evoked by the motion direction change during each trial type, we computed a FRI between the responses in the two time periods for each neuron (see Materials and methods). We plotted the average FRI as a function of the average pre-event firing rates (Fig. 2C). Lower pre-event firing rates are associated with trial types when the distractor was of lower contrast. This analysis illustrates two main points. First, the motion direction change evoked the strongest changes in firing rates when the AP-pattern was presented alone in the RF (see diamond symbols in Fig. 2C), an effect that was significantly potentiated when the direction change was attended (red or blue) compared with when it was ignored (black; index = 0.3 vs. 0.18, Wilcoxon signed-rank test,  $Z = 2.32$ ,  $P = 0.02$ ). Second, in both conditions, the responses evoked by the direction change were systematically reduced as the distractor's contrast increased (i.e. as the pre-event firing increased). Moreover, we found the same negative correlation between the magnitude of response change after the event (i.e. FRI) and the pre-event response strength (Fig. 2C, red and black line;  $r^2 > 0.8$ ,  $P < 0.004$ ). Thus, the motion direction change evoked the strongest response change (i.e. index  $> 0$ ) when the AP-pattern was paired with low-contrast distractors producing firing rates that fall at the lower tail of a neuron's contrast tuning curve profile. Noticeably, the response evoked by the direction change was significantly higher than the pre-event response only when the change was attended (see asterisk symbols over data points,  $P < 0.05$ , Wilcoxon signed-rank test).

We also examined whether attention modulated the latency of the direction change-evoked response, as was recently reported for changes in MT neurons (Galashan *et al.*, 2013). To determine response change latency in the attended and ignored conditions, we fitted a function to each neuron's average response during trials with the AP-pattern presented alone in the RF (see Materials and methods; Khayat *et al.*, 2006, 2009), as this situation yielded the strongest post-event response change in both conditions. In the analysis, we included cells for which we obtained a reliable fit ( $r^2 > 0.5$ ,  $n = 42$ ), and estimated the latency as the time point where the function reached 33% of its maximum (see single-cell example in insert of Fig. 2D). We found that in most of these neurons the response to the direction change occurred at a slightly shorter latency when the change was attended vs. ignored (Fig. 2D; mean of distribution = 120 vs. 134 ms,  $n = 42$ , Wilcoxon signed-rank test,  $Z = -2.55$ ,  $P = 0.01$ ). At the population level, the fitted function on the average response in which we included all cells ( $n = 62$ , see dashed trace in Fig. 2A) yielded a latency of 106 and 115 ms, in the attended and ignored conditions, respectively. This latency difference also held when determined with a significance criterion ( $P < 0.05$ , paired  $t$ -test). Here, we defined the latency as the first of seven successive bins with a significant difference in response relative to the pre-event period (91 vs. 103 ms; see thick marks over dashed trace in Fig. 2A). Thus, on average, responses of MT neurons to a transient motion direction change occurred slightly earlier and were stronger when the change was attended.

### Neuronal DS

To examine how reliable the response of MT neurons signaled the direction change event, we computed the DS for each neuron and trial type. The DS is a ROC-based analysis (see Materials and methods) that measures the probability that an ideal observer could reliably detect, on a trial-by-trial basis, the direction change from the spike counts after the change relative to a reference time period immediately before the change (i.e. pre-event period; Bosking &

Maunsell, 2011; Smith *et al.*, 2011). Figure 2E shows the average DS to the motion direction change as a function of the neurons pre-event responses to the different stimulus combinations. As for the changes in firing rates, we found that the neuronal DS was most prominent in the absence of a distractor, and was also significantly stronger in the attended vs. the ignored condition (Fig. 2E, red and black diamond symbols; DS = 0.65 vs. 0.59, Wilcoxon signed-rank test,  $Z = 2.82$ ,  $P = 0.005$ ). Thus, MT neurons can signal a motion direction change in a stimulus more strongly in the absence of a nearby distractor and when the stimulus is attended.

In both behavioral conditions, even though the neuron's sensitivity increased with increases in distractor's contrast, the presence of the distractor systematically attenuated the neuronal DS (Fig. 2E; attended condition, red slope,  $r = -0.98$ ,  $P = 0.00003$ ; ignored condition, black slope,  $r = -0.79$ ,  $P = 0.01$ ). However, the DS remained consistently above chance level in the attended condition and in the presence of low-contrast distractors evoking responses falling on the lower segment of the neuron's contrast tuning curves (asterisk symbols over red data points,  $P < 0.05$ , Wilcoxon signed-rank test). These results indicate that the responses of MT neurons, selective for a nearby distractor's features, can reliably signal, on a trial-by-trial basis, the direction change when such distractors weakly contribute to the neuron's response.

In the above analysis, we computed the DS using a fixed post-event time period, from 100 to 200 ms after the stimulus direction change. This analysis period was intended to cover most of the direction change-evoked responses. However, neuronal responses to the direction change still yielded somewhat different latencies across cells, especially between the attended and ignored conditions, as shown in target-alone trials (Fig. 2D). Thus, to examine whether the observed difference in DS between conditions might arise from differences in the latency of the change-evoked response, we recomputed the DS in neurons in which we could obtain a latency measure ( $n = 42$ ) using a 100-ms time window aligned to the onset of each neuron's response to the direction change. The DS in these neurons using this 'dynamic' window was stronger in the attended compared with the ignored condition (0.68 vs. 0.6, Wilcoxon signed-rank test,  $Z = 2.63$ ,  $P = 0.008$ ), as was the case for the DS computed using the fixed window (0.67 vs. 0.59,  $Z = 2.91$ ,  $P = 0.004$ ). Thus, the higher neuronal DS to changes in attended targets relative to unattended ones was unlikely due to fluctuations in response latency.

### Other factors that may influence neuronal DS

#### Overall level of firing rate

Our previous results show that low-contrast nearby distractors interfere the least with the neuron's DS to the direction change. However, one alternative explanation for this effect is that the DS is correlated with the level of firing rate preceding the change rather than with the contrast of the distractor. This hypothesis would predict that neurons with low firing rates would show the largest increases in response after the change relative to neurons with high firing rates. Furthermore, because firing rates are always lower at low-stimulus contrast, this effect may also explain the larger DS corresponding to low- compared with high-contrast distractors.

We tested this hypothesis by correlating the pre-event firing rates with the DS associated to stimuli-evoking responses at either the lower (Fig. 3A; distractor contrast = 0.02%, mean response = 11.5 Hz) or the upper end (Fig. 3B; contrast = 14%, mean response = 44.4 Hz) of the neurons' tuning curve. In both cases, the

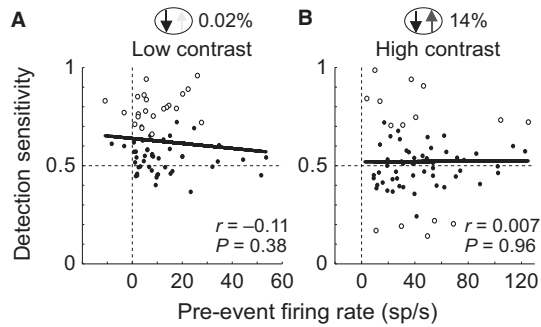


FIG. 3. Relationship between neuronal detection sensitivity (DS) and firing rates in the attended condition. DS of each neuron vs. the pre-event firing rates when falling on the lower (A) or upper (B) tail of the contrast tuning profile. Spontaneous activity (mean in 100-ms time period before stimulus onset) was subtracted from each response. The stimuli evoking these firing rates are illustrated on top. Open circles depict DS values significantly different from chance as determined by a permutation test. Black circles, non-significant DS.

firing rates varied considerably from cell-to-cell, but no correlation was observed between the DS and the level of firing rates ( $r^2 < 0.012$ ,  $P > 0.3$ ). Thus, although the DS was stronger overall at the lower tail of the contrast response function (0.62 vs. 0.52), it was not governed by the absolute response rate. Consequently, neurons that fired with lower rates did not necessarily detect the direction change better.

#### Response variability preceding the change

We next examined whether changes in response variability across trials were predictive of a neuron's DS. Recent studies showed that reducing stimulus contrast increases neuronal trial-to-trial response variability (Purcell *et al.*, 2012; Ponce-Alvarez *et al.*, 2013), which may have an impact on change-detection. To examine this issue, we determined the Fano factor (i.e. the ratio of the variance to the mean of spike counts across trials) in the pre-event period during trials associated with the low- (0.02%) and high- (14%) contrast distractors. The average Fano factor was higher in trials with low- compared with high-contrast distractors (1.5 vs. 1.3, Wilcoxon signed-rank test,  $Z = 2.48$ ,  $P = 0.013$ ). However, we found no correlations between Fano factors and the DS of the neurons (Fig. 4;  $r^2 < 0.08$ ,  $P > 0.1$ ), indicating that response variability preceding the change did not affect the DS on a cell-by-cell basis.

#### Response normalization

Response normalization can be conceptualized as a canonical operation in which excitatory inputs into a given neuron are weighted by the overall amount of excitatory and inhibitory inputs (Heeger *et al.*, 1996; Simoncelli & Heeger, 1998). One indicator of the degree of response normalization a neuron undergoes is to quantify the drop in response to a preferred stimulus when an anti-preferred stimulus is added inside its RF. Such a drop in response is likely due to the anti-preferred stimulus recruiting a large proportion of inhibitory relative to excitatory inputs into a neuron.

We hypothesize that if a neuron receives strong inhibitory inputs, its ability to increase its firing rate after the direction change may be constrained relative to a neuron that receives weaker inhibitory inputs. A prediction derived from this hypothesis is that units with stronger response suppression when adding the anti-preferred to the preferred stimulus in the RF would show a smaller increase in firing

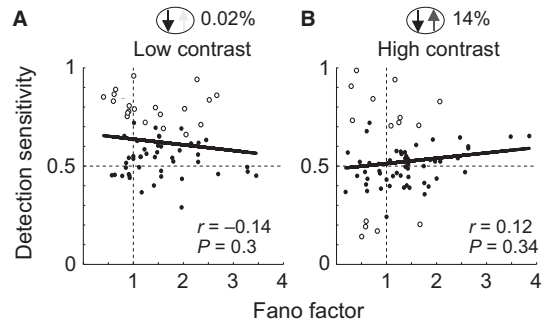


FIG. 4. Relationship between neuronal detection sensitivity (DS) and Fano factor in the attended condition. DS of each neuron vs. the pre-event Fano factor during trials with low- (A) or high- (B) contrast distractors. Same conventions as Fig. 3.

rate after the change and thus a lower DS. We tested this prediction by computing a suppression index (SI) for each unit, defined as:  $1 - \text{FR}_{\text{pair}} / (\text{FR}_{\text{AP}} + \text{FR}_{\text{pref}})$ , where  $\text{FR}_{\text{AP}}$ ,  $\text{FR}_{\text{pref}}$  and  $\text{FR}_{\text{pair}}$  represent the pre-event firing rates after subtracting the spontaneous activity (100 ms period before stimulus onset) evoked by the AP-pattern alone, the preferred pattern alone, and the stimulus pair, respectively. These firing rates were computed during trials when the animal was attending outside the RF. SI values of 0 indicate that the addition of the AP- to the preferred pattern in the RF produced the same firing rate as the sum of the individual firing rates evoked by each pattern alone. A negative SI would indicate a larger response when both stimuli were presented together relative to when presented alone. Here several scenarios are possible (e.g. increase in response to each stimulus of the pair, or decrease in the suppression produced by the AP-pattern alone in the RF when the preferred stimulus is added). However, because few cells in our sample show negative SI, we cannot distinguish between these scenarios. Positive SI values indicate that adding the AP-pattern to the preferred pattern decreases the response relative to the sum of individual responses (e.g. produce an increase in response normalization).

Figure 5A shows the average pre-event firing rates to the AP-pattern (left bar), the preferred pattern (right bar), and the pair (middle bar). Figure 5B plots the DS of the neurons (mean = 0.65) as a function of the SI (mean = 0.25) during trials with only the AP-pattern inside the RF. This condition was used because it avoids the possible influence of the varying-contrast distractor on the response. There was a significant negative correlation between SI and DS (slope =  $-0.26 \pm 0.08$ ,  $r = -0.6$ ,  $P < 10^{-6}$ ), indicating that neurons with the lower responses to the pair of stimuli indeed exhibit smaller increases in firing rate after the direction change. These results suggest that inhibitory interactions induced by the presence of the stimulus pair in the RF constrain the ability of MT neurons to signal changes in motion direction.

#### Relationship between neuronal activity and behavior

So far, the analyses have illustrated how the responses of MT neurons to a transient motion direction change in the AP-pattern vary with distractor contrast and the allocation of attention. However, because we recorded from a specific population of MT neurons and with a specific stimulus configuration, an important issue to consider is whether the observed response changes are contributing to the monkeys' task performance (Britten *et al.*, 1996; Thiele *et al.*, 1999; Cook & Maunsell, 2002; Purushothaman & Bradley, 2005; Cohen & Newsome, 2009; Price & Born, 2010; Bosking & Maunsell, 2011; Smith *et al.*, 2011).

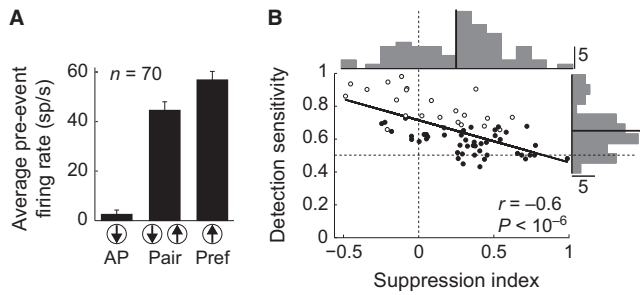


FIG. 5. Relationship between neuronal detection sensitivity (DS) and the strength of response suppression produced by the anti-preferred pattern (AP-pattern). (A) Average population response during the pre-event period evoked by the AP-pattern alone (AP), the preferred pattern alone (Pref) or by both (Pair). Error bars, SEM. (B) DS to the target change measured with the AP-pattern alone inside the receptive field (RF) vs. the suppression index (SI) for all cells. The SI reflects the strength of suppression a cell undergoes when two stimuli are inside its RF. The line represents the linear regression fit. Histograms for each variable are also plotted, with the solid black line denoting the mean of the distribution.

In order to examine this issue, we considered the recording sessions that contributed to the attended condition ( $n = 70$ , see Materials and methods) and separated the trials associated with the two lowest contrast distractors (0.02 and 0.1%, which showed the higher DS) into fast and slow RT trials relative to the median RT (Purcell *et al.*, 2012; Galashan *et al.*, 2013). For each neuron, we then aligned the single trial response to the RT, and quantified the FRI and DS over a 100-ms time window relative to the RT (from 200 to 100 ms before the RT). In order to perform this analysis over a sufficient number of trials and recording sessions, we combined trials from both contrast levels before rejecting recording sessions with less than five trials per RT group. This resulted in the inclusion of 61 sessions, with 5–19 trials (median = 10) per RT group and session.

Figure 6A shows the fast (black bars) and slow (white bars) RTs pooled over trials with low-contrast distractors (0.02 and 0.1%). On average, monkeys responded to the target direction change 43 ms faster in fast RT trials compared with slow RT trials. One likely explanation for the variability in RTs is small trial-to-trial fluctuations in attentional effort or alertness. Another possibility, however, is within-trial fluctuations due to variable trial durations and direction change onset times (e.g. longer trials would lead to shorter RTs). We examined this possibility by testing whether there was a correlation between the animal’s RT and the time of the direction change event during trials of a recording session. In all but one recording session ( $r = -0.59$ ,  $P = 0.002$ ), we found no significant ( $P > 0.05$ ) relationship between the two variables, thereby indicating that in our task the timing of the event did not bias the animal’s RT.

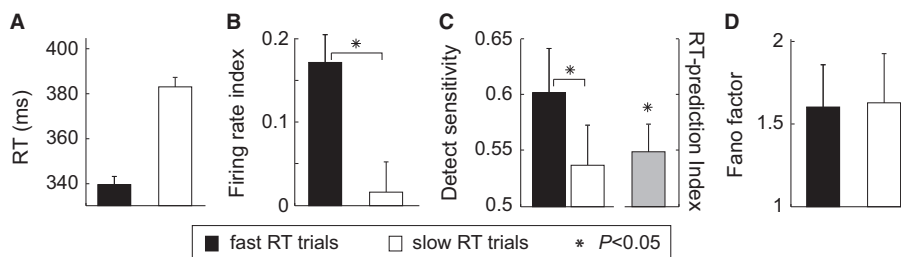


FIG. 6. Correlation between neuronal activity and response times (RTs) of animals in the attended condition. (A) Average fast (black bars) and slow (white bars) RTs during trials in which the target anti-preferred pattern (AP-pattern) was paired with low-contrast distractors (0.02 and 0.1%). (B) Average firing rate index (FRI) during fast and slow RT trials. Asterisk symbol denotes significant difference. (C) Average detection sensitivity (DS) in each RT group and average RT-prediction index (gray bar). (D) Average pre-event Fano factor for each RT group. Error bars, SEM in (A, B, D), and 95% bootstrap confidence interval in (C).

The average FRIs (Fig. 6B) and DS (Fig. 6C) were significantly higher during fast RT trials compared with slow RT trials (black vs. white bars, asterisk symbol,  $P < 0.02$ , Wilcoxon signed-rank test), suggesting that larger changes between pre- and post-event neuronal activity were associated with faster RTs. We also directly contrasted neuronal activity during fast vs. slow RT trials by computing the RT-prediction index. This index describes the probability that an ideal observer could predict whether the animal will respond fast or slow based on the neuronal responses to the change. To do this, we compared the distribution of the response difference between the post- and pre-event periods during fast RT trials against the distribution of the response difference during slow RT trials. Note that this index differs from the DS in that it compares the evoked activity during trials with different behavioral outcomes (slow and fast RTs) rather than comparing the activity between the pre- and post-event periods. We found that the RT-prediction index was significantly above the 0.5 chance level (Fig. 6C, gray bar;  $P = 0.005$ , Wilcoxon signed-rank test), indicating that trial-to-trial changes in response rate between pre- and post-event periods were predictive of RTs.

A recent study reported that MT neurons exhibit a reduction in their response variability prior to a speed change during trials in which the animals responded fast relative to trials in which they responded slower (Galashan *et al.*, 2013). We thus examined whether there was a relationship between neuronal response variability and RT by computing the Fano factor for each unit and RT group during the pre-event period before averaging across neurons. Unlike that study, we did not find any significant difference in Fano factor between fast and slow RT trials (Fig. 6D; 1.6 vs. 1.63,  $P = 0.79$ , Wilcoxon signed-rank test), indicating that in our data set response variability did not predict the animal’s RTs. Moreover, within each RT group, we found no correlation between the pre-event Fano factor and the magnitude of response change (FRI) or the strength of DS ( $r^2 < 0.04$ ,  $P > 0.1$ ). Thus, the neuron’s response variability before the target event did not co-vary with the strength of the neural signal after the motion direction change.

### Discussion

Our study showed that the presence of nearby distractors interfered with the ability of monkeys to detect transient direction changes in a moving target, an effect that decreased when decreasing distractor contrast. This was accompanied by a similar effect on the ability of MT neurons to detect transient direction changes (DS). Moreover, directing attention away from a changing stimulus decreased neuronal DS. The neuron’s DS was inversely correlated with the degree of response suppression/normalization a given cell underwent when adding an anti-preferred stimulus to a preferred stimulus inside the RF.



### Effects of distractors on change-detection

Our results agree with previous reports of distractors positioned near a target interfering with performance and event-related potentials during change-detection tasks (Pinilla *et al.*, 2001; Felisbert *et al.*, 2005; Pöder, 2008; Allard & Cavanagh, 2011; Michael *et al.*, 2011; Niedeggen *et al.*, 2012). Our study further shows that the degree of distractor interference decreases when lowering its contrast. This effect may be explained by the relative increase in target saliency when the distractor's contrast decreases, which may facilitate allocating attention to the target and the perception of its attributes (Wright, 2005).

### Effects of visual attention on the DS of neurons

A recent study examined the effects of attention on responses of MT neurons to speed changes in a single target stimulus (Galashan *et al.*, 2013). The authors reported that attention increases the amplitude of the change-evoked response and shortens response latencies, thus increasing the ability of cells to signal the event. Our data replicated this result for responses evoked by motion direction changes in a single target inside the RF. One alternative explanation for the higher neuronal DS when the stimulus in the RF was attended relative to when it was ignored, is that attention increases neuronal responses preceding the change and thus decreases response variability and improves the signal-to-noise ratio of the change-evoked response (McAdams & Maunsell, 1999; Galashan *et al.*, 2013). This explanation, however, does not apply to situations with our stimulus pairs, where attending to the target produced a decrease rather than an increase in neuronal response prior to the direction change (Khayat *et al.*, 2010), and response variability before the change did not correlate with neuronal DS.

A novel result of our study was that the presence of a distractor inside the RF decreased the ability of MT neurons to signal transient direction changes in the target. This effect was less pronounced for low-contrast distractors and decreased when directing attention to the target. These results are compatible with a mechanism in which attention decreases the effective contrast of unattended stimuli by decreasing the strength of inputs into MT neurons (Martinez-Trujillo & Treue, 2002; Khayat *et al.*, 2010).

It may be that our results apply to our stimulus configuration, and to neurons that are strongly selective for the distractor (motion in the preferred direction) and weakly selective for the target (motion in the anti-preferred direction). In these neurons, we find an increase in response following the target change. One may ask whether similar effects would be observed when both the target and distractor moved in the neuron's preferred direction. In the latter scenario one would anticipate that a direction change of 30° would cause a response decrease rather than increase (Bosking & Maunsell, 2011). The effects of distractors in such response decreases require further investigation.

The effects of attention on the responses to the direction changed we have observed here may be related to documented changes in RF profiles, for example, shifting the RF center toward an attended stimulus, previously reported, which would effectively exclude a nearby distractor (Womelsdorf *et al.*, 2006). Importantly, our data suggest that the magnitude of the RF shift is dependent on distractor contrast.

### Effects of response normalization

When an anti-preferred stimulus is paired with a preferred stimulus inside an MT neuron's RF, the cell's response is suppressed rela-

tive to when the preferred stimulus appears alone. This phenomenon can be explained by response normalization mechanisms (Snowden *et al.*, 1991; Britten *et al.*, 1996; Heeger *et al.*, 1996; Simoncelli & Heeger, 1998). In our experiment a measure of response normalization strength is the amount of response suppression produced by the pair preferred + AP-preferred stimulus presented inside the RF relative to the preferred stimulus alone. We found that neurons with the strongest suppression exhibited the weakest DS. This may be due to the amount of inhibitory drive (response normalization) into a neuron triggered by the presence of the stimulus pair that constrains response increases following transient changes in sensory inputs.

Moreover, we found that trials with low-contrast distractors were associated with larger DS relative to trials with high-contrast distractors. Because response normalization increases with increasing stimulus contrast (Britten *et al.*, 1996; Heeger *et al.*, 1996), the effect of low-contrast distractors on DS could be explained by a lower amount of response normalization. Interestingly, it has been proposed that visual attention affects response normalization in visual neurons (Reynolds & Heeger, 2009). In our target and distractor trials, the effects of attention reported here could be associated with an overall decrease in the contribution of distractor inputs into MT neurons, which would also decrease response normalization (Khayat *et al.*, 2010; Niebergall *et al.*, 2011).

Previous studies have reported that decreasing stimulus contrast increases trial-to-trial variability in a neuron's firing rate (Purcell *et al.*, 2012; Ponce-Alvarez *et al.*, 2013), therefore improving coding of stimulus attributes (Churchland *et al.*, 2010). Considering that low-contrast distractors increased trial-to-trial response variability (i.e. Fano factor) in our sample of MT neurons relative to high-contrast ones, it may appear contradictory that they impaired the DS of neurons the least. However, response variability neither influenced neuronal DS nor the detection performances of animals (i.e. RTs), indicating that, at least in our task, response variability was not an influential factor.

### Role of area MT on motion change-detection

Electrophysiological studies in humans have reported activation of area MT during the detection of changes in motion attributes, hence suggesting that neurons in this area play a role in this type of task (Pazo-Alvarez *et al.*, 2004; Martinez-Trujillo *et al.*, 2007; Prieto *et al.*, 2007). Moreover, studies in monkeys have demonstrated a correlation between MT neurons activity and performance during motion tasks (Britten *et al.*, 1996; Thiele *et al.*, 1999; Cook & Maunsell, 2002; Purushothaman & Bradley, 2005; Cohen & Newsome, 2009; Price & Born, 2010; Bosking & Maunsell, 2011; Smith *et al.*, 2011; Galashan *et al.*, 2013). Indeed, in the sample of MT neurons we recorded from (i.e. neurons encoding the target direction as anti-preferred and the distractor direction as preferred), the changes in firing rates following a transient motion direction change and the reliability of this signal change across trials (neuron's DS) was predictive of changes in reaction time. Thus, the recorded neuronal activity likely played a role in the performance of animals.

In sum, our data provide a neural correlate for distractor interference on change-detection performance. We propose that, in MT neurons, the main effect of a distractor, sharing the same RF with a target, is an increase in the amount of inhibitory drive into the neurons, consequently, constraining the amount of signal change following a transient change in the sensory input. Factors, such as attention and the contrast of a distractor, can modulate such an

inhibitory drive and therefore influence neuronal and behavioral change-detection performance.

### Conflict of interest

The authors declare that they have no conflict of interest.

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### Abbreviations

AP-pattern, anti-preferred pattern; DS, detection sensitivity; FS, fixation spot; IE, inverse efficiency; MT, middle temporal area; RDP, random dot pattern; RF, receptive field; ROC, receiver-operating characteristic; RT, response time; SI, suppression index.

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