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Task-specific shaping of feature-based attention in area MT

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June 2016

Abstract

Visual perception depends on the effective prioritization of visual information in order to concur with the current behavioral context. Depending on the context's requirements, it is important to facilitate the processing of a certain feature (e.g. motion) in some situations, while in others another feature (e.g. color) is more crucial. We here address the question whether and how the specific requirements of a visual task influence modulation of neuronal activity by feature-based attention (FBA). We recorded neuronal responses from monkey motion-sensitive medio-temporal area (MT) in response to spatially attended or unattended motion stimuli, while monkeys were required to detect an instantaneous speed- or color-change of a pre-cued target stimulus. We found a strong influence of task requirements on several parameters of MT single cell responses: If the task required attention to speed, mean firing rates were higher, and response variability and latency to otherwise identical visual stimuli was lower as compared to the task requiring attention to color. This was evident even with attention directed to the stimulus outside the receptive field (RF) of the recorded neuron, moving in a direction 180 deg away from the preferred direction inside the RF. Importantly, this task-specific response modulation in the

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processing of visual motion was preceded by a spatially global and tuning-independent shift in the baseline activity of MT neurons before onset of visual stimuli. The results provide single cell support for the hypothesis of a feature dimension-specific top-down signal emphasizing the processing of an entire feature class.

Introduction

Neuronal processing of visual information depends on the observer's perceptual requirements (Huk and Heeger, 2000; Jack et al., 2006; Chen et al., 2008). Several mechanisms involved in this selective, goal-directed processing have been proposed and assigned to different forms of visual attention (Knudsen, 2007; Bisley, 2011). Feature-based attention (FBA), in particular, renders the capability to process preferentially a certain quality of the visual environment. For example, human imaging studies showed higher activity in early visual cortex in response to color hues, motion directions, shape, or orientation of a stimulus if they matched the currently attended feature of another object (Corbetta et al., 1991; Saenz et al., 2002; Liu et al., 2007).

At the level of single cells, FBA is characterized by a firing rate (FR) change of neurons that are well-tuned to the attended feature attribute. For example, directing attention towards the preferred motion direction of a direction-selective neuron in area MT increases the response of that neuron irrespective of the current spatial focus of attention (Treue and Martínez Trujillo, 1999). In contrast, the neuron's response is unmodulated (or even weakened) if the attended motion direction deviates by more than 90 deg from its preferred direction (Martínez Trujillo and Treue, 2004). Importantly, this effect seems to be independent from the actual task: On the population level, FBA-induced FR changes were essentially identical in a motion task requiring detection of direction changes and in a color-change task, during which direction was irrelevant (Katzner et al., 2009). Only on the level of single cells, some neurons were showing higher activity during the motion task, while others were more active during the color task (see also Chen et al., 2012).

These results indicate that FBA spreads along the attended object, modulating the response of direction-selective neurons independent of the behavioral relevance of motion, i.e. independent from task requirements (Katzner et al., 2009). Yet, numerous imaging, EEG, and psychophysical studies provide evidence that non-spatial attention effects are not mandatorily bound to the attended object but may be dominated by the behavioral relevance of a single feature (see Wegener et al., 2014 for literature overview and a conceptual model). For example, reaction times (RT) to both speed and color changes were found to be significantly different in two versions of a task requiring either a more feature-directed or a more object-directed deployment of attention (Wegener et al., 2008). Considering that RTs to such speed changes correlate with the attentional modulation of MT responses (Galashan et al., 2013), we wondered whether FBA effects in area MT are likely to be independent from the specific task at hand. We investigated this issue by recording MT responses to instantaneous speed changes using essentially the same task requirements as in

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our previous psychophysical study. In the first task, monkeys were required to detect speed changes - a feature MT neurons are highly sensitive to (Nover et al., 2005; Traschütz et al., 2015). In the second task, using identical visual stimulation, monkeys were required to detect color changes – a feature for which MT is only weakly sensitive (Thiele et al., 1999; Croner and Albright, 1999). Based on the previous results (Katzner et al., 2009; Chen et al., 2012), both tasks were expected to elicit a tuning-dependent but task-independent influence of FBA, inside and outside the spatial focus of attention. Yet, analysis of numerous response parameters revealed clear differences between the speed and the color task, both at the level of evoked and spontaneous activity - suggesting a highly flexible, task-dependent shaping of FBA.

Material and Methods

Electrophysiological recordings. All surgical and experimental procedures followed the Regulation for the Welfare of Experimental Animals issued by the Federal Government of Germany, and were approved by the local authorities. Extracellular recordings were obtained from two male adult rhesus monkeys (*Macaca mulatta*) using tungsten microelectrodes (0.8 - 5 MOhm, 125 µm shank diameter; Frederic Haer, Bowdoin, ME). Surgery was performed under Propofol/Fentanyl anesthesia and under strictly aseptic conditions, as previously reported in detail (Wegener et al., 2004). The recording chamber was placed over the middle temporal sulcus; coordinates for electrode penetrations were estimated from structural magnetic resonance imaging scans. During recordings, area MT was identified by the high proportion of direction selective neurons, the size/eccentricity ratio of RFs and the depth of the recording site (Maunsell and Van Essen, 1983; Desimone and Ungerleider, 1986; Mikami et al., 1986). The amplified electrode signal was sampled at a frequency of 25 kHz and band-pass filtered between 0.7 and 5 kHz, using either a custom-made hardware filter or an equiripple FIR filter in forward and reverse direction. Online detection of spikes was achieved by thresholding. At the beginning of each recording session, one or two electrodes were lowered through a guide tube penetrating the *dura mater* until the electrode's tip reached the desired depth in area MT. Prior to cell recordings, the tissue was allowed to settle for about 30 min.

Visual Stimulation. Visual stimuli were presented on a 22 inch CRT monitor (1280 × 1024 pixels, 100 Hz refresh rate), placed 83 cm from the animal. Stimuli were shown on a grey background (luminance: 10 cd/m^2), and consisted of two high-contrast, drifting Gabors (spatial frequency: 2 cycles/deg), enveloped by a Gaussian with 0.75 deg at half height. Gabors had a mean luminance of 10 cd/m^2 and drifted with 2.17 deg/sec. Speed and color changes were achieved by abruptly increasing the speed to 4.17 deg/sec or changing the color to an isoluminant pale yellow. Eye-movements were monitored with a custom-made eye-tracking device with a spatial resolution of 0.2 deg. Prior to cell recordings in the behavioral paradigms, monkeys performed a dimming task at fixation to determine basic response characteristics of each unit. RF size and location were mapped manually using a moving bar. If two electrodes were used simultaneously, we searched for units with largely overlapping RFs. Each units' direction tuning was measured using Gabor gratings moving into one of 24 different directions.

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Behavioral task. Monkeys were trained to perform two variants of a feature-change detection task (Fig. 1*A*). They had to attend either inside or outside the RF or the recorded unit, and were required to detect either a speed or a color change. This 2*2 design allowed gathering data under the four experimental conditions illustrated by the inlet in Figure 1*E*. The monkey initiated a trial by maintaining fixation on a central fixation point (0.14° side length) and pressing a lever. The color of the fixation point indicated the task type (red: speed-change detection, yellow: color-change detection). 1050 ms after pressing the lever (or 350 ms for some recording sessions), a rectangular spatial cue indicating the location of the behaviorally relevant stimulus was displayed for 700 ms and outside the RF of the recorded neuron(s), followed by a 200 ms delay period. Subsequently, two static Gabor gratings appeared simultaneously. One grating was placed inside the RF and the other one at a mirror-inverted position in the opposite hemifield. 200 ms later, both gratings started to move intrinsically. If we recorded from two electrodes at the same time, the stimulus was placed in the joint RF of the units and motion direction of the RF stimulus was chosen to drive one of the recorded units with its preferred direction. Motion direction of the stimulus outside the RF was in opposite direction. If neurons had very different preferred motion directions, we chose a motion direction capable to drive both units efficiently. Thus, for a number of neurons we obtained data following stimulation with motion directions deviating to some degree from their preferred motion direction.

Following motion onset, monkeys had to attend the cued location and feature dimension and to signal detection of the target event (either a speed or a color change) by releasing the lever within 150 ms and 750 ms after the stimulus change. Target events occurred pseudo-randomly between 660 ms and 5500 ms after motion onset. Prior to these changes, up to three distractor events may have occurred, all of which had to be ignored. These distractor events consisted of a change in the currently relevant feature dimension at the uncued location, and/or a change in the irrelevant feature dimension at the cued and/or the uncued location. Their number and sequence varied pseudo-randomly. These trials increased the attentional demand for the monkeys and allowed us to verify that they were following the cue instructions. Throughout the trial and until 300 ms following the lever release, monkeys had to keep fixation within a circular eye window of 2 deg diameter, centered on the fixation point. To support selective attention to the relevant feature dimension (instead of a more global attention to any change at the attended object), speed-changes and color changes were presented block-wise. The task order was alternated between recording sessions. We aimed to collect 25 successful trials of each experimental condition during which the speed change at the RF location was the first change event. This was behaviorally relevant only in the attend-in condition of the motion task, but irrelevant during the color task and the two attend-out conditions. Only these trials entered data analysis, because they allowed comparing the different attention conditions in response to identical visual stimulation. All other trials were disregarded.

Data analysis. Data were analyzed using Matlab R2011b and later releases (The MathWorks, Natick, MA), using both in-built and custom-made functions. Spikes were detected and sorted semi-automatically as previously described in detail (Galashan et al., 2011). Spike thresholds were set by four times the median of the absolute values of the high-pass filtered signal (Quiroga et al.,

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2004), where applicable, otherwise by three times the signal's SD. Occasionally, these thresholds had to be corrected manually. Preferred motion direction and significant direction tuning of the spike-sorted data were estimated offline using a response reliability approach (Grabska-Barwinska et al., 2012).

We collected data from 303 units, for which we obtained a sufficient visual response (> 1 SD above spontaneous activity and > 10 Hz) and at least 10 trials per experimental condition (mean: 25.1). 61 (20%) of these were excluded from data analysis due to slow electrode drifts over the course of the session. Electrode drifts were identified based on lab notes during recordings and careful visual inspection of the data, as well as by semi-automated procedures taking the mean FR over the course of the session into account. From the 243 remaining units, another 56 were not analyzed because they did not fulfill all of the following inclusion criteria: i) behavioral performance in both tasks above 75% (14%), ii) significant direction tuning (5%), iii) deviation between stimulating and preferred motion direction below 90 deg (3%). The final dataset consisted of 187 units gathered in 165 recording sessions. For 116 of these units, their preferred direction was within 15 deg of the stimulating motion direction (mean deviation: 7.1 deg), estimated by offline analysis of the spike-sorted data. For the remaining units, preferred and stimulating motion direction differed between 15.4 – 72.5 deg (mean: 30.9 deg, $N = 71$). All results derived from the entire database hold true if considering only units stimulated within 15 deg of their preferred motion direction.

Spike-density functions (SDF) were calculated within a 100 ms time window, shifted by 1 ms and smoothed by a Gaussian kernel (σ = 20 ms). Population responses were computed by subtracting each neuron's mean baseline activity from its response, normalizing the response to the mean FR of all conditions during the period 400 ms prior to the speed change, and averaging over the normalized responses of all individual units. Individual time bins of the difference-SDFs were considered significant if the 95% confidence interval did not contain 0 ($\alpha < 0.05$, two-tailed). Modulation indices (MI) were defined as:

$$MI = \left(\overline{FR}_{cond1} - \overline{FR}_{con}\right) / \left(\overline{FR}_{cond1} + \overline{FR}_{cond2}\right)$$

For investigating task-specific response differences, cond1 and cond2 relate to each unit's pool of trials from the speed-change and the color-change task, respectively (TCI). Analogously, for spatial attention cond1 and cond2 relate to each unit's trials from the attend-in and attend-out conditions (SAI).

Response latencies were calculated as the point in time at which the transient FR increase following the speed change reached 75% of its maximal peak (Galashan et al., 2013). Peak responses were required to occur between 20 and 300 ms after the speed change. Latencies were only calculated for units responding with a significant FR increase to the acceleration of the motion stimulus (Wilcoxon signed rank, $\alpha < 0.05$).

Trial-to-trial variability was measured by calculating the Fano factor (FF, mean normalized variance of spike counts) in successive, non-overlapping time windows during the 250 ms prior

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to the speed change. Window width varied between 5 ms and 125 ms, increased stepwise by 1 ms. For each width, the FF is reported as the mean of all windows. To investigate whether FF effects depended of FR differences between conditions, a rate-matching procedure was applied by searching for groups of 10 trials per experimental condition and unit, for which the mean FR did not differ by more than 1 Hz. This was done for 10 successive, non-overlapping 50 ms windows during a 500 ms period starting 250 ms before the speed change. For each of the windows we found such trial combinations for minimally 178 of 187 units, and 186 neurons were considered for the statistical analysis of the pre-change epoch, during which FRs were relatively stationary.

Spike-count correlations (SCC) were computed for 38 pairs of simultaneously recorded units, using the same integration windows as for the FF. We only considered units recorded at different electrodes. For each pair, the raw spike counts were converted to z-scores, and the SCC was calculated as the Pearson correlation of z-scores across trials. Since this measure is sensitive to outliers, we excluded data segments which were above 3 SD of the mean of a given window and unit.

To investigate tuning-dependent differences as a function of spatial attentional and task demands, stimulus preferences of individual neurons were related to the actual stimulus properties. For direction preference, this was based on the deviation between stimulus direction and a unit's preferred direction. For speed preference, we considered the transient FR change following the speed-up of the stimulus as an indicator for the match between stimulus and preferred speed. Because in area MT, most neurons are low-pass or follow a log-Gaussian shaped response profile (with preferred speeds in the range of base and target speeds as used in our experiments, or above) (Lagae et al., 1993; Nover et al., 2005), large transients unambiguously indicate neurons with a preferred speed well above the stimulating speed before the change (Traschütz et al., 2015). In turn, neurons with a small transient are likely to be driven by a speed that is more similar to their preferred speed, unless they have an extremely narrow or very broadband response profile. The transient's amplitude was calculated by dividing the mean FR during the 250 ms after the speed change by the mean FR during the 250 ms before the speed change, taken from the attend-in speed task. Direction preference and speed preference-sorted neurons were distributed to two groups of well-matching and less-matching neurons. For each subgroup (and for the individual neurons of the groups) demixed principal component analysis (dPCA) (Brendel et al., 2011; Kobak et al., 2014) was performed to quantify the amount of explained variance for the relevant response variables (time, spatial attention, task, and interaction of spatial attention and task). Demixed PCA was run using the original Matlab code as provided by the authors (https://github.com/machenslab/dPCA). In contrast to standard PCA, dPCA considers the data labels such that principal components depend on task parameters, and allows demixing of data with arbitrary combinations of task parameters. In our experiments, task parameters correspond to the two spatial attention conditions SA, the two task conditions TC, and time T. The number of available data points X can be thought of as a SA-by-TC dimensional trajectory of length T in N-dimensional space, where N corresponds to the number of recorded units. By considering the labels of each data point, dPCA decomposes X into independent parts to estimate the variance attributable to one of the parameters T, SA, and TC. Thus, X_T captures the

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variance due to the passage of time, independent from spatial attention and task, while X_{SA} captures the variance due to spatial attention that cannot be explained by X_T. In turn, X_{TC} describes the variance due to task conditions that cannot be explained by time and spatial attention condition, and $X_{SA/TC}$ describes the variance due to interaction between spatial attention and task condition that is not explained by the previous parameters. Since dPCA requires the same number of time bins T for all trials, the steady-state response between 200 ms after motion onset and 200 ms before the speed change was re-stretched to 260 time bins for each trial. For the shortest trials, this conformed to the original SDF resolution of 1ms/bin; for the longest trials each bin represents the SDF over a period of 4.4 ms. After re-stretching, each trial was described by a vector of 910 ms length, lasting from motion onset to 250 ms after the speed change. To avoid overfitting, dPCA on each of the datasets was performed by adding a regularization term λ, as described in Kobak et al. (2014).

