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Research Report

Stimulus complexity modulates contrast response functions in the human middle temporal area (hMT+)

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ABSTRACT

The brain systems that support motion perception are some of the most studied in the primate visual system, with apparent specialization in the middle temporal area (hMT+ in humans, MT or V5 in monkeys). Even with this specialization, it is safe to assume that the hMT+ interacts with other brain systems as visual tasks demand. Here we have measured those interactions using a specialized case of structure-from-motion, point-light biological motion. We have measured the BOLD-contrast response functions in hMT+ for translating and biological motion. Even after controlling for task and attention, we find the BOLD response for translating motion to be largely insensitive to contrast, but the BOLD response for biological motion to be strongly contrast dependent. To track the brain systems involved in these interactions, we probed for brain areas outside of the hMT+ with the same contrast dependent neural response. This analysis revealed brain systems known to support form perception (including ventral temporal cortex and the superior temporal sulcus). We conclude that the contrast dependent response in hMT+ likely reflects stimulus complexity, and may be evidence for interactions with shape-based brain systems.

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1. Introduction

Motion is an effective sensory cue for visual scene segregation. Motion information facilitates the separation of figure from background, aids in seeing objects that would otherwise be effectively camouflaged, and surfaces that would be otherwise imperceptible. The means by which our visual system analyzes these motion signals has been the topic of much scientific investigation, and has resulted in the identification of at least a dozen distinct brain areas in the primate visual system sensitive to moving events (e.g., Sunaert et al., 1999). Depending on task demands, these motion-sensitive brain areas must interact with other perceptual and cognitive brain systems to bring these visual experiences into awareness.

In the laboratory we can create so-called 'structure-from-motion' (SFM) displays that depict two-dimensional shapes and three-dimensional surfaces from the movement patterns of small tokens, typically lines or dots (Hildreth et al., 1995; Wallach and O'Connell, 1953). A particularly interesting example of SFM is point-light biological motion, in which body movements are easily recognized from the kinematics of small tokens representing the joints (Johansson, 1973; Pinto and Shiffrar, 1999; Troje, 2002). Point-light animations have been an intensely investigated form of SFM, in part because the neural system that supports biological motion recognition

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extends beyond motion sensitive cortex, into more complex multi-modal cortex (the superior temporal sulcus) and into parts of the brain that support object recognition (ventral temporal cortex, Grossman and Blake, 2002; Michels et al., 2005; Thompson et al., 2005). The existence of extensive neural networks supporting awareness of complex motion patterns promotes interactions between neural systems supporting motion processing and those supporting shape perception.

In these experiments, we compare the neural response from the motion sensitive human MT, and its surrounding complex (the hMT+, which includes the human homologues to MST, FSTv, FSTd and other motion sensitive regions), across a variety of motion patterns, including complex motion patterns that depict form. The middle temporal area (MT, or V5 in monkey) plays a particularly critical role in motion perception, with over 90% of the neurons highly tuned to direction of motion (Lagae et al., 1993; Zeki, 1980), and the region as a whole being closely associated with the awareness of motion and the perceived direction of those moving events (Huk and Heeger, 2002; Salzman et al., 1990; Zihl et al., 1983). In addition, most MT neurons are cue-invariant such that they encode motion signals over many image features (Stoner and Albright, 1992), effectively signaling motion across a wide range of visual patterns. The neural response from MT also saturates at relatively low luminance contrasts (Tootell et al., 1995b), allowing these motion signals to be analyzed over a wide range of viewing conditions.

Here we take advantage of the characteristic insensitivity to luminance contrast as a means to measure the range of BOLD response in hMT+ and other brain systems during perception of complex motion patterns. We measure BOLD-contrast response functions when observers view simple coherently translating motion and complex point-light biological motion. On the basis of previous findings (Tootell et al., 1995b), we anticipate finding shallow BOLD-contrast response functions for the coherent translating motion. However, because point-light biological motion perception requires visual integration over space and time (Neri et al., 1998) and is known to recruit regions of cortex specialized for form (e.g., Thompson et al., 2005), we anticipate that these influences will be apparent in the BOLD-contrast response profile.

As a means for comparison and to control for possible low-level feature differences in our two stimuli (e.g. size-dependent effects in the contrast responses in MT, Pack et al., 2005), we have included measurements using a third condition, a small collinear triad of dots. To test the generality of our findings, we have also measured the BOLD-contrast response functions across a range of conditions designed to measure the effects of attention and task specificity, and have included measurements of a non-biological SFM stimulus.

Our results reveal the hMT+ BOLD-contrast response function to depend on the complexity of the visual stimulus, with translating coherent and collinear motion yielding the predicted BOLD response invariant to contrast, but biological motion being strongly contrast dependent. This effect is somewhat attenuated when the biological figure is masked in noise, but is not explained by task or by functional subdivisions of the hMT complex. Contrast dependent BOLD signals during biological motion perception were also evident in ventral temporal cortex and the superior temporal sulcus. We did not find these contrast-dependent responses for a non-biological SFM stimulus. These findings reveal the neural signature of integrated shape and motion analysis in the middle temporal cortex supporting biological motion perception.

2. Results

2.1. *BOLD-contrast response functions in the human MT+*

We measured the BOLD response in hMT+ as a function of contrast for three types of motion: coherent motion, collinear motion, and point-light biological motion. For each condition, we computed a statistical contrast testing for non-zero increasing slope in the BOLD response as function of luminance contrast using the generalized linear model. The results from these measurements are shown in Fig. 2, with the corresponding statistics in Supplemental Table 1.

For the coherent motion conditions, the BOLD-contrast response functions in hMT+ in three of four subjects did not differ significantly from zero, and thus were considered to be invariant to contrast. This finding replicates previous reports of BOLD saturation at low contrast levels (Tootell et al., 1995b) and weak hMT+ response at isoluminance (Wandell et al., 1999). We found similar results with the collinear motion, with slopes of the BOLD-contrast response functions not significantly different from zero in two of four subjects. Further, if the slopes did reach significance, they were still considerably shallow (approximately one fifth the slope of the biological motion condition, Supplemental Table 1).

In the biological motion condition, the hMT+ BOLD-contrast increased sharply as a function of contrast, with significantly increasing slopes in all subjects ($p<.001$, Bonferroni corrected for multiple comparisons). For all subjects, the slopes were steeper for the biological motion as compared to the other conditions, and at the highest contrast levels the neural response for biological motion more than doubled the amplitudes measured during the coherent or collinear motion. These measurements demonstrate that the previous results of hMT+ BOLD response saturating as a function of contrast do not generalize to complex biological motion.

2.1.1. *Additional ROIs*

As a means for comparison, we isolated four additional ROIs outside of the hMT+ associated with biological motion (the STSp, ITS and FFA) and visual processing more generally (V1/V2). The posterior STS is the single brain area most commonly implicated in neuroimaging studies of biological motion perception (for review, see Allison et al., 2000). We targeted this brain area using a standard biological motion localizer (see Experimental procedures). From this localizer scan we also isolated the inferior temporal sulcus (ITS), a brain area

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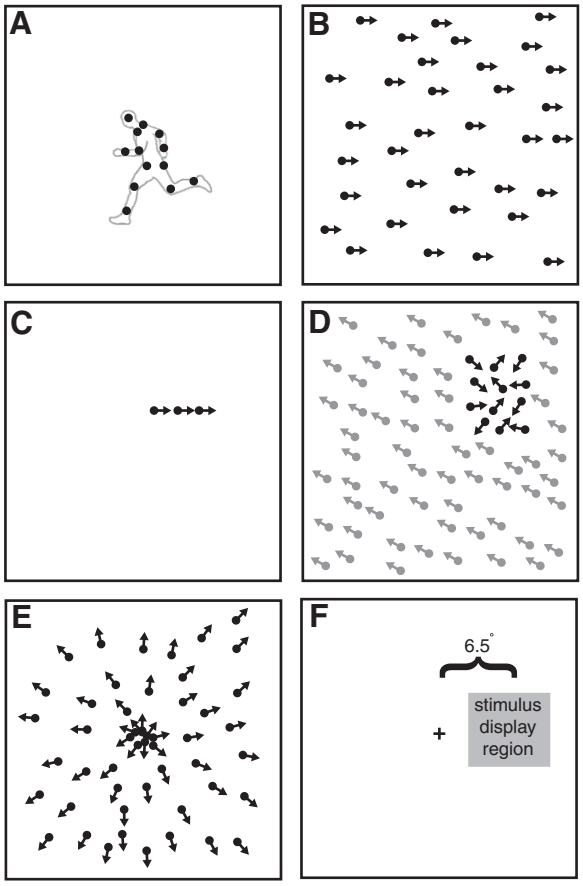

Fig. 1 – Schematics of the stimuli. (A) Single frame of a point-light biological motion animation (BIO). The outline of the actor is shown above, but was not visible in our experiments. (B) Single frame of a coherent motion RDK (COH). (C) Single frame of a rightward moving collinear triad (3DOT). (D) Single frame of a structure-from-motion (SFM) stimulus. The perceived shape was created by randomizing the direction of dots (which otherwise moved coherently) within a virtual rectangle, with the virtual region translating leftward or rightward on each frame. For ease, the signal dots in these images are denoted as black and background dots as gray, but in the actual experiment all dots were yellow against a gray background. (E) Single frame from an optic flow (FLOW) stimulus with contracting and expanding dots. (F) Spatial layout of the experiment, where the experimental stimuli (A–E) were centered 6.5° in the periphery. Stimulus displays region shaded in gray.

more generally involved in perception of dynamic shapes (Pyles et al., 2007; Thompson et al., 2005). Using a different localizer, we identify the fusiform face area (FFA), which is known to overlap with the fusiform body area, previously shown to be involved in the recognition of the human bodies implied by biological motion (Grossman et al., 2004; Peelen and Downing, 2005). Finally, in a separate localizer we isolated the region of early visual cortex (V1/V2) along the calcarine sulcus corresponding retinotopically to the region of space in which the stimuli were presented. Estimates of the BOLD-contrast responses from each of these ROIs for the three motion conditions are shown in Fig. 3 (with individual subject data shown in Supplemental Fig. 2) and the corresponding statistics in Supplemental Table 1.

During the biological motion conditions, the BOLD response in the STSp and ITS both increase steeply, with a slope significantly different from zero in all subjects ($p<.001$, corrected, in both ROIs). The BOLD-contrast response during the coherent and collinear motion conditions was more shallow, with a slope not significantly different from zero across our group of subjects ($p>.05$, corrected). At the highest contrast levels, the BOLD response for biological motion more than doubled that for the coherent and collinear motion. Thus the pattern of brain responses we observed in the STSp and ITS is very similar to that found in the hMT+, with the complex biological motion driving stronger BOLD responses at higher contrasts.

The FFA revealed a different pattern of BOLD responses, with BOLD-contrast response functions for the biological and coherent motion having slopes not significantly different from zero ($p>.05$, corrected). In early visual cortex, we replicated previous findings of contrast-dependent responses for coherent motion ($p<.001$, corrected, e.g., Boynton et al., 1999). But the slopes for the BOLD-contrast response functions for the biological and collinear dot conditions did not reach significance ($p>.05$, corrected). This may be due to the relatively small number of tokens carrying the contrast signal in the biological motion and collinear dot motion condition, as compared to the coherent motion. If so, it is interesting that this signal-to-noise factor does not affect the BOLD-contrast response functions in the more dorsal and lateral brain areas.

2.1.2. *Whole-brain analysis*

To expand our previously targeted analysis, we conducted a whole-brain GLM on the biological motion conditions, testing for linearly increasing BOLD response as a function of contrast. We must caution that this analysis is not statistically independent from the previous ROI analysis because it is being computed with the same underlying data, on some of the same voxels, and is motivated by the findings generated from our ROI analysis (for discussion on circularity in hypothesis testing common in brain imaging analysis, see Kriegeskorte et al., 2009). Nonetheless, this whole-brain analysis is intended to reveal the extent to which the observed contrast-dependent BOLD response exists beyond the targeted brain areas. The results from this analysis are shown in Fig. 4.

This whole-brain GLM analysis revealed a number of significant (FDR<.005) brain areas with contrast-dependent BOLD signals during biological motion perception, including the posterior portion of the STS (STSp), a region located along the inferior temporal cortex corresponding to hMT+ (and possibly including the extrastriate body area, EBA) that extends onto the lateral ventral surface, and, in some subjects, a ventral region partially overlapping with fusiform face and body areas. These are all brain areas corresponding to those identified in previous studies as having neural signals selective for biological motion perception (Peuskens et al., 2005; Pyles et al., 2007; Vaina et al., 2001), and are hypothesized as the major nodes in the network of brain areas supporting biological motion perception (Giese and Poggio, 2003).

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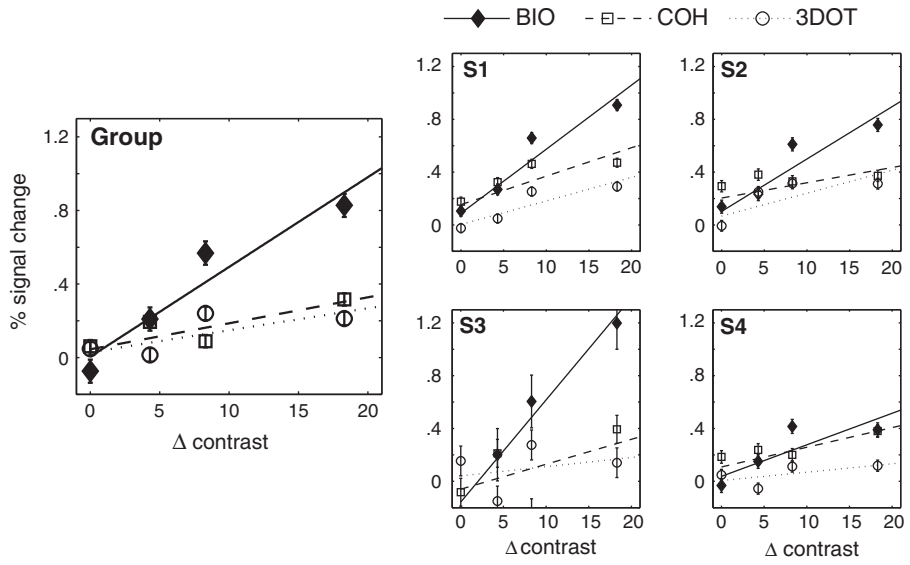

Fig. 2 – The hMT+ BOLD-contrast response functions for coherent (COH), collinear (3DOT) and point-light biological motion (BIO). Percent signal change is estimated from the best-fit beta weights for a generalized linear model with predictors for each condition and baseline normalization. Error bars depict +/−1 standard error of the mean.

2.2. *The effects of task demands*

In this experiment, we considered that our three tasks may inequitably tap attentional resources. Actively attending to motion features is known to boost the BOLD response in hMT for simple RDK displays (Saenz et al., 2002; Sunaert et al., 2000), and because biological motion is more inherently "interesting" than the simpler motion stimuli, subjects may be more motivated to analyze the complex features (which may be either local, dynamic features, or global structural features; e.g. Lu and Liu, 2006; Thurman et al., 2010). We also know from previous research that even though recognizing biological motion in point-light displays subjectively appears to be trivially easy, it does in fact demand attentional resources (Thornton and Vuong, 2004). Therefore, in a control experiment we counterbalanced the inequitable attention demands of the three tasks by calibrating difficulty.

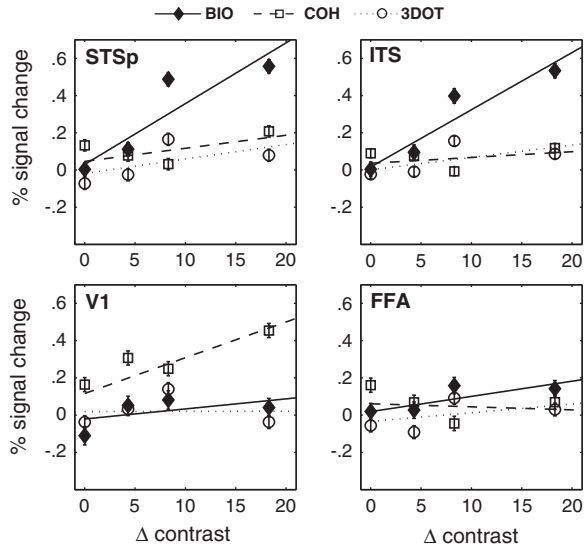

Fig. 3 – The BOLD-contrast response functions for additional ROIs. STSp: superior temporal sulcus, posterior extent. ITS: inferior temporal sulcus. FFA: fusiform face area. V1/V2: early visual cortex, corresponding retinotopically to the parafoveal position of our stimuli. Percent signal change is estimated from the best-fit beta weights for a generalized linear model with predictors for each condition and baseline normalization. Error bars depict +/−1 standard error of the mean.

To achieve this, we employed a method from previous psychophysical experiments to manipulate the signal-to-noise ratios in each of the displays (Garcia and Grossman, 2008). The SNR levels of the biological motion and collinear motion were manipulated by adding masking noise dots (see Experimental procedures), while the SNR levels of the coherent motion were set by adjusting the proportion of dots moving coherently. The coherence and noise tolerance levels for each task and subject were computed in the laboratory (Table 1), with performance subsequently monitored in the scanner. Both collinear motion and biological motion required increasing the number of dots at high contrast levels to fix performance. Because direction discriminations on coherent motion are optimized at very low contrast levels (Garcia and Grossman, 2008), the coherence levels across our contrast measures were essentially fixed at 22% to achieve fixed performance.

In general, subjects were able to maintain threshold accuracy with these more difficult tasks in the scanner, although performance on the biological motion task was below our targeted threshold (Supplemental Table 3). Results from these experiments are shown in Fig. 5A (with individual subject results in Supplemental Fig. 3A).

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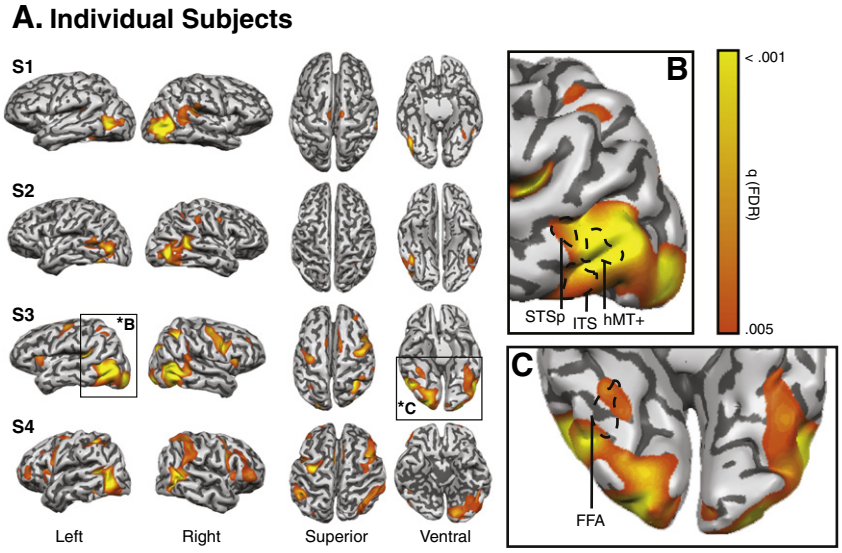

Fig. 4 – (A) Individual subject statistical maps generated from the biological motion conditions (BIO). Color maps show the statistically significant regions (corrected for multiple comparisons with the FDR, FDR<.005) of a general linear model analysis testing for contrast dependent neural responses (increasing BOLD response for increasing luminance contrast levels). Inserts show the expanded selections from the (B) lateral surface and (3) ventral surface of S3's left hemisphere, with the independently localized ROIs outlined in black.

Adjusting task difficulty had little effect on the BOLD-contrast response profiles for any of the conditions. Slopes of the hMT response functions for the difficulty-equated coherent and collinear motion conditions were not significantly different than zero ($p=0.38$, $p=0.24$, uncorrected, respectively). The hMT and STS responses for the masked biological motion remained contrast dependent ($p<.001$), with slopes still higher than the coherent and collinear motion conditions, as found in the uncalibrated conditions in Experiment 1 (Fig. 2). We conclude that for the range of SNR tested, the boost in BOLD response for biological motion does not reflect a tendency to attend more carefully to the biological motion stimulus, nor inequitable attention demands across the tasks.

2.3. *Working memory demands*

In a second control experiment, we consider the effect of the task itself on our measurements. In all of our previous experiments, subjects had made a 1-back discrimination on the point-light animations, but left–right direction discriminations for the coherent and collinear motion. The unique task for the point-light biological motion condition was chosen because of its use in previous neuroimaging studies (Grossman and Blake, 2002; Peelen et al., 2006), and because many of the actions do not have obvious directional decision points. For example, a jumping jack viewed in the fronto-parallel plane is not clearly a 'leftward' or 'rightward' stimulus. This is true for many of the natural actions in our dataset. The unfortunate consequence of these different tasks is that the 1-back task had a working memory demand that did not exist for our other motion conditions. This working memory component could, in principle, be the source of the steep BOLD-contrast response functions we observed for biological motion (e.g., Zaksas et al., 2001).

We conducted a neuroimaging experiment to test the hypothesis that working memory demands incurred by 1-back tasks are contrast-dependent, while direction discriminations without working memory demands are not. To do this, we collected BOLD-contrast response functions for the coherent and collinear motion while subjects performed a 1-back task on each trial. All other parameters were identical to the previous measures. Results from these measurements are shown in Fig. 5C (with individual subject results in Supplemental Fig. 3B).

When subjects performed a 1-back task on the coherent and collinear motion, we found weak BOLD-contrast response functions in hMT that were nonetheless significantly different than zero ($p<.001$, corrected). By way of comparison, these response functions rose an average of .01 units of percent BOLD signal change, with each 1% increment in contrast (the slope estimates). This is roughly 75% more shallow slope than generated by biological motion using the same task. Similar to

Table 1 – Mean noise dots (BIO, 3DOT) or coherence level (COH) for the fixed performance set of experiments. Parentheses indicate standard deviation. (–) indicates subjects cannot discriminate the biological motion at isoluminance.

	Noise/coherence		
Contrast	BIO	Condition COH	3DOT
Iso	–	34 (13)	83 (66)
4%	25 (12)	23 (6)	96 (52)
8%	32 (6)	20 (3)	146 (72)
18%	47 (7)	23 (4)	177 (68)

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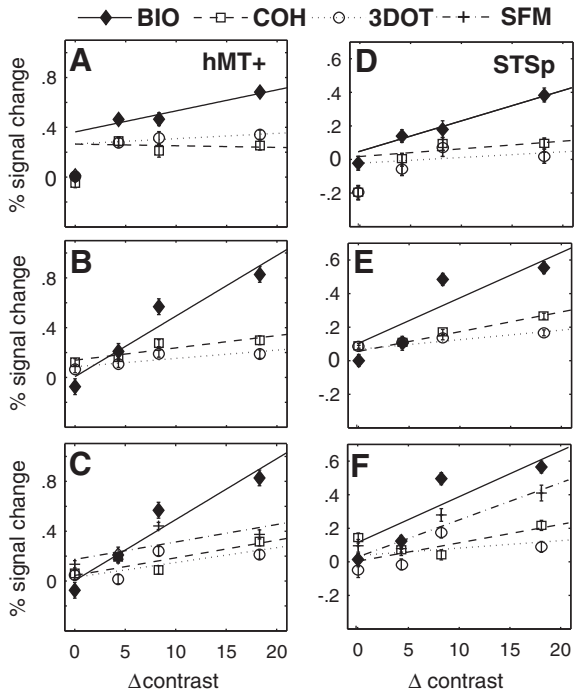

Fig. