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Motion opponency and transparency in the human middle temporal area

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Abstract

Motion transparency is the perception of multiple, moving surfaces within the same retinal location (for example, a ripple on the surface of a drifting stream), and is an interesting challenge to motion models because multiple velocities must be represented within the same region of space. When these motion vectors are in opposite directions, brief in duration and spatially constrained within a very local region, the result is little or no perceived motion (motion opponency). Both motion transparency and motion opponency inhibit the firing rate of single middle temporal area (MT) neurons as compared with the preferred direction alone, but neither generally influences the firing rate of primary visual cortex neurons. Surprisingly, neuroimaging studies of human middle temporal area (hMT+) have found less activation due only to motion opponency and an increase in neural responses for motion transparency. Here we parametrically manipulate the local balance between competing motion vectors and find an interaction between motion opponency and transparency in the population blood oxygen level-dependent (BOLD) response. We find reduced BOLD amplitude for motion opponency throughout visual cortex, but weakened responses due to perceptual transparency that is most apparent only within the hMT+. We interpret our results as evidence for two distinct mechanisms mediating opponency and transparency.

Introduction

In everyday scene segmentation, the human visual system is faced with the task of disentangling superimposed motion signals. Shadows cast over moving objects, reflections on windows and fish moving beneath the water's rippled surface are all naturally occurring examples for which multiple directions of motion share the same space. Collectively, we refer to the perceptual experience of multiple directions of motion perceived in the same retinal position as motion transparency. If those velocity signals are opposing and strictly balanced within a small local region, individuals report perceiving directionless flicker with no clear sense of motion or transparency (motion opponency, e.g. Qian *et al.*, 1994a). Both of these situations pose a computational challenge for the visual system because the competing motion signals must be represented in the same regions of retinotopic cortex.

The perceptual experiences of motion transparency and opponency are believed to be the result of pooling and normalizing velocity-selective responses in the visual cortex, specifically within the middle temporal area (MT or V5 in monkeys, hMT+ in humans). Virtually all neurons in MT are velocity-tuned, a property inherited from direction-tuned neurons in primary visual cortex (V1). Afferents from V1 are believed to be pooled such that inputs from neurons tuned to different local velocities are compared, typically modeled as the summation of positively and negatively weighted inputs (i.e. summed within a given spatio-temporal frequency band, from which other spatio-temporal frequency bands are subtracted). This input activity level is then normalized by the overall activity levels in the region and rectified to produce physiologically plausible non-negative outputs (e.g. Adelson & Bergen, 1985; van Santen & Sperling, 1985; Simoncelli & Heeger, 1998). As such, these models resolve the aperture problem inherent to V1 simple cells via an intersection of constraints (Adelson & Movshon, 1982; Huk & Heeger, 2002), predict mutual inhibition of locally opponent vectors observed during motion opponency (effectively through subtraction of opposing directional signals within the local neighborhood, Qian & Andersen, 1994; Simoncelli & Heeger, 1998), and predict inhibition of MT neuronal responses during motion transparency (through the divisive normalization stage, Snowden *et al.*, 1991). Because both motion opponency and transparency reduce the responses of direction-selective MT pattern neurons (namely, those neurons with firing patterns that reflect the intersection of constraints, not the velocity of the components), it is the population response that appears to distinguish the two perceptual states.

Measurements of the population response in human visual cortex during opponency and transparency, however, are few and not easily interpreted in the context of the current single-unit physiology and computational literature. Therefore, in the present study we measure the human visual cortex population response for opposing velocity signals, systematically manipulating the balance from completely opponent to perceptually transparent. Our measurements include parametric manipulations of motion opponency that have not yet been tested in human neurophysiological studies. With these added parametric measures, the results clearly reveal two distinct brain

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states supporting motion opponency and motion transparency. Weak blood oxygen level-dependent (BOLD) responses in motion opponency are apparent throughout visual cortex, while a suppressed neural response during motion transparency is isolated to human MT. These findings support the notion that different computational mechanisms drive perceived opponency and transparency, and may reveal the spatial structure of the integration zone for local motion afferents.

Materials and methods

Participants

Five individuals (three men, two women, aged 20–33 years) participated in both the behavioral and the neuroimaging portions of the experiment. All observers had normal or corrected-to-normal vision, and gave informed, written consent. The study was approved by the University of California, Irvine Institutional Review Board, and was in accordance with the Declaration of Helsinki.

Stimuli

All animations were displayed using Matlab (Mathworks, Natick, MA, USA) in conjunction with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997), and schematics of the stimuli are shown in Fig. 1. Four conditions were constructed to measure the effects of locally balancing and unbalancing motion signals on perceptual transparency and opponency. All conditions (unless otherwise noted) consisted of 200 circular black dots subtending 0.05° visual angle, randomly placed within a foveal 10° aperture (resulting in a dot-density of approximately 4 dots/degrees^2). Dots moved at a speed of 2.5 degrees/s against a white background with a mean intensity of approximately 46.2 cd/m^2, and an effective contrast of 83%. All conditions consisted of limited lifetime dots such that each dot was visible for no more than 53 ms (traversing a maximum of 0.13°), at which time the dots (or dot-pairs, depending on condition) were replotted to a new, randomly selected location within the aperture. Because the phase of the lifetime was randomized among all the dots, the displays have an apparent 'twinkling' in addition to any perceived directional signal.

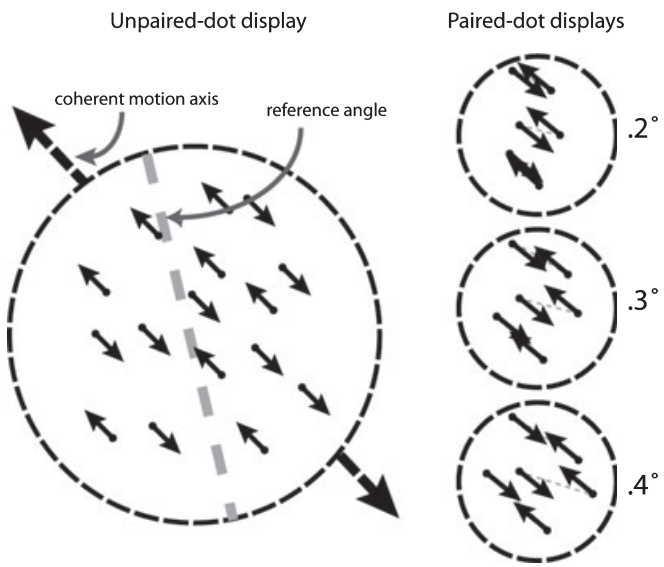

FIG. 1. Schematic of the stimuli used in the unpaired and paired-dot conditions. Subjects made a 2AFC clockwise/counterclockwise orientation discrimination on each 10° display. Dots were plotted as either unconstrained RDKs (transparent condition) or dot-pairs varied in proximity (represented by the legend to the right) where three paired-dot conditions of varying proximity were used (0.2°, 0.3°, 0.4°). Subjects were asked to estimate the target angle, based on the feedback given for each trial. In the example above (transparent unpaired dot condition), the correct answer would be 'counterclockwise'.

The four conditions were as follows. (i) Paired-dot displays were constructed as modified from Qian *et al.* (1994a) such that the distance between dots within a given pair varied parametrically with average displacements of 0.2, 0.3 and 0.4° (but never exceeded 0.303, 0.404 or 0.506°, respectively). These distances were chosen on the basis of previous reports of very weak perceived motion at the smallest displacement, and clear motion transparency at the largest displacement (Qian *et al.*, 1994a). The relative position of the two dots within the pair was randomized within a circular aperture to prevent possible orientation or texture cues from being predictive of the motion direction. In pilot studies, we observed that without this additional consideration, subjects were able to judge angular deviations on the basis of the relative alignment of the dots. We also considered previous reports that have detailed the joint function of dot lifetime and dot-pair proximity in perceived motion cancellation (Muckli *et al.*, 2002). Our smallest dot-pair proximity, in conjunction with the brief lifetime of the dots, was set well within the lifetime and proximity ratio (i.e. distance and stretch) expected to result in motion opponency. (ii) The Unpaired dots were constructed by randomly plotting pairs of dots with no constraints on the spatial proximity of the two dots within the pair. These sequences were essentially two overlapping coherent random dot kinematograms (RDKs), with equal numbers of dots moving in opposite directions. Observers commonly report these displays to appear as two transparent surfaces. (iii) Unidirectional motion was constructed as a 100% coherent RDK (all dots moving in the same direction). These displays consisted of a single plane of motion from the Unpaired condition, and thus had half the number of dots (100 dots as opposed to 200). (iv) Semi-coherent motion (50% Unidirectional) was constructed by modifying the Unidirectional motion displays such that half the dots on each frame were randomly selected to move coherently in the same direction, while the other half moved incoherently. Using this non-fixed path technique, observers cannot track a single dot through its lifetime to determine the direction of motion, and instead must integrate globally over the spatial extent of the display. Partially coherent motion generally results in higher thresholds for perceived motion direction (e.g. Ball & Sekuler, 1980; Williams & Sekuler, 1984).

In our displays, the positions of the dot-pairs were randomized across the aperture, with no constraints as to the specific distances between them. It is possible that due to the stochastic nature of our motion displays, some dot-pairs were positioned in sufficiently close proximity to other dot-pairs that instances of motion opponency (pairs within 0.3°) may have been created in what would otherwise be a non-opponent display. The probability of this is increased by our relatively high dot density (4 dots/degree^2), and would result in, for example, local instances of motion cancellation even in the Unpaired (transparent) dot displays. To quantify this, we conducted simulations with our displays to measure effective cancellation, in which we computed the Euclidean distance between a given dot and all the other dots moving in the opposite direction. If a dot with opposing motion existed within the local motion cancellation zone (thresholded at 0.3°), these two were deemed to be a balanced pair and were considered to be effectively cancelled. We computed the probability of balanced motion for each display (Paired and Unpaired) 10 000 times. Results are shown in Supporting information, Fig. S1 (A). From these simulations we found that each of our displays yielded a range of opponency between dots. Some proportion of this opponency was a

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function of our experimental manipulation (the proximity of the dot-pairs), and some was due to chance. So, in our motion opponent displays (the smallest dot-pair proximity at average distance of 0.2°), the vast majority of motion signals were within the motion cancellation zone. A small percentage of dot-pairs originated on the outskirts of the maximal radius, and moved away, resulting in 12% of the dots being unbalanced. In contrast, the larger dot-pair proximities (dot-pair proximities of 0.3 and 0.4°) yielded higher proportions of unbalanced motion (62 and 84% unbalanced motion, respectively). Moreover, these simulations revealed that even the Unpaired displays had a proportion of dots cancelled (73% unbalanced), simply by chance. supporting Fig. S1 (B) reconfigures the data shown in Fig. 2 to be aligned by the proportion of unbalanced motion, as computed from these simulations. Even with the cancellations due to dot density taken into consideration, neural signals in occipital cortex still follow the same pattern (inverted-U), as is discussed in the results.

Procedure

Neuroimaging experiments

Neuroimaging data were collected on a 3T Philips Intera Achieva Magnetic Resonance system located at the University of California, Irvine. Visual displays were projected with a Christie DLV1400-DX DLP projector controlled by a G4 dual-processor Macintosh computer equipped with Matlab (Mathworks, Inc.) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Subjects viewed the animations via a periscope mirror mounted on an eight-channel birdcage headcoil, directed at a screen positioned behind the subject's head.

For each individual we collected a high-resolution (T1-weighted, MPRAGE) whole-brain anatomical image used for co-registration of the functional data. Functional data were collected using single-shot T2*-weighted parallel imaging (SENSE reduction factor R = 1.5; gradient EPI, TE = 30 ms, flip angle = 70°, LR phase-encoding, interleaved acquisition) with slices that covered nearly the entire brain (27 oblique axial slices aligned to the anterior and posterior commissures, 1.8 × 1.8 × 4-mm voxels, TR = 2000 ms).

Regions of interest (ROIs) were identified using standard localizers. Human MT+ (hMT+; the complex of motion-selective brain areas that likely includes the human homologs to monkey MT, medial superior temporal area (MST), and fundal area of the superior temporal sulcus (FST) was localized as the brain area on the ascending branch of the inferior occipital sulcus that was more activated during 14-s intervals of RDK optic flow motion (randomly switching between inward and outward motion) as compared with 14-s intervals of stationary dots. Statistical threshold for significance was set using the false discovery rate (FDR) as a correction for family-wise error rate ($P < 0.01$, FDR-corrected), which controls the proportion of expected false positives and has the advantage of being adaptive to the signal levels in data while still correcting for multiple comparisons (Genovese *et al.*, 2002).

Because the computational models of motion opponency and transparency draw from neurophysiological measurements of monkey MT, we isolated human MT proper from its satellite areas based on the retinotopic properties of its response (Dukelow *et al.*, 2001; Huk *et al.*, 2002; Smith *et al.*, 2006). While the human MST and surronding areas (hMST+) have bilateral receptive fields, the hMT proper BOLD response is dominated by contralateral motion, and thus we can differentiate these two regions on the basis of their response to ipsilateral optic flow. To achieve this, subjects viewed the same motion display as above, displaced 11° into the ipsilateral or contralateral hemifields. Each block was repeated five times for each position

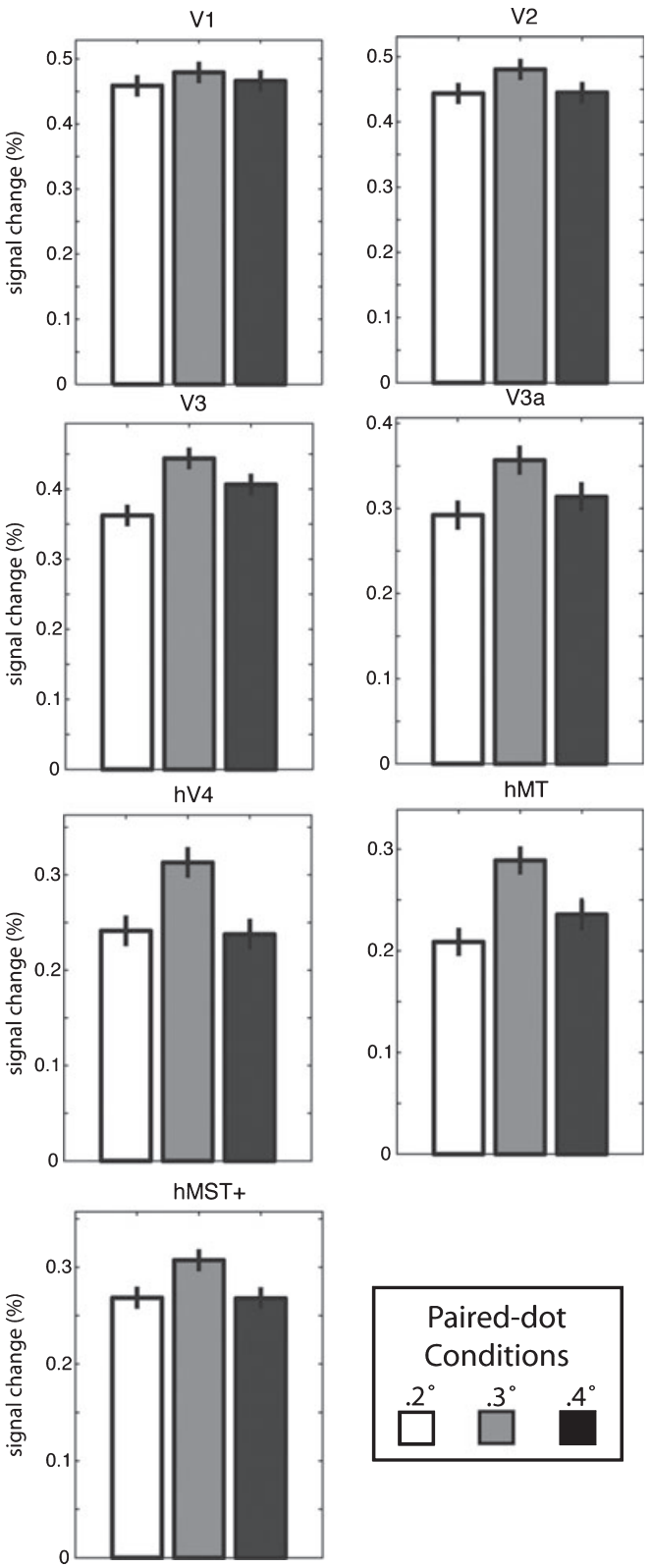

FIG. 2. The BOLD response from V1 and hMT (top row) and other retinotopic regions (V2, V3, V3a, hV4, hMST+) for parametric manipulations of motion transparency. Percentage signal change was estimated with general linear model beta estimates. Neural responses estimated for the opponent motion (0.2°) and locally unbalanced (0.3°, 0.4°) conditions. Error bars indicate standard error of the estimates. GLM contrasts were used for model comparisons and revealed behavior in agreement with the interaction model (inverted U-shape) for all brain regions except V1.

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within the 5.1-min scan. The hMT/MST+ localizer was repeated 3–6 times for each participant.

We delineated the early visual areas (V1–V3, V3a, hV4) using a traveling wave analysis (Engel *et al.*, 1994). Subjects viewed 24-s sequences of a high-contrast, contrast-reversing checkerboard wedge (15° wide, 11.1° maximum length) rotating at a rate of one cycle every 24 s. The wedge made nine complete rotations within each scan, and each traveling wave scan was repeated twice. Phase-encoding maps were generated by visualizing the lags of the correlated (thresholded at $P < 0.05$, FDR-corrected) neural response on the individual's inflated cortical sheet in BrainVoyager (Brain Innovations, Inc.). Centroids of the Talairach coordinates for each ROI can be found in supporting Fig. S2.

The neural responses for our experimental conditions were measured in separate scans. The experimental scans consisted of two 18-s blocks of each stimulus condition (Paired dots: 0.2°, 0.3°, 0.4°; Unpaired dots) and two fixation blocks, all randomly interleaved. Within each stimulus block, subjects viewed nine 1-s animations with a 1-s inter-stimulus interval. To maintain attention, subjects engaged in a demanding two-alternative-forced-choice (2AFC) task in which they made clockwise/counterclockwise discriminations on the angle of motion in each animation, relative to a reference angle. To minimize confusion in the responses, the reference angle for each scan was chosen between a maximum 45° leftward or rightward tilt from the vertical meridian. The direction of the motion stimuli deviated +/−5, 15 or 30° from the reference angle, spanning the range of values obtained in our psychophysical portion of the experiment (described below). To maximize accuracy on the few trials in a scan, the reference angle was constant throughout each scan and shown to the subjects prior to the scan onset as a stationary line bisecting the circular stimulus aperture window. Subjects were not given feedback on the trial-by-trial accuracy of their discriminations, but were shown their overall performance for the entire scan at the end of each run.

In separate scans, subjects viewed 18-s blocks of the Unidirectional motion (100 and 50%), plus 18-s fixation intervals. Each of the 6.3-min scans was repeated 6–10 times, resulting in a minimum of 162 data points estimating the BOLD response for each angular deviation, for each condition and for each subject.

A multi-subject general linear model was used to analyse the BOLD response within each ROI. Regressors were designed from boxcar protocols of each stimulus condition (Paired dots: 0.2°, 0.3°, 0.4°; Unpaired dots, 100 and 50% Unidirectional) and were convolved with a difference-gamma hemodynamic response function. To minimize error, the mean intensity of each scan was included as a regressor to exclude any large-scale scanner-introduced variability in the signal. Signal change is computed as the best-fit beta estimate, with baseline normalization. All statistical comparisons were conducted as general linear model (GLM) contrasts.

In a second analysis, we computed an additional whole-brain GLM statistical map, with the aim to reveal brain areas that are significantly correlated with the inverted-U pattern observed in the ROIs (as detailed below). The ROI-based approach was driven by predictions in the computational literature and by previous single-unit physiological reports using similar experimental conditions. However, a strength of functional magnetic resonance imaging (fMRI) is in the ability to reveal larger patterns in the overall brain response, which would otherwise not be captured in an ROI-based analysis. Therefore, the whole-brain analysis presented in supporting Fig. S3 should be considered as complementary to the ROI-based analysis. One must be cautious, however, because the statistical contrasts used in these analyses are chosen by our findings in the ROI-based analysis, and therefore they are somewhat circular and not entirely independent (e.g. Kriegeskorte *et al.*, 2009).

Psychophysical experiments

Psychophysical thresholds for each motion condition were measured in separate experiments in the laboratory. All psychophysical experiments were displayed on a ViewSonic Graphics Series 220fp monitor controlled by a G4 dual-processor Macintosh computer equipped with Matlab and the Psychophysics Toolbox. Participants were seated 66 cm from the screen with their chin comfortably situated on a headrest to minimize movement during data collection. Participant responses were collected on a standard keyboard.

We measured the minimum angular deviation resolved by the observers for each of our stimulus conditions, with measurements blocked by condition (Paired dots: 0.2°, 0.3°, 0.4°; Unpaired dots; 100% Unidirectional motion; 50% Coherent motion). Using the method of single stimuli (Morgan *et al.*, 2000), observers made a 2AFC orientation discrimination on each trial, indicating whether the direction of motion was clockwise or counterclockwise from an implied (unseen) mean reference angle. Feedback was given on incorrect trials. Discrimination performance was measured on a range of angular deviations from the reference angle (+/− 1.1, 2.9, 5.7, 11.5, 22.3 and 45.3°). The threshold minimum angular deviation required for 80% accurate discrimination was estimated from Weibull fits of the psychometric functions. To minimize the likelihood of adaptation to reference angle and nearby, adjacent directions of motion, observers took mandatory breaks every 40 trials and the reference angle was changed after every 100 trials. To ensure that subjects were able to ascertain the reference angle for each block of trials, participants estimated the reference angle by orienting a bisecting line through a circular aperture before every reference angle change.

To determine whether our findings could be predicted by deviations in eye movements across our different conditions, we also collected eye movement measurements on two subjects in separate laboratory experiments (supporting Fig. S4). Subjects viewed four types of animations (Paired dots: 0.2°, 0.3°, 0.4°; Unpaired dots) in 16-s blocks, simulating the block design in the scanner. Eye movements were recorded using a Sensomotoric Instruments iViewX system. Following the removal of eye blink artifacts, the standard deviation from the mean eye position (foveal fixation) in both the horizontal and the vertical directions was computed for each condition type. In all conditions, the standard deviation of eye movements stayed well within 1° of fixation, with a slight monotonic decrease in amplitude as a function of dot-pair proximity. These findings are unlikely to explain the inverted-U shape BOLD response we measured in visual cortex.

Results

This study seeks to measure the human population response of motion-selective hMT and surrounding visual cortex during motion opponency and transparency. Both opponency and transparency are associated with reduced neuronal firing rates in velocity-tuned monkey MT neurons, but neither is effective at modulating the firing rates of V1 neurons (Snowden *et al.*, 1991; Qian & Andersen, 1995). The population responses in MT are believed to capture the dramatic perceptual differences between the two states (with little perceived motion in opponency, two sliding surfaces in transparency).

To measure these population responses, we have modified the limited lifetime random dot kinematograms from Qian *et al.* (1994a) to vary systematically the perceived motion transparency of the displays. This was achieved by manipulating the spatial proximity between locally opposing dot-pairs from the most locally balanced pairs (opponent motion, with opposing dots paired within 0.2°) to locally unbalanced motion (opposing motion within 0.3 and 0.4°). We

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compare our measurements with completely transparent, unidirectional and partially incoherent motion. We also compare our parametric measurements with those acquired at low contrast and with smaller stimuli, the former of which is known to alter the balance of excitation and inhibition in the pooling of inputs throughout the visual system (Levitt *et al.*, 1994), while the latter is associated with increased surround suppression in MT (Pack *et al.*, 2005).

Although motion opponency and transparency have both been linked specifically to MT, the measurements reported here include the entirety of occipital retinotopic cortex, including V1, V2, V3, V3a, hV4, hMT and hMST+ (the full-field, direction-selective satellite areas surround MT proper). For all of our measurements, we extracted the BOLD response from the ROIs and estimated the amplitude using a GLM.

Parametric manipulation of balanced motion signals

We compared the neural response for each of our Paired-dot conditions (0.2°, 0.3°, 0.4°) and computed a GLM contrast to test the prediction that neural response in hMT would increase monotonically with weaker opponency. This prediction is based on a computational mechanism that pools afferents (with excitatory and inhibitory weights on the basis of spatio-temporal tuning) within some spatial neighborhood that effectively corresponds to a receptive field. This model would predict no difference in BOLD responses for these three conditions, provided all inputs are weighted equally within that neighborhood. Alternatively, it is reasonable to suppose stronger competition between more local opposing motion signals, thus predicting a monotonic pattern of brain responses. The results from these measurements are shown in Fig. 2 with significance threshold corrected for multiple comparisons using family-wise error rate-corrected, $\alpha = 0.007$.

No brain area we measured in visual cortex reached significance for the monotonically increasing (or decreasing) models of brain response ($P > 0.05$, corrected). Instead, we find an inverted-U pattern of brain responses across occipital cortex, with weak responses for the opponent motion (locally balanced within 0.2°) and transparent motion (paired within 0.4°), and the strongest response at the intermediate dot-pairs (0.3°). To test for statistical significance of this pattern, we computed a GLM with the interaction contrast [–1 2 –1]. In all of the visual areas we measured except V1, the BOLD response was significant for this interaction model ($t > 3.0$, $P < 0.004$ for all brain areas, V1: $t = 0.782$, $P = 0.43$).

These results replicate previous findings of weak neural responses in this region during motion opponency in hMT+ (Heeger *et al.*, 1999; Muckli *et al.*, 2002) and extend them to most of the visual cortex. Our measurements also reveal an inverted-U interaction between parametric shifts in locally balanced motion signals, suggesting a shift in the population response between two computational mechanisms as the perceptual state moves away from opponency and towards transparency.

Motion transparency vs. coherent motion

Transparent motion, in particular, has been linked to inhibited neural firing of individual MT neurons in monkeys as compared with motion in the preferred direction alone (e.g. Snowden *et al.*, 1991). This is one of the defining features of MT functional specialization. We therefore measured the BOLD response to completely Unpaired (transparent) motion and for coherent, Unidirectional motion. The Unpaired transparent motion was generated by removing any constraints on the spatial proximity of balanced motion signals, resulting in two perceived surfaces of coherent motion sliding on top of each other. Unidirectional motion was generated from a single plane of coherent motion. Results from these measurements are shown in Fig. 3.

As predicted by the single-unit physiology, the BOLD response in hMT was higher for Unidirectional motion than for the Unpaired transparent motion, despite having half the dot density ($t = 1.9$, $P = 0.06$). Our finding of the population BOLD response matches that found in single-units (Snowden *et al.*, 1991; Qian & Andersen, 1994) and in monkey BOLD measurements (Nelissen *et al.*, 2006), but run counter to previous measures of motion transparency in the human MT+ (Muckli *et al.*, 2002). Our findings are also predicted by the network inhibition models of hMT (Qian *et al.*, 1994b; Simoncelli & Heeger, 1998) and by attention-based models of neural competition in visual cortex (Desimone & Duncan, 1995; Reynolds *et al.*, 1999).

In contrast to the hMT response, for nearly all of the other occipital brain areas we measured, we found stronger BOLD response to the Unpaired transparent motion as compared with the Unidirectional motion (V1, V2, V3, hV4 all $P < 0.05$), or equivalent neural responses between the two (V3a, $t = 1.7$, $P = 0.10$; hMST+, $t = 0.78$, $P = 0.43$). This finding is perhaps not surprising given that the Unpaired transparent motion is likely to engage twice as many neurons as the Unidirectional coherent motion, namely the two populations of neurons supporting the two directions of motion, in comparison with half as many neurons which would be engaged during the Unidirectional coherent motion. This hypothesis is supported, in part, by the finding that incoherent motion elicits a stronger BOLD response in V1 than coherent motion, whereas the opposite pattern of activity is found in hMT+ (Martinez-Trujillo *et al.*, 2005).

Quantifying inhibition due to motion transparency

Because the suppressed neural response during transparency was most strongly isolated to hMT, we hypothesized that this measure may reflect relative strength of neuronal firing in the velocity-tuned neurons underlying the BOLD response. To estimate quantitatively the neural activity underlying the BOLD response during motion transparency, we considered a psychophysical study that found the strength of a motion after-effect generated by transparent displays to be approximately equivalent to that generated by 50% coherent motion (Lankheet & Verstraten, 1995). With this as a rough psychophysical estimate of energy equivalence, we compared the global BOLD response from within hMT to that generated by an RDK with only 50% coherence. The results from this experiment are shown in Fig. 3.

We find the neural response in hMT for 50% coherent motion to be significantly reduced ($t = 2.9$, $P < 0.01$) as compared with 100% Unidirectional motion, and equivalent to that generated by transparent motion ($t = 1.4$, $P = 0.17$). V3a and hMST+ also had stronger neural responses for the 100% Unidirectional motion as compared with the 50% coherent motion (although these brain areas did not exhibit suppression during the Unpaired, transparent motion). V1, V2, V3 and hV4 all had equivalent neural responses for the Unidirectional motion at each coherence level ($P > 0.05$).

Opponency and transparency for low contrast and small stimuli

Both motion opponency and transparency are modeled as components of the pooling of V1 afferents (with excitatory and inhibitory weights) to MT pattern responses and the subsequent divisive inhibition (Simoncelli & Heeger, 1998). We therefore considered that our parametric measures may reflect a tradeoff between these two computations, as revealed in the population BOLD response. This

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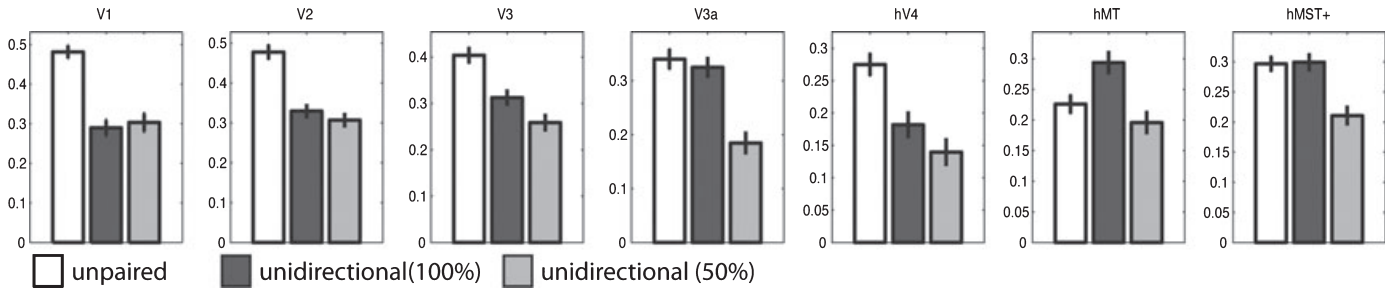

FIG. 3. The BOLD response from retinotopic regions (V1, V2, V3, V3a, hV4, hMT, hMST+) for Unpaired transparent motion, unidirectional 100% coherent motion, and unidirectional 50% coherent motion. Percentage signal change was estimated with GLM beta estimates. Error bars indicate standard error of the estimates.

would imply that our parametric measures reveal estimates of the spatial neighborhood over which opposing directional signals are integrated. Our current results suggest that beyond 0.2°, much smaller than the average receptive field size in MT, these velocity signals are effectively unbalanced. To determine whether spatial neighborhood is indeed the factor estimated by these parametric measures, we implemented two psychophysical manipulations designed to modify the size of the integration zone.

In single MT units, the optimal receptive field size is strongly contrast-dependent, with most neurons exhibiting smaller receptive fields (shaped by less inhibitory influences in the surrounding region) at high contrasts, and large receptive fields (increased spatial summation) at very low contrast levels (Pack *et al.*, 2005). Because motion opponency is dependent on the spatial neighborhood of the opposing velocity signals, we hypothesize that the local neighborhood required to induce balanced motion should also be contrast- and size-dependent. This hypothesis predicts that the inverted-U observed in hMT as a function of dot-pair proximity signals should attenuate with low contrast, and intensify with smaller stimuli.

To test this hypothesis, we measured BOLD responses to our Paired-dots at the same three dot-pair displacement levels (0.2°, 0.3°, 0.4°) at low contrast levels (7.2% root mean square contrast) and with smaller stimuli (4° of visual angle, as compared with 10°, Martinez-Trujillo & Treue, 2002; Pack *et al.*, 2005). The results from this experiment are shown in Figs 4 and 5.

At low contrast, we find overall that the BOLD response across visual cortex is slightly reduced in amplitude as compared with our previous high-contrast conditions. Most importantly, however, we do not find the same inverted-U as a function of our parametric manipulation of local dot balance (Fig. 4). The GLM contrast testing the interaction model revealed no significant effects in any brain area ($t < 1.0$, $P > 0.30$), eliminating the inverted-U as observed in the high-contrast conditions. These results support the notion that the weak motion opponent response observed at high contrasts are dependent on the summation fields, which expand at low contrasts. In other words, previously unbalanced motion signals are now effectively integrated and balanced within a larger region.

Reducing the stimulus size also had the overall effect of lowering the BOLD response. We attribute this reduction primarily to the retinotopic nature of the ROIs we measured in occipital cortex. However, reducing stimulus size also had the effect of reversing the inverted-U, with the exception of hMT and hMST+ (Fig. 5).

Psychophysics

In a final set of experiments, we considered the behavioral importance of the reduction in BOLD response we observed as a function of motion transparency. Specifically, we asked whether the reduced response we observed in hMT and throughout visual cortex came at a cost. What are the behavioral consequences of motion opponency and transparency? To determine this, we measured the resolution with which observers were able to make angular discriminations for all of our conditions. Using the method of single stimuli, we measured the minimum angle for which subjects could discriminate direction of motion from a reference angle (see Methods, Fig. 1). The results from these experiments are shown in Fig. 6.

The psychophysical thresholds we observed for the parametric unbalancing of the motion signals were strongly decoupled from the BOLD responses measured in hMT. While the BOLD response revealed an interaction between motion opponency and motion transparency, psychophysical thresholds generally improved monotonically as a function of transparency (Fig. 6A). On average, observers required at least 14.9° angular deviation to discriminate reliably the direction of opponent motion displays, but only 11.8 and 9.3° for the slightly unbalanced dot-pairs. As a means for comparison, the best performance in these conditions is comparable with performance for the transparent motion RDKs (threshold = 9.98°) or with those measured with a single field of coherent motion (threshold = 11.43°). All of these thresholds were much better than achieved with 50% coherent motion (threshold = 21.63°).

These psychophysical results can be compared against those measured in the low-contrast and small stimulus conditions (Fig. 6B and C, respectively). In the low-contrast conditions, psychophysical angular thresholds were much worse than in the high-contrast conditions, particularly for the opponent motion condition. Behaviorally, this bears out the prediction that summation zones effectively enlarge at low contrast, with the consequence of impairing velocity discriminations. With the smallest stimuli at high contrast, psychophysical performance was overall better than for low contrast, but did not vary as a function of dot-pair proximity.

Discussion

Motion opponency and transparency present a computational challenge to the visual system because multiple directions of motion must be resolved within the same retinal location. Previous neurophysiological investigations of these perceptual experiences have targeted computations within MT, with opposing velocities generally reducing the firing rate of individual neurons. Computationally, this is achieved by both excitatory and inhibitory pooling of V1 afferents, and by divisive inhibition (followed by a rectification stage) based on overall activity level (Simoncelli & Heeger, 1998). Here we find weak BOLD responses for opponency and transparency, consistent with predictions based on the single-unit literature. However, we also showed that

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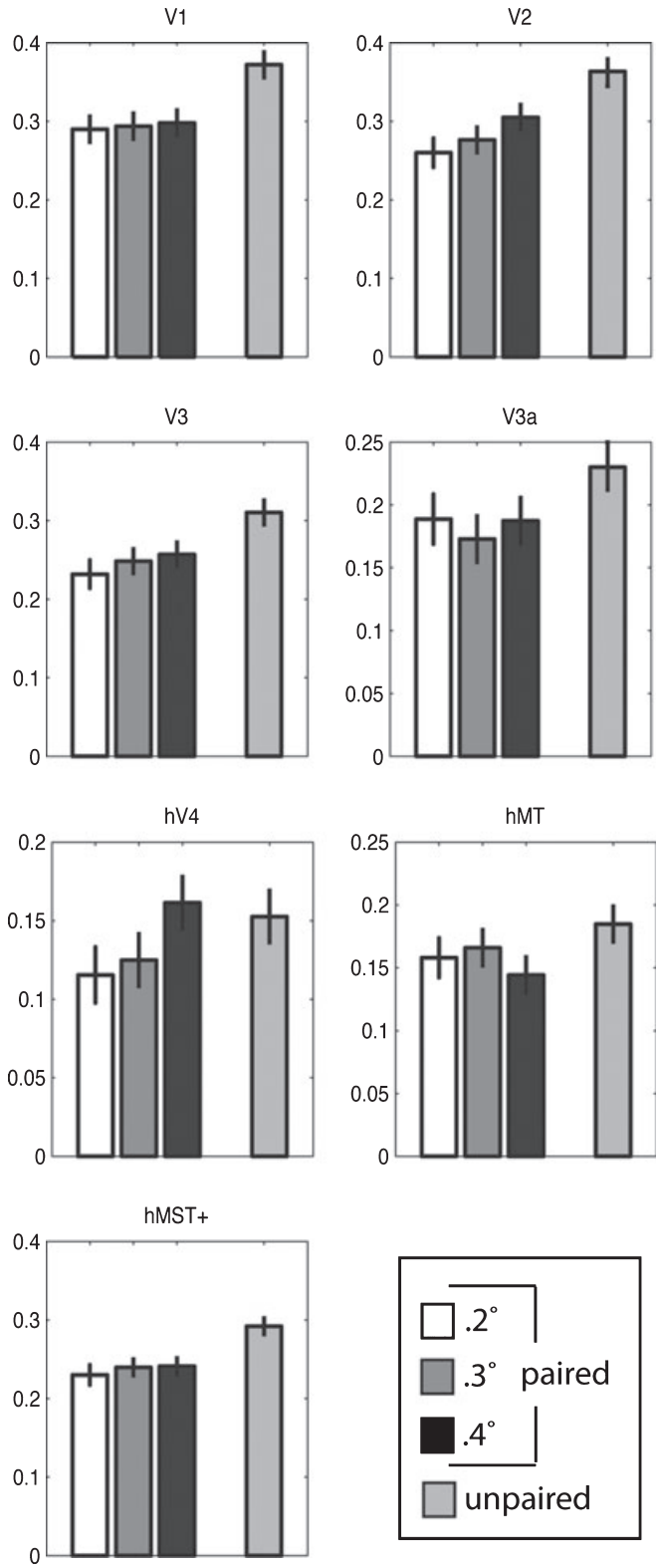

FIG. 4. The BOLD response from V1 and hMT (top row) and other retinotopic regions (V2, V3, V3a, hV4, hMST+) for parametric manipulations of motion transparency at low contrast (7.2% root mean square contrast). Percentage signal change was estimated with GLM beta estimates. Error bars indicate one standard error of the estimates.

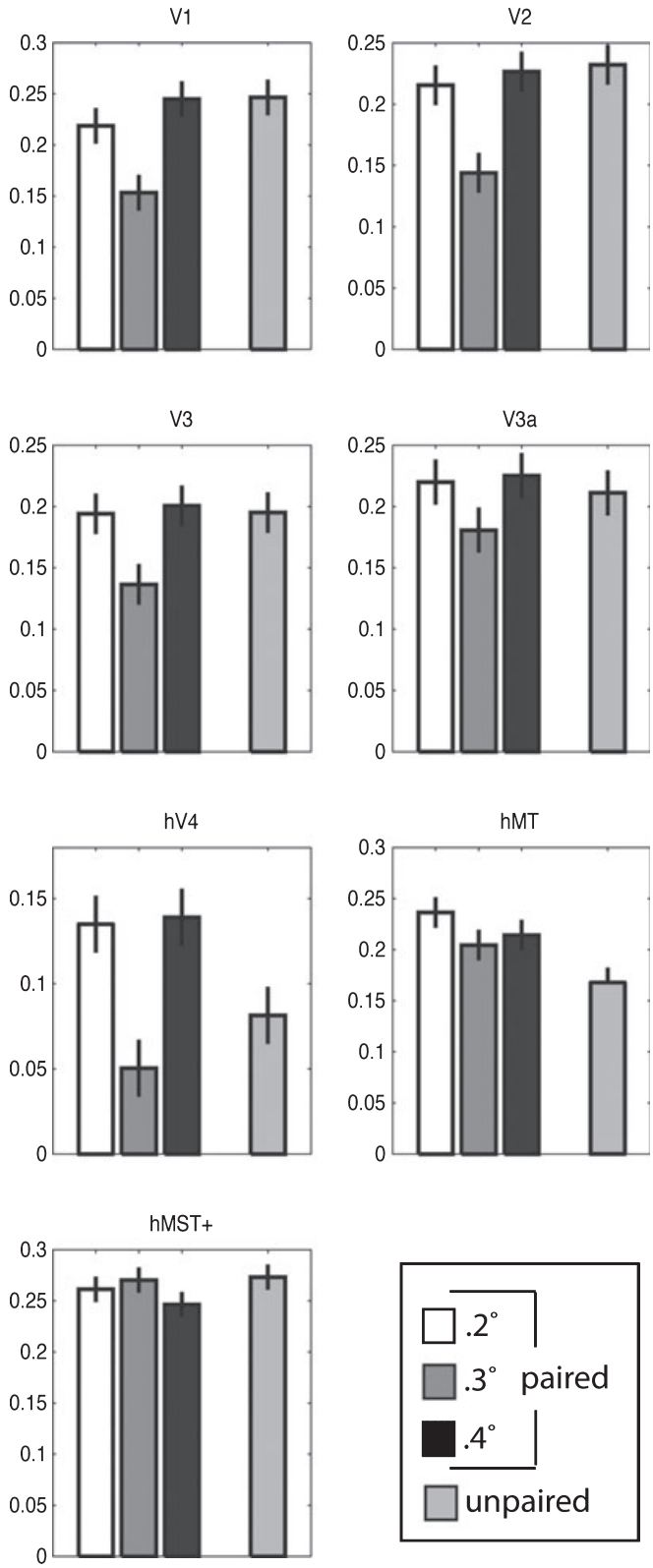

FIG. 5. The BOLD response from V1 and hMT (top row) and other retinotopic regions (V2, V3, V3a, hV4, hMST+) for parametric manipulations of motion transparency for smaller stimuli (4° circular aperture). Percentage signal change was estimated with GLM beta estimates. Error bars indicate one standard error of the estimates.

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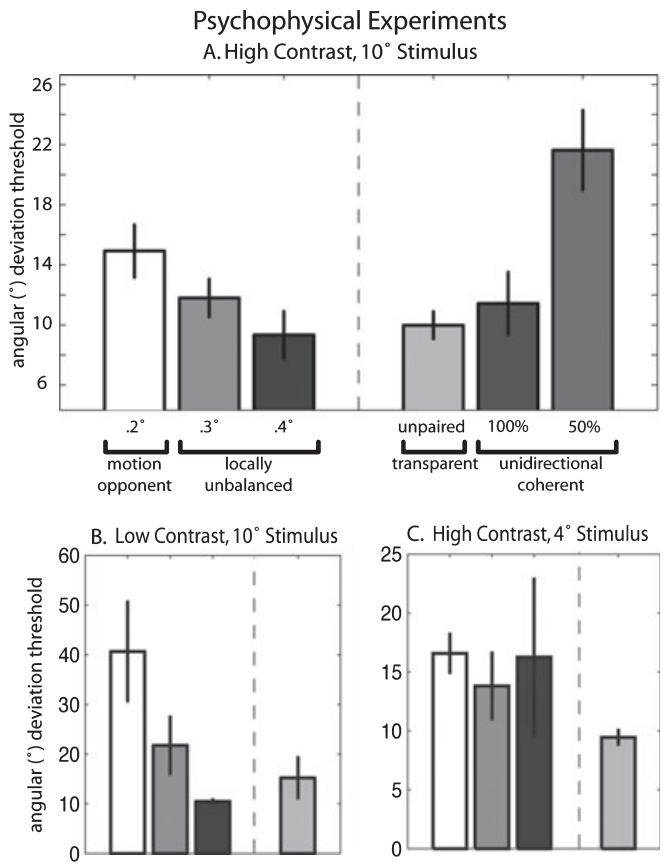

FIG. 6. Performance in psychophysical experiments estimating angular thresholds (80% accuracy) in a blocked 2AFC experiment. (A) Psychophysical thresholds for high-contrast, 10° stimulus condition. Left: psychophysical thresholds of motion opponent (0.2°) and locally unbalanced (0.3°, 0.4°) paired-dot stimuli. Right: performance on the Unpaired transparent and unidirectional Coherent displays (100%, 50%). (B) Psychophysical thresholds for low-contrast, 10° stimulus. (C) Psychophysical thresholds for high-contrast, 4° stimulus. Error bars indicate standard error.

parametric manipulations of the local balance between the opposing motion signals yield an inverted U-shaped interaction in the population response between motion opponency and motion transparency. We believe the apex of the inverted-U reflects the size of the spatial neighborhood over which afferents are being pooled and balanced (the subtractive inhibition component), with the weak BOLD responses for transparent motion competition between populations of velocity-tuned neurons (the divisive inhibition component). In support of this, we were able to demonstrate that the inverted-U pattern is effectively eliminated by lowering the contrast levels of our displays (a manipulation that alters the local balance between excitation and inhibition).

Our measurements also find the interaction between opponency and transparency throughout the visual cortex, not just in hMT, with the exception of V1. This provides evidence that the neural computations reflected in the BOLD interaction as a function of locally unbalanced velocity signals are likely not specific to neural computation within hMT. This is in contrast to the weak BOLD response to transparency, which had the effect of reducing the BOLD response most dramatically in human MT proper. Indeed, hMT was the only brain area in which we measured weaker neural responses for transparent motion as compared with unidirectional motion. We also showed that the completely Unpaired transparent motion yields a BOLD response in hMT that is roughly equivalent to displays with half the motion energy. hMT was the only brain area with these distinctive functional features, and likely reflects some functional specialization in this area for transparent motion that does not exist in other regions of the occipital cortex.

We do not attribute our pattern of results to arousal or selective attention, which generally boost or reduce the BOLD response across the visual cortex as a whole (e.g. Saenz *et al.*, 2002). We also do not attribute our results to task difficulty, which was equivalent across the opponent, transparent and coherent motion trials despite the different levels of neural suppression. Instead we interpret our data as reflecting two distinct mechanisms for opponency and transparency in the visual cortex. Our data are consistent with single-unit measurements and computational models of motion opponency and transparency, and expand those findings to parametric manipulations in the strength of transparency.

Motion opponency

A critical feature of our data is the pervasiveness with which suppression during motion opponency is distributed throughout the visual cortex. Currently, inhibition of MT neuronal firing rates during motion opponency is predicted from the pooling of directionally selective V1 afferents, in which velocity-tuned inputs for opposite directions are subtracted (or summed, with negative weights) and effectively cancel (Simoncelli & Heeger, 1998). The basis for implicating MT in this computational stage comes from the large numbers of neurons tuned to pattern velocity (as opposed to velocity of the individual components, Rust *et al.*, 2006) and the inhibition of directionally tuned MT units during motion opponency (with little impact on directionally tuned V1 neurons, Qian & Andersen, 1994). These findings have been replicated in measurements of the human MT complex, hMT+ (Heeger *et al.*, 1999).

Although not disputing these previous findings, our measurements reveal the impact of motion opponency throughout the visual cortex. We found weak BOLD responses in all visual areas, except V1, for the locally paired opposing motion. These results suggest that pooling of directionally selective inputs (as predicted by the two-stage models) is not a feature specific to motion-selective MT.

The spatial extent over which the opponent motion signals must be balanced in order to achieve psychophysical motion cancellation (perceptually, and for the reduced neurophysiological responses) is very small, approximately 0.2°. This restricted integration zone is a fraction of the size of the receptive field of MT neurons, which subtend approximately 5–10° (Felleman & Kaas, 1984; Mikami *et al.*, 1986). If the computation underlying motion opponency is specific to MT, it must reflect some directionally opponent subunits within the neuron's receptive field (e.g. Livingstone *et al.*, 2001; Majaj *et al.*, 2007).

When our results are considered in conjunction with the small size of the integration zone, these findings may be taken as evidence for a more general pooling mechanism of velocity-tuned inputs in visual processing. This would suppose a more generalized mechanism of feed-forward pooling, not a mechanism specific to MT. Because of the enhanced antagonism that may result from the cascade of non-linearities in feed-forward connections from V1 to MT (Rust *et al.*, 2006), it is reasonable to suppose that the local suppression we have measured originates very early in visual processing. Likewise, the restricted spatial integration zone over which this antagonism operates (a fraction of a degree of the visual angle) is consistent with opponent processing of early velocity signals within the many-to-one pooling of feed-forward inputs.

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Motion transparency

A second critical feature of our data is the pattern of brain responses in hMT during motion transparency as compared with unidirectional motion. In transparent motion, individuals typically report a perceived depth-ordering to the moving surfaces, with one appearing to pass in front of the other (Stoner *et al.*, 1990). In situations where the motion energy between the two surfaces is balanced, the surfaces may perceptually 'switch' positions in depth (Snowden & Verstraten, 1999). Motion transparency is thus effectively a perceptual competition between two objects in the same region of space. In the laboratory the cues that construct the surfaces can be carefully controlled and balanced, but this is rarely the case in the natural world. More typically the transparency cues are not perfectly balanced, and additional features (e.g. occlusion, contrast, context) may bias the neural competition in favor of one velocity plane or the other.

The motion transparency competition has been modeled by pooling the direction-tuned pattern neurons across disparity-tuned channels (Qian *et al.*, 1994b), which is effectively the same as feature-based neural competition often described in attention models, with the features in this instance being motion-defined surfaces (e.g. Desimone & Duncan, 1995; Kastner & Ungerleider, 2000; Wannig *et al.*, 2007). Our results show that this competition is likely instantiated in the neural computations in hMT. It is the neural response in this region in particular where the BOLD response for transparent motion was reduced as compared with unidirectional motion.

Our finding of a reduced BOLD response during motion transparency is consistent with a neuroimaging study in non-human primates (Nelissen *et al.*, 2006), but directly contradicts the single previous neuroimaging study of motion transparency in humans (Muckli *et al.*, 2002). The non-human primate study explored transparency with kinetic texture patterns that varied in width, with the smallest distances in the velocity bands effectively creating instances of opponent motion. These researchers also find an inverted-U shape as a function of pattern width in the monkey MT BOLD response, and a strong reduction in BOLD response for motion transparency as compared with unidirectional motion. The human study, however, used limited lifetime RDKs much like ours and reported stronger neural signals in hMT+ for motion transparency as compared with unidirectional (coherent) motion (and even weaker responses for opponent motion). These authors attributed their results to more neurons excited during motion transparency than during unidirectional motion, without any evidence for inhibition.

There were a number of differences in the design of Muckli *et al.*'s (2002) study as compared with ours that may explain the differences in findings, the most significant of which is the task. The previous experiment asked subjects to identify the quadrant in which patches of motion differed in direction from the surrounding motion (a localization task with shifts in spatial attention). In contrast, our subjects were asked to make a foveal direction discrimination judgment (feature-based). Thus, it may well be that location-based attention and feature-based attention influence the population BOLD response in hMT quite differently. It is not unreasonable to believe that the covert shifts of attention required in the localization task may have boosted the neural response in retinotopic hMT, regardless of direction tuning of those neurons. In contrast, our feature-based task likely served to boost the signal of a select group of neurons, namely those tuned to velocities surrounding the reference angle. Our findings, in conjunction with those of Muckli *et al.* (2002), suggest that computational models of motion transparency must take into account the strong influence of attention in computing mutual inhibition.

Behavioral impacts

Together, our findings implicate two distinct mechanisms supporting perceived motion opponency and motion transparency. Behaviorally, the consequence of these two mechanisms is striking. The impact of motion opponency on psychophysical thresholds is significant, with observers requiring larger angular differences to discriminate different directions in the locally balanced displays. Motion transparency came without a perceptual cost, with angular discriminations for two surfaces being as accurate as those for one. Thus, it appears that motion opponency has a destructive influence on the neural representation of velocity, while transparency can serve to strengthen those representations.

Note that some human psychophysical experiments have found a cost in representing spatially overlapping transparent motion, with poorer velocity discriminations for transparent surfaces than for unidirectional motion (Curran & Braddick, 2000; Braddick *et al.*, 2002). The differences between their results and ours may be due to the redundancy of the task-relevant information in our two velocity cues, which differed by 180° and thus were both perfectly predictive of the correct response. Subjects may have engaged in a strategy of actively attending to only a single motion-defined surface, which would have been sufficient to make the discrimination judgments accurately. It is therefore possible that had we explicitly required subjects to attend actively to both surfaces we may have found a behavioral cost.

If, indeed, subjects were using a single plane of motion to make the psychophysical discriminations, then our BOLD measurements may reflect this strategy. In such a case our patterns of BOLD signals could be interpreted to reflect the effects of attention-based competition, which is known to exert local inhibition (Reynolds *et al.*, 1999; Kastner & Ungerleider, 2000). There is much similarity between feature-based attention competition models and those that directly pit neural populations supporting opposing directions of motion (Snowden, 1989). Thus, our results are entirely consistent with such an interpretation.

An important implication of our findings is the difficulty with which one can infer behavior from a pattern of BOLD responses within a given brain area. Consider, for example, our psychophysical findings in conjunction with previous reports of the impact of attention on the spiking rate of the neurons. Previous single-unit studies have documented higher neuronal firing rates when a monkey performs difficult perceptual tasks as compared with easy tasks (Spitzer *et al.*, 1988). Thus, one could hypothesize that our difficult psychophysical conditions, namely the locally balanced opponent motion and the low-contrast manipulations, would serve to induce higher firing rates in velocity-tuned neurons. This may indeed have been the case, although our measurements did not reveal higher population responses for these conditions. This is just one example of a mechanism that may reflect indirect mapping between the fMRI BOLD measurements and spiking activity.

Our fMRI measurements also reveal a dissociation between psychophysical performance and BOLD amplitude when considered within the context of a single, specialized brain area, or ROI. Single units in monkey MT have been strongly linked to the behavioral choice of that monkey when a decision is rendered on the basis of motion signals (Britten *et al.*, 1992). Human neuropsychological studies have also demonstrated the critical role of the middle temporal area in perceived motion (Zihl *et al.*, 1983). We found that the suppression in brain responses across retinotopic cortex was a better predictor of psychophysical behavior than the output from a single cortical area. We do not intend this interpretation to provide a revision to the functional specialization of hMT, but instead believe this reflects the inherent limitations of fMRI measurements, which are correlative

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in nature and not diagnostic of critical regions of information processing. Due to the indirect nature of the BOLD measurement, the underlying source of which is an active area of investigation, one must be cautious in drawing a direct link between neural response measured by fMRI and perception.

Computational mechanisms and neural inhibition

The link between BOLD response and behavior may be strengthened by the use of converging evidence acquired from other methodologies. Computational models of motion analysis clearly implicate inhibitory mechanisms (through both subtractive and divisive normalization) supporting motion opponency and transparency. Our findings mirror this, with both opponent and transparent displays resulting in weaker BOLD hMT responses than Unidirectional motion. Although we cannot conclusively attribute our findings to active inhibition across the population of neurons underlying the BOLD response, it is reasonable to suggest that the weak BOLD responses we are measuring reflect this inhibition.

As with all fMRI studies, one must be cautious in attributing changes in the BOLD response to specific neuronal mechanisms such as spiking and active inhibition. It could be argued that the decreases in BOLD response we observed may in fact be the result of *decreased* inhibition. This conclusion would be drawn under the assumption that inhibition has the effect of increasing local metabolic activity (for a review, see Logothetis, 2008), which would outweigh any contributions of changes in spiking rate to the population response (Bartels *et al.*, 2008).

There is a an ongoing debate in the literature regarding the relative influence of inhibition and spiking and the BOLD rseponse, but the current consensus is that there are five times fewer cortical inhibitory synapses than excitatory (DeFelipe & Farinas, 1992), and inhibitory mechanisms are likely to be less metabolically demanding on the whole (Waldvogel *et al.*, 2000). However, because fMRI measurements are highly correlated with both spiking activity and with local field potentials (Logothetis *et al.*, 2001), it remains unclear the extent to which inhibition may shift this integrated response (Lauritzen, 2001).

In working through these issues, computational models provide a framework within which these data can be interpreted. Inhibition of MT neuronal responses during motion transparency (and, by inference, the population-based hMT BOLD response) is predicted by models that establish competitive relationships among networks of neurons tuned to opposite directions of motion within the same regions of retinal space (Snowden, 1989), and is proposed to be the mechanism by which depth segregation is imposed when depth ordering is perceived in ambiguous situations, such as motion transparency (Nawrot & Blake, 1991). These competitive networks may be driven by the bottom-up input of disparate motion signals, or be engaged by feature-based attention, which modulates the gain of the individual features in attention-based motion-defined surface segregation (e.g. directions or color, Treue & Martinez Trujillo, 1999). In either way, the end result appears to be a strengthening of the neural representation of at least one of the two surfaces. Supporting this idea, the perceptual thresholds for motion discrimination improved as dot-proximity increased, and observers could make as fine discriminations for the transparent motion displays as they could for single planes of coherent motion.

Conclusion

In summary, we observe two mechanisms operating in visual cortex during perceptual transparency, both of which suppress the hMT BOLD response relative to uniform, coherent motion. This could lead one to conclude that the same underlying patterns of neuronal firing in hMT exist in the two conditions. But when the neuroimaging data are interpreted as a more global pattern and within the context of the psychophysical results, it is clear that the BOLD response reflects two unique brain states. When opponent motion signals are locally balanced, the BOLD response throughout the visual cortex is reduced and observers have difficulty perceiving the direction of motion signals. We suggest that this reflects the subtractive pooling of opponent directional signals within a very small region of visual space, and that this is a general feature of early visual processing. But when those opponent signals are locally unbalanced to induce perceptual transparency, the BOLD signal is suppressed in hMT. It is in this region only that multiple motion-defined surfaces yield half the neural response of that generated by a single surface.

Supporting information

Additional supporting information may be found in the online version of this article:

Fig. S1. A. Simulation revealing the distribution of locally opponent motion in each of the dot displays.

Fig. S2. Talairach coordinates for the regions of interest.

Fig. S3. Grouped whole-brain GLM analysis after Tailarach transformation.

Fig. S4. Vertical and horizontal eye displacements for each stimulus condition.

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Abbreviations

2AFC, two-alternative-forced-choice; BOLD, blood oxygen level-dependent; FDR, false discovery rate; fMRI, functional magnetic resonance imaging; GLM, general linear model; hMT, human middle temporal area; hMST+, human medial superior temporal area and surrounding areas; MT, middle temporal area; ROI, region of interest; V1, primary visual cortex.

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