Statistics. Statistical analysis was performed using non-parametric tests (balanced Friedman test, two-sided Wilcoxon signed rank test, Kruskal-Wallis test). Confidence intervals (CI) were obtained by bootstrapping the data with 5000 re-samples using the bias-corrected and accelerated percentile method (Efron and Tibshirani, 1993; DiCicio and Efron, 1996). For dPCA, periods of significant classification were computed by 100 iterations of stratified Monte Carlo leave-group-out cross-validation, as implemented in Kobak et al. (2014).

Results

Behavioral task and performance. Monkeys were trained on two variants of a feature-change detection task, and neuronal processing in area MT was investigated as a function of task requirements and spatial deployment of attention (Fig. 1*A*,*B*). In both variants of the task, stimuli consisted of two grey Gabor patches with inherent motion. One Gabor was placed inside the RF of the recorded unit while the other one was inversely mirrored across the fixation point. The monkeys' task was to detect either an instant 100% speed change or a sudden isoluminant color change to yellow. Each trial started with the appearance of a fixation point, indicating the task type by color (yellow: color task, red: speed task), followed by a spatial cue to signal target location (0.5 s). With a delay of 0.5 s, the two Gabors appeared simultaneously and started to move 0.2 s later. The Gabor within the RF moved approximately in the preferred direction of the recorded unit, and the other one moved in opposite direction. Color and speed changes occurred at pseudo-random points in time 0.66 s to 5.5 s after motion onset. They had to be ignored by the monkeys unless they were cued. The rationale of this 2*2-design was to implement two different task conditions that direct attention either towards or away from the motion domain, at a location inside or outside the neuron's receptive field (RF). Speed- and color-change trials were presented block-wise and the order of blocks was balanced over recording sessions. Both monkeys performed very well (M1: 87.1% ± 7.8 SD; M2: 97.9% ± 3.7 SD), with no difference between attend-in and attend-out trials (Friedman test, M1: $\chi^2(1) = 1.7$, $P = 0.19$; M2: $\chi^2(1) = 0.06$, $P = 0.81$). Monkey M1 also performed similarly during speed- and color-change trials, while M2 had a slightly but significantly better performance for speed changes (Friedman test, M1: $\chi^2(1) = 0.63$,

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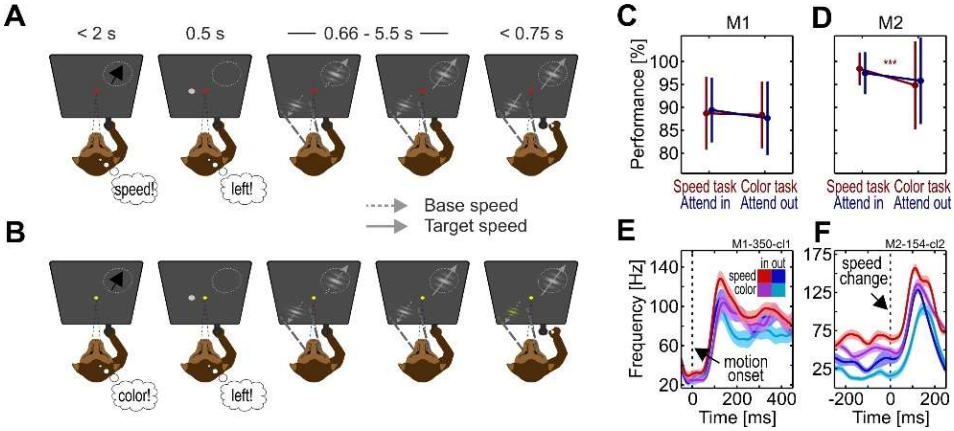

Figure 1. Behavioral paradigm, performance, and firing rates across task periods. ***A, B***, Example trials of the speed change task (*A*) and the color change task (*B*). The exact timing of a trial is provided in Material and Methods. Circle, RF of the recorded neuron; black arrow, preferred direction; Gray dashed arrow, motion direction at base speed; gray straight arrow, motion direction at increased speed; thin dashed line, gaze direction; bold dashed line, direction of spatial attention. Note that visual stimulation is identical across tasks until the first change (here: RF stimulus speed-up, fourth panel from left in both tasks). ***C, D,*** Mean performance (correct responses/sum(correct responses, false alarms, misses)) of monkey M1 and M2. ***E, F,*** Responses of two example units. Color scheme indicated by the inlet in (*E*) is used throughout the article. In, attend inside RF; out, attend outside RF; speed, detect speed change; color, detect color change.

$P = 0.43$; M2: $\chi^2(1) = 15.23$, $P < 10^{-4}$) (Fig. 1*C*, *D*).

Task-specific firing rate modulation. We investigated task-dependent modulations of MT responses by comparing neuronal activity depending on whether motion was relevant or irrelevant for the task. Visual stimulation was identical across tasks until the first feature change (Fig. 1*A*,*B*), such that neuronal activity within the two spatial attention conditions is expected to be the same, unless dependent on task requirements. Specifically, for attention directed to the RF, the motion direction of the attended Gabor matched the preferred direction of the recorded neuron, which is hence expected to receive the same attentional gain in both tasks if FBA spreads to task-irrelevant features (Katzner et al., 2009). For attention directed to the stimulus outside the RF, the attended motion direction is 180 deg apart from the stimulating, preferred motion direction of the recorded neuron, which is then expected to receive no motion direction-related gain in any of the tasks (Martínez Trujillo and Treue, 2004). Contrary to this prediction, the responses of the single unit shown in Figure 1*E* (with responses aligned to motion onset) show a clear influence of task demands. When the monkey was attending to speed, FRs were considerably higher than when he was attending to color, both inside and outside the spatial focus of attention. Likewise, the multi-unit shown in Figure 1*F* (with responses aligned to the speed change), was more active in the speed task throughout the period before the speed change as well as during the transient response following the speed-up of the RF stimulus. In all trials contributing to these SDFs, the speed change was the first change event, i.e. visual stimulation was identical across all experimental conditions.

These units are representative of the population of MT neurons (187 units, M1: 24 single

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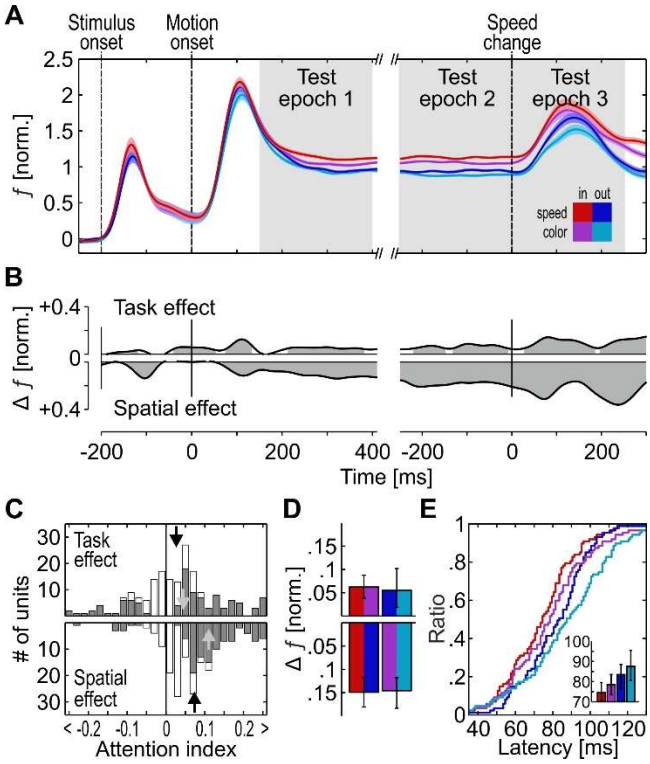

Figure 2. Task-specific modulation of firing rates. ***A***, Population SDF (N = 187) during all task periods in each of the four conditions. Shaded areas: SEM. ***B***, Time course of mean spiking difference depending on task and spatial allocation of attention. Gray shading indicates significantly different time bins. ***C***, Distribution of TSIs (top) and SAIs (bottom). Open bars, all units; gray bars, significantly modulated units. Black arrows, median AIs of all units; Gray arrows, median AIs of significantly modulated units. ***D***, FR difference between conditions. Top, task effect; bottom, spatial attention effect. Left and right color in each bar indicate the attentional conditions, which were subtracted. ***E***, Cumulative distribution of response latencies during test epoch 3. Inlet: median latencies; error bars, 95% CI.

units, 46 multi-units, M2: 57 single units, 60 multi-units). FRs were consistently higher in the speed task than in the color task (Fig. 2*A*). This task-specific difference already showed up during the response to static stimuli. It was of smaller magnitude than the effect of spatial attention, but remained clearly present throughout the trial (Fig. 2*B*). Similar to the effect of spatial attention, not only the steady-state response during stimulation with base speed, but also the response to the speed change was different between tasks. It was highest during the attend-in condition of the speed task and weakest for the attend-out condition of the color task (Fig. 2*A*). Statistical testing was carried out by a non-parametric ANOVA applied to the collapsed data of three 250 ms test-epochs (grey-shaded areas in Fig. 2*A*). Both the factor task and the factor spatial attention had a highly significant influence on the FR of the MT population (Friedman tests, task: $\chi^2(1) = 11.85$, $P < 10^{-3}$; spatial attention: $\chi^2(1) = 86.59$, $P < 10^{-19}$) (Fig. 2*C*). Individual testing of the single epochs confirmed this finding (Friedman tests, all $\chi^2(1) > 5.34$, all $P < 0.0209$).

These task-dependent differences were carried by a large number of neurons showing higher activity during the speed task. 55% of all neurons had significantly different FRs between tasks (Friedman tests, $P < 0.05$), and 71% of these were more active in the speed task. We calculated an index for task-specific response differences (TCI) to test the sign and strength of the modulation of individual units. The TCI is positive for neurons having higher activity during the

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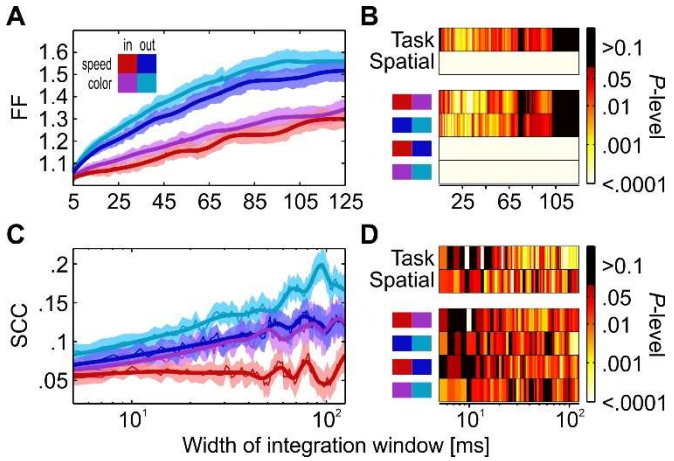

Figure 3. Variability of responses depending on attentional condition. ***A, B,*** Fano Factor of spike counts for integration windows between 5 ms and 125 ms width (*A*), and color-coded *P*-values for Friedman tests (top rows) investigating the factors task and spatial attention, and Wilcoxon tests (bottom rows) comparing single conditions (*B*). Color coding ranges between *P*-values of 10^{-4} and 10^{-1}. Larger and smaller values are colored black and white, respectively. ***C***, Spike-count correlation of 38 pairs of simultaneously recorded neurons for different integration windows. ***D***, Statistical outcome depending on the width of the integration window. Conventions as in (*B*).

speed task (see Material and Methods). Collapsed over the three 250 ms time epochs, the median TCI of the entire population was 0.031, and the distribution of index values was significantly greater than zero (Wilcoxon signed rank test, $Z = -3.65$, $P < 10^{-3}$) (Fig. 2*C,* upper panel). The median TCI of the individual epochs 1 - 3 was 0.011, 0.037, and 0.03, respectively, and all distributions were significantly different from zero ($Z < -2.3$, $P < 0.0217$). We also calculated a spatial attention index (SAI) for comparison. 57% of all neurons were significantly modulated by spatial attention, and 92% of these were more active during the attend-in conditions. The collapsed median SAI of all neurons was 0.07 (Fig. 2*C*, lower panel), and the median SAI of the individual epochs was 0.049, 0.075, and 0.076. All distributions were significantly different from zero ($Z < -6.74$, $P < 10^{-10}$).

We next tested statistically whether the task effect was spatially global or, alternatively, restricted to the spatial focus of attention, and compared the firing rates between the two tasks and the two spatial attention conditions separately (Fig. 2*D*). Besides a spatial attention effect in both tasks (Wilcoxon signed rank test: both $Z > 8.81$, $P < 10^{-17}$) and a task effect for the attend-in condition ($Z = 3.78$, $P < 10^{-3}$), we found significantly higher FRs in the speed task for attention directed outside the RF ($Z = 3.12$, $P = 0.0018$), also if restricted to the mere population of single units ($Z = 3.23$, $P = 0.0012$, $N = 81$). These results also hold true for the individual animals (M1: all $Z > 2.15$, all $P < 0.0313$, $N = 70$; M2: all $Z > 2.31$, all $P < 0.0206$, $N = 117$). Thus, neuronal responses where consistently higher in the speed task, even when the attended motion direction was opposite to the preferred motion direction of the recorded neurons.

Task-dependence of neuronal latencies. We next asked whether response parameters other than the mean FR were influenced by task requirements. Because spatial attention has a significant effect on response latencies (Sundberg et al., 2012; Galashan et al., 2013; Khayat and Martinez-Trujillo, 2015), and latency correlates with reaction time (Galashan et al., 2013), we hypothesized that MT responses to speed changes should be more rapid if speed is behaviorally

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relevant. To this end, we analyzed the latency of the transient FR increase in response to the speed change of all neurons for which their speed tuning promoted an identifiable response peak in each of the four conditions (N = 87). In the attend-in conditions of the speed and the color task, the median latencies were 75 ms and 79 ms, respectively, and in the corresponding attend-out conditions, they were 84 ms and 88 ms, respectively (Fig. 2*E*). A Friedman test on the factors task and spatial attention revealed a significant influence of both factors (task effect: $\chi^2(1) = 5.08$, $P = 0.0242$; spatial attention: $\chi^2(1) = 14.3$, $P < 10^{-3}$). *Post-hoc* Wilcoxon signed rank tests confirmed the task effect both with attention directed towards the RF and away from it, and also confirmed the influence of spatial attention on MT neuronal response latencies for both tasks (all $Z > 2.14$, all $P < 0.0326$). Thus, MT neurons respond faster in a task requiring attention to motion, independent of the spatial focus of attention.

Task requirements and neuronal variability. Given the key function of spatial attention in facilitating the neuronal representation of behaviorally relevant content, task-dependent modulations are expected to serve a similar function. Therefore, we next asked whether they also apply to neuronal response fluctuations, as recently shown for spatial attention (Cohen and Newsome, 2008; Galashan et al., 2013). We calculated the Fano factor (FF) of each unit, and the spike-count correlation (SCC) of 38 simultaneously recorded pairs of units. Because independent and correlated response variability fluctuates on a range of time scales, both FF and SCC depend on the width of the integration window over which spikes are counted (Smith and Kohn, 2008). To obtain an unbiased estimate, we used multiple window sizes (5 ms to 125 ms bin width, increased stepwise by 1 ms).

We applied this analysis to the period 250 ms prior to the speed change (while FRs were relatively stationary). Both the FF and SCC varied significantly as a function of behavioral condition (Fig. 3*A*,*C*). For example, for a window size of 50 ms we found significantly different FFs between tasks both for attention inside and outside the RF (Wilcoxon signed rank test, $Z > 2.29$, $P < 0.0222$, $N = 187$). Likewise, the SCC of both spatial conditions was significantly smaller in the speed task ($Z > 2.94$, $P < 0.0033$, $N = 38$). Testing other window sizes demonstrated that the statistical outcome of the FF was consistent among most widths below 100 ms, indicating a reduced trial-to-trial variability in the speed task (Fig. 3*B*). For the SCC, statistical differences were found for the majority of integration windows, independent of the spatial focus of attention (Fig. 3*D*). For comparison, we also calculated the effect of spatial attention and found a corresponding and very robust influence. The effect on the FF was highly significant ($Z > 5.1$, $P < 10^{-4}$) for all window sizes, and SCC results were consistent among most windows (Fig. 3*B*, *D*). Spatial attention had a stronger influence on the trial-to-trial variability than the task type, but their effect on the SCC was about equally strong. We also tested whether the FF modulation was mainly due to differences in FR, or alternatively, independent from these. We applied a mean-matching procedure to five non-overlapping 50 ms time windows and estimated the FF for an integration window of 50 ms. FFs were smaller during the speed task (Friedman test, $\chi^2(1) = 4.77$, $P = 0.029$, $N = 186$) and for attention directed to the RF ($\chi^2(1) = 33.21$, $P < 10^{-8}$). *Post-hoc* tests revealed a significant task effect inside the RF (Wilcoxon signed rank, $Z = 2.37$, $P = 0.0177$), but not so for attention directed away ($Z = 1.08$, $P = 0.2821$). Spatial attention had a significant effect in both

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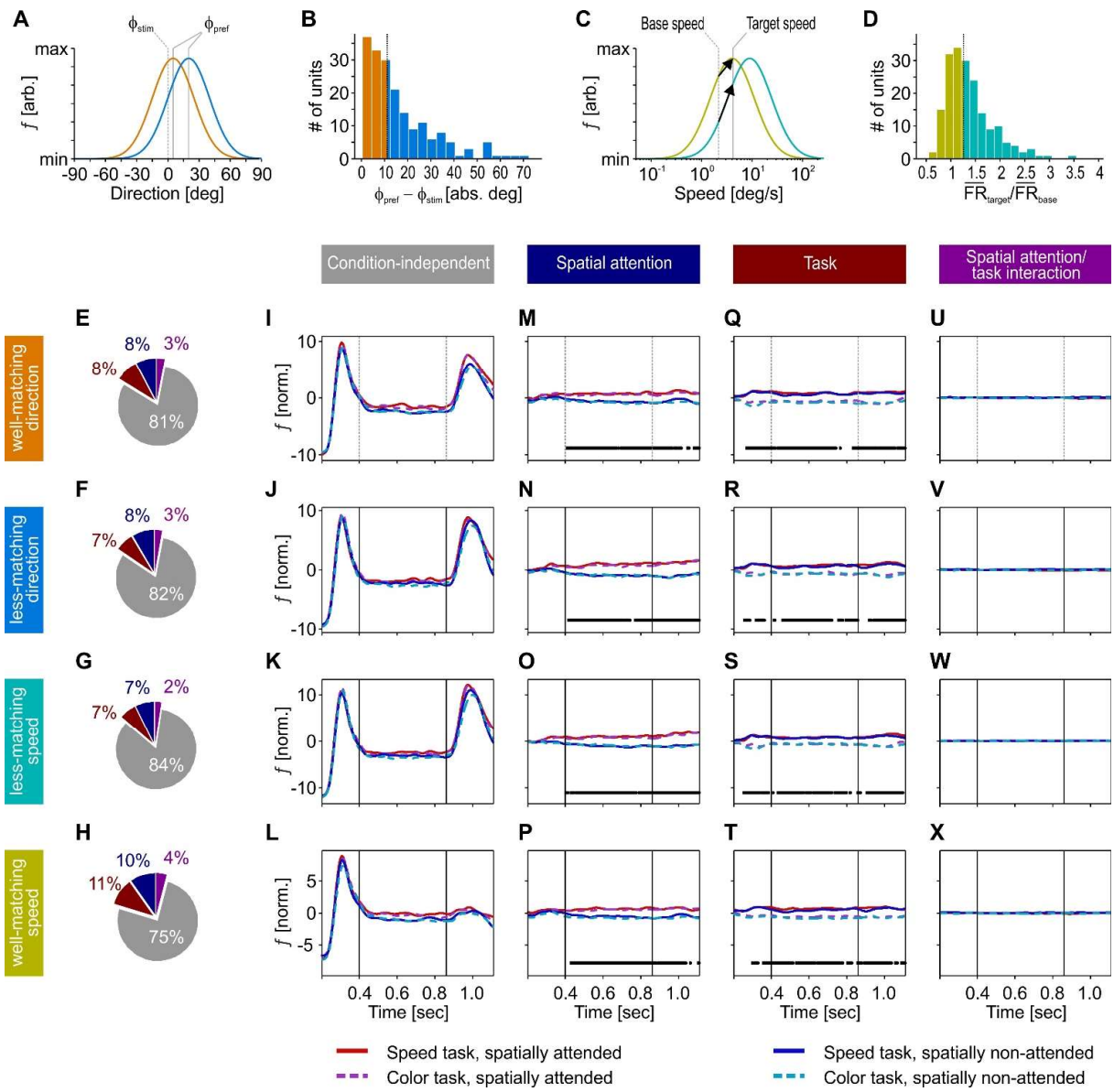

Figure 4. Influence of motion and speed preference on task-dependent response modulation. ***A***, Sketch of two direction-tuning curves with small and larger deviation between preferred direction ϕ_{pref} and stimulus direction ϕ_{stim}. ***B***, Distribution of neurons depending on the absolute deviation ϕ_{pref} - ϕ_{stim}, split by median (straight vertical line). Orange bars, well-matching neurons; blue bars, less-matching neurons. ***C***, Sketch of two log-Gaussian shaped speed-tuning curves. Yellow line, speed-dependent responses of a neuron for which the base speed of the stimulus (dashed vertical line) is close to preferred and target speed (straight vertical line) is preferred; green line, speed-dependent responses of a neuron preferring higher speeds; black arrows, vectors indicating the FR increase for a jump from base to target speed, as expected from each neuron's speed tuning. Note that the to-be-expected FR change of the sub-optimally driven neuron is about twice the size of the well-driven neuron. ***D***, Distribution of transients with different amplitude, as expressed by the ratio between the post-change response and the pre-change response (test epochs 3 and 2 in Fig. 2), split by median (straight vertical line). Yellow bars, putatively well-matching neurons; blue bars, less-matching neurons. ***E-H***, Percentage of explained variance for neuronal populations sorted by either direction preference or speed preference, estimated by dPCA. Colors in pie plots correspond to variance explained independent of condition (grey), by spatial attention (blue), task condition (red), and interaction between spatial attention and task (purple). ***I-L***, Deconstructed spike trains showing explained variance essentially independent of condition, due to the passage of time. Colored lines correspond to the four experimental conditions, as indicated at the bottom of the figure. ***M-P***, Deconstructed spike trains showing explained variance due to spatial attention, ***Q-T***, task condition, and ***U-X***, interaction of spatial attention and task. Black lines indicate periods of significant classification.

tasks ($Z > 4.22$, $P < 10^{-4}$). Thus, reductions in trial-to-trial variability occur independent of changes

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in FR for both task-specific and spatially attended information, yet presumably restricted to the attended location.

Tuning-related differences in attentional and task-specific modulation. So far, the FR analysis demonstrates task-specific response differences regarding mean FR, trial-to-trial variability, and latency of the transient FR increase following the speed-change. As this is different from the results of previous work (Katzner et al., 2009; Chen et al., 2012), we wondered whether they may depend on the neurons' tuning properties, or alternatively, appear to be independent from these. It is important to note that the experimental design of the study was not chosen to test systematically the influence of task demands as a function of neuronal tuning. Yet, if the stimulus features deviate from a neuron's preferred features, investigating the size of the task effect as a function of this deviation may provide important insights into such a possible dependency. Therefore, we sorted all neurons according to i), the deviation between their preferred motion direction and the actual stimulus direction (Fig. 4*A*), and ii), the size of the transient following the speed change as an indicator of the match between stimulus base speed and a neuron's preferred speed (Fig. 4*C*) (see Methods). Based on this, we distributed all units into two groups of well-matching (N = 94) and less-matching (N = 93) preference, either by direction or by speed (Fig 4*B, D*), re-stretched all trials to a common number of time bins, and performed a dPCA (Brendel et al., 2011; Kobak et al., 2014) on these groups to investigate how much variance of the response can be explained in terms of task parameters (see Methods). Based on 20 components, dPCA explained between 81% and 90% of the total variance in the four groups, which was slightly below standard PCA (95% - 97%). For all groups, most of the variance (75 – 84%) was explained by the stimulus' time course (from motion onset to 250 ms following the speed change), independent of condition (Fig. 4*E* - *H*). Spatial attention explained between 7 and 10% of the variance, and task conditions explained another 7 to 11%. The remaining part of explained variance was due to the interaction between spatial attention and task (2 – 4%). Reconstructed neuronal responses (Fig. 4*I* – *X*) were different regarding the condition-independent component of well-matching units when data were sorted according to the putative speed preference (due to a missing deflection of the response following the speed change, Fig. 4*L*), but where otherwise very similar between groups. Independent of the sorting criteria, spatial attention was significantly classified after the firing rate reached a steady state level, about 200 ms after motion onset, and during the remaining response period (Fig 4*M* – *P*). Yet, explained variance by task developed sooner than for spatial attention, allowing significant classification of the task already during the initial motion onset transient and lasting again until the end of the response (Fig. 4*Q* – *T*). Thus, dPCA on groups with well-matching and less-matching feature preferences confirmed the previous analyses showing the significant influence of task requirements on neuronal responses in MT. However, the group-wise analysis did not provide evidence for a dependence of this effect on the tuning properties of the neurons, at least within the range of deviations between preferred and stimulus features we covered. In terms of explained variance, task and spatial attention had about equally strong effects on neuronal responses in each of the groups.

To investigate this in more detail, we performed dPCA also for single neurons, again sorted by feature preference (Fig. 5, inner bar plots). For almost all of the units, both the task and the

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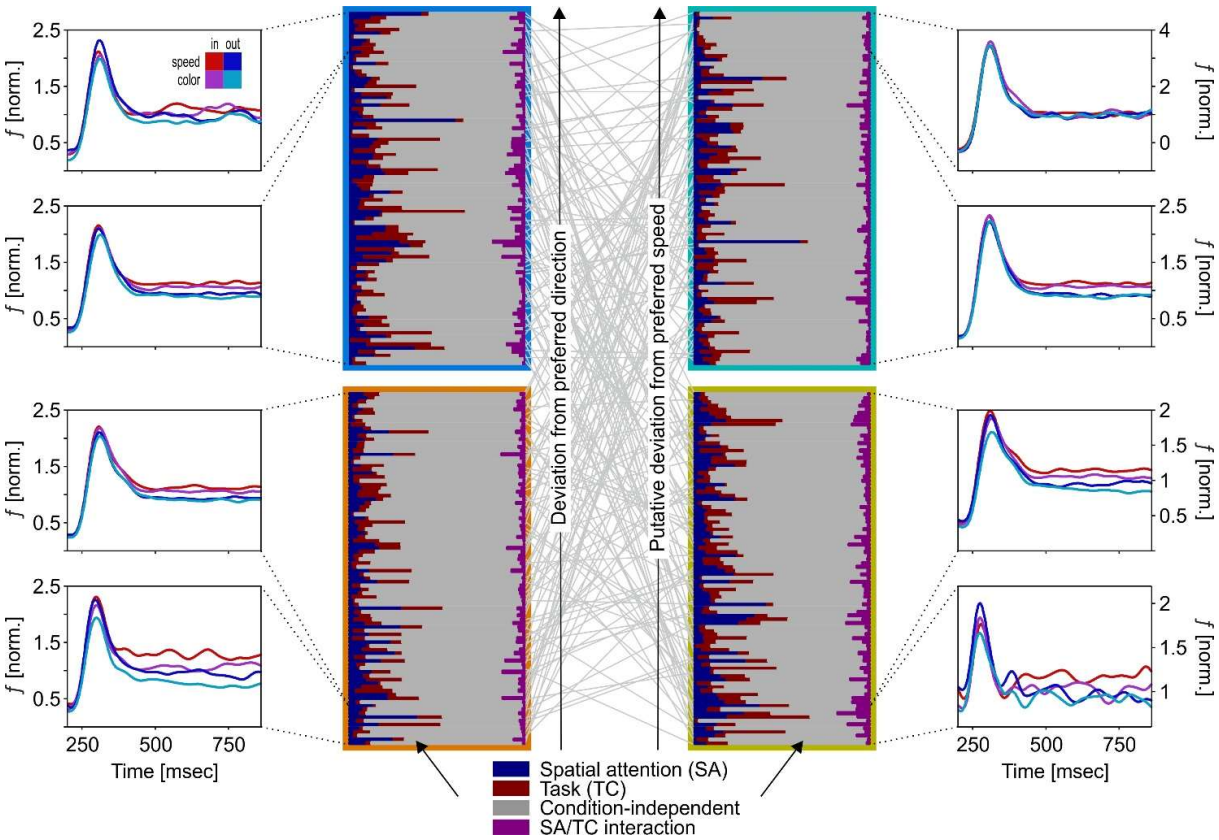

Figure 5. Explained variance of differently tuned units and SDFs for subgroups of neurons sorted by feature preference. Inner bar plots show the ratio of explained variance independent of condition, and due to spatial attention and task, and their interaction. Frame colors correspond to the four tuning groups, as in Fig. 4. Left-hand bar plots show units sorted according to the deviation between stimulus direction and preferred direction, with the best-matching neurons at the bottom. Right-hand bar plots show the same units, sorted by their putative speed tuning. Grey lines identify the rank of each unit in both sorting procedures. Lower and upper SDFs show the averaged, re-stretched spike train of the 10 best-matching and 10 least-matching units, respectively. SDF plots in-between represent the averaged spike trains of the remaining units.

spatial attention condition explained some of the variance, but to a different degree. Yet, if sorted for their feature preference, there was no obvious pattern distinguishing the two groups of well-matching and less-matching neurons. For direction preference, the mean deviation between stimulus and preferred direction was 5.7 deg and 26.7 deg for well-matching and less-matching direction preference, respectively; yet the effects of task and spatial attention were significant in both groups (TCI and SAI distributions significantly different from zero; Wilcoxon signed rank tests, all $Z > 2.32$; all $P < 0.02$). However, comparing the averaged, re-stretched SDFs of the 10 least-matching neurons (47 – 72.5 deg deviation) and the 10 best-matching neurons (0.4 – 1.2 deg deviation) indicated a stronger influence of both task and spatial attention when the motion direction of the RF stimulus matched the neurons' tuning preference (SAI, 0.109 : 0.037; TCI, 0.047 : 0.025) (Fig. 5, upper and lower panel on left side). This apparent tendency towards stronger effects at well-matching neurons also shows up if neurons were sorted according to the size of their speed-change transient (i.e. their putative speed tuning). Note that we used the same speed throughout the experiments and did not constrain recordings to well-matching neurons. Thus, neurons were usually not driven by their preferred speed, and the deviations between stimulus

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speed and preferred speed cover a much broader range than for direction. In contrast to the explained variance by dPCA, the TCI distribution was significantly different from zero only for the putatively well-matching neurons (Z = 3.66, $P < 10^{-3}$), but not for less-matching neurons (Z = 1.5, P = 0.134). The SDFs of the 10 best-matching neurons, the 10 least-matching neurons, and those of the two groups in-between show continuously smaller modulation by task (TCI: [0.046 0.04 0.014 0]), while the effect of spatial attention remained relatively stable (SAI: [0.041 0.071 0.065 0.025]) (Fig. 5, right panels).

As neurons were sorted according to two different criteria, we also checked how these criteria combine. The lines between the bar graphs in Figure 5 indicate that both groups of direction preference-sorted neurons contain about equal numbers of neurons for which the stimulus speed was well matching with their putative preferred speed. Thus, it is possible that the significant task effect for neurons with a less-matching stimulus direction was predominantly carried by the subgroup of neurons well-tuned to the stimulus speed. Therefore, the data do not exclude the possibility that the task effect is more pronounced for well-tuned neurons, even though the dPCA for the population of neurons (Fig. 4) does not provide strong support for this. Yet, as speed was the behaviorally relevant feature, this finding would be in line with the feature-similarity gain hypothesis (Treue and Martínez Trujillo, 1999; Martínez Trujillo and Treue, 2004), stating that FBA selectively addresses neurons that are tuned to the attended feature attribute. Future experiments that systematically test the relation between stimulus and neuronal tuning properties are needed to address explicitly whether this task-specific modulation is tuning-dependent.

Feature dimension-specific modulation of spontaneous activity. The previous section showed that a significant part of the explained response variance in area MT could be attributed to task-specific effects. What is the underlying mechanism causing this systematic response difference? Regarding the hint from the previous analysis that well-tuned neurons may develop a stronger task effect, one hypothesis is that top-down signals target MT neurons in a highly specific manner, emphasizing the response of those neurons well-tuned to the attended feature (Wagatsuma et al., 2013). An alternative hypothesis is a more general, feature dimension-specific top-down modulation, presumably addressing the entire cortical module that is most sensitive to the relevant feature dimension, supported by the finding that part of the variance of all our recorded neurons is explained by task dependencies. To distinguish between these alternatives, we investigated the spontaneous activity before onset of the spatial cue. During this epoch, monkeys already knew the task type due to the color of the fixation point, but not the to-be-attended motion direction of the upcoming target. We found that FRs in the speed task were increased by 8.3% (Friedman test, $\chi^2(1) = 43.46$, $P < 10^{-10}$, N = 187), while no such differences showed up if the same trials were sorted according to their later spatial condition ($\chi^2(1) = 1.97$, P = 0.16). We then investigated whether this baseline shift affected neurons differently, depending on their tuning (Fig. 6). We found, however, that neurons of all tuning groups were more active in the speed task. Note that regarding direction tuning, monkeys could not build an expectation about the upcoming target motion direction, and only knew that motion instead of color was relevant. The fact that both well-tuned and less-tuned neurons had a highly significant increase in baseline activity

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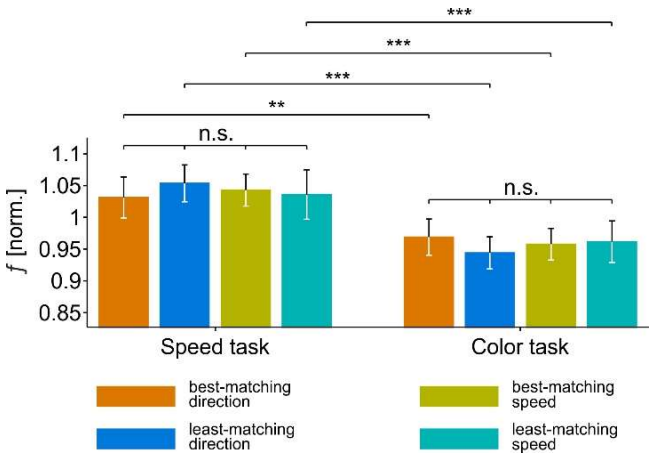

Figure 6. Normalized spontaneous activity depending on direction and speed-tuning preferences. Errors bars, 95% CI; *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$; n.s.: not significant.

supports the hypothesis that in the speed task, MT received an early, general boost targeting neurons independent of their tuning. In contrast, monkeys could well anticipate the relevant speed, since this was the same inside and outside the spatial focus of attention. Yet, even neurons with the largest transients (for which the stimulus base speed was clearly away from their preferred speed) showed the same baseline increase than putatively well-tuned neurons. Neither in the speed nor in the color task, there was any statistical difference between tuning groups (Kruskal Wallis tests, both $\chi^2(3) < 1.87$, $P > 0.59$), but for each tuning group the across-task comparison revealed a highly significant baseline shift (Wilcoxon signed rank tests, all $Z > 3.17$, all $P < 0.0015$). This suggests that baseline activity in MT is actively adjusted as a function of task requirements. Yet, subtracting the spontaneous activity in a condition-specific manner does not eliminate the task-dependent modulation seen in the population SDF (Friedman test, $\chi^2(1) = 12.7$, $P < 10^{-3}$, $N = 187$; *post-hoc* Wilcoxon signed rank tests inside and outside spatial focus of attention: $Z > 2.97$, $P < 0.029$), indicating that task-dependent differences in the evoked response get significantly amplified during later visual processing, and do not constitute a pure reflection of an early, additive baseline shift.

Discussion

Location-independent, feature-directed attention plays a crucial role in everyday life. A considerable amount of our knowledge about its neuronal mechanisms has been gained by experiments examining the processing of feature attributes, e.g. a specific color hue or motion direction (Treue and Martínez Trujillo, 1999; McAdams and Maunsell, 2000; David et al., 2008) and several models of visual attention built on attribute-specific top-down modulations (Corchs and Deco, 2004; Wagatsuma et al., 2013). Yet, psychophysical and EEG visual search experiments suggested that location-independent processing of visual features depends on selection weights

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allocated to the feature dimensions defining the potential target stimulus (Found and Müller, 1996). For example, subjects searching for a singleton in a multi-item display show decreased detection performance and increased RT if the singleton is defined in a different feature dimension as in the preceding trial, accompanied by a shorter N2pc component of the EEG (Töllner et al., 2008). In contrast, no switch-costs are observed if a target switch occurs between different feature attributes of the same dimension (Gramann et al., 2010). While these results provide evidence for a bottom-up weighting of feature dimensions (priming), they are also subject to top-down processes: validly cueing the feature dimension of a search target improved target detection, even if the cued feature attribute did not match (Müller et al., 2003). Similar to the Dimensional Weighting Account, the "Guided Search" model (Wolfe, 1994) proposes that observers may prepare for searching a target in a specific feature dimension by adjusting the output weights of different feature channels.

Our results are well in line with the notion that processing of visual features depends on dimensional weighting. Depending on the task, i.e. depending on the relevance of the feature dimension motion to detect the required feature change, responses of motion-sensitive neurons in area MT were differently shaped in numerous aspects. We found a higher activity of MT neurons in the speed task, independent from the spatial focus of attention and even if the stimulating motion direction was opposite to the attended motion direction. We also found a reduced response variance, both in terms of the trial-to-trial variability of individual neurons and the spike-count correlations of neuronal pairs. Furthermore, neuronal response latencies to the speed change depended on attention assigned towards or away from the motion domain.

These results are different from two previous MT studies investigating the effect of FBA as a function of task requirements (Katzner et al., 2009; Chen et al., 2012). Here, switching between tasks requiring attention to either motion or color did influence the activity of individual neurons, but no task-related FR differences showed up at the population level. The results were taken as an indication that FBA spreads along the attended object, selectively influencing neurons tuned to feature attributes of the attended object (i.e. its motion direction), even if not explicitly attended (Katzner et al., 2009). In contrast, in the present study the MT population was significantly facilitated if motion was task-relevant, independent of the spatial focus of attention. Thus, feature-directed attention may result in either a more object-based or more feature-based processing of visual information, indicating a highly adaptive and flexible nature of attentional control. This difference in results is mirrored by many human studies on feature- and object-based attention, showing that irrelevant features of an attended object may be co-selected (Duncan, 1984; O'Craven et al., 1999; Blaser et al., 2000; Rodríguez et al., 2002; Schoenfeld et al., 2003; Wannig et al., 2007; Ernst et al., 2013), but also that this co-selection is not mandatory (Fanini et al., 2006; Nobre et al., 2006; Cant et al., 2008; Polk et al., 2008; Wegener et al., 2008; Serences et al., 2009; Taya et al., 2009; Xu, 2010; Freeman et al., 2014). For example, using similar task and stimulus conditions as in the present neurophysiological experiments, we showed that task-irrelevant features of an attended object may be suppressed in a task enforcing feature-directed attentional deployment as compared to another task enforcing object-directed attention (Wegener et al., 2008). These results may reflect the competitive activation of two attentional control systems,

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facilitating feature-based or object-based processing, or alternatively, two different states of a common control system. The latter view is supported by the finding that the processing of co-selected, unattended features is not only facilitated at the attended object but also at unattended objects (Boehler et al., 2011; Wegener et al., 2014), arguing against a strict object-based effect of attention. Assuming task-dependent top-down weighting of feature channels and object-related interaction across feature channels, we recently provided a conceptual framework to explain switching between more feature-based and more object-based processing in a single control system (Wegener et al., 2014). Thus, we presume that the result difference between our and the previous experiments (Katzner et al., 2009; Chen et al., 2012) is most likely due to differences in task settings. However, future experiments addressing the specific conditions under which non-relevant object features become either co-selected or suppressed are needed to gain a better understanding of the underlying control mechanism.

An important characteristic of the task-dependent attentional modulation described here is its time course. First, in the speed task, MT responses were significantly facilitated already before visual stimulation. This is in accordance with results from neuroimaging studies demonstrating increased baseline activity in areas V4 and MT when attention was directed either to color or to motion, respectively (Chawla et al., 1999), and with the finding of enhanced activation at visually unstimulated regions in human MT+, when subjects attended to motion at a remote location (Serences and Boynton, 2007). Second, during the evoked response, task-dependent response facilitation was evident during the initial motion onset transient, before modulation by spatial attention became statistically reliable (Fig. 4). This earlier effectiveness of feature-related modulation and the confinement of spatial attention to the later steady-state response is in line with results from area V4 (Hayden and Gallant, 2005). The time course of task-related response differences suggests an early, spatially global, and tuning-independent boost of neuronal activity in the cortical module most sensitive to the feature dimension of the upcoming target. Based on neuroimaging results, it has been suggested that such attention-dependent preparatory activity supports the activation of target-specific neuronal populations (Stokes et al., 2009), possibly shifting neurons representing the task-relevant information into their optimum dynamic range (Chawla et al., 1999).

However, the increase in baseline activity cannot account on its own for a comprehensive interpretation of our results, because task-dependent response differences were still evident after subtracting baseline activity for each experimental condition separately (which eliminates additive effects of a baseline shift). Thus, the ongoing facilitation of MT responses in the speed task became significantly amplified during the evoked response. Since the feature-similarity gain hypothesis assigns FBA effects depending on the matching between a neuron's tuning and the attended feature (Treue and Martínez Trujillo, 1999; Martínez Trujillo and Treue, 2004), we asked whether task-dependent facilitation during the evoked response is similarly constrained to neurons preferring the attended stimulus feature. Even though our study was not designed to investigate a tuning-dependent difference of a task-specific modulation, we tried to made use of the fact that first, stimulus directions sometimes deviated from the preferred direction of a unit, and second, that stimulus speed was chosen independently from the speed tuning of the units.

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Based on dPCA, a significant part of the variance was explained by the task, independent of the tuning, but for the population PSTH for neurons sub-optimally tuned to the stimulus speed, FR differences did not reach significance. Thus, it is possible that the amplification of dimension-based facilitation is more pronounced for neurons well-tuned to the task-relevant feature attribute, but future experiments will be needed to investigate this in more detail.

Based on human EEG data, we recently showed that dimension-specific and attribute-specific attention effects possess distinct spatiotemporal profiles (Gledhill et al., 2015). During the selection negativity period of the event-related potential, dimension-specific effects first developed at prefrontal electrode sites and then moved to posterior sites over visual cortex, while attribute-specific effects developed with some delay on top of the dimension-specific modulation at occipital electrodes. Thus, dimension-specific and attribute-specific attention effects were activated by the same task, but each showed a unique spatio-temporal pattern. The single-cell data from monkey MT now provide corresponding evidence for an initial dimension-specific boost of activity followed by a later amplification within MT, suggesting that feature-based attention (with the term feature including both the dimension and the attribute) consists of an early, tuning-independent top-down signal into the visual area most sensitive to the relevant feature, followed by a later tuning-dependent process potentially arising within this area.

Acknowledgements:

The work was funded by DFG Grants KR 1844/1-2 and WE 5469/2-1, and two ZF Grants from the University of Bremen. The authors declare no competing financial interests. The authors acknowledge support by Peter Bujotzek, Sunita Mandon, Deniz Parmuk, Ramazani Hakazimani, and Katrin Thoß regarding various aspects of the study.

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Conceptualization: D.W. and A.K.K.; Methodology: D.W., A.K.K., B.S., and F.O.G.; Software: F.O.G., B.S., A.K.K., and D.W.; Formal Analysis: B.S. and D.W.; Investigation: B.S., F.O.G., and M.P.; Writing – Original Draft: D.W. and B.S.; Writing – Review & Editing: D.W. B.S., and A.K.K.; Funding: D.W. and A.K.K.; Supervision: D.W. and A.K.K.

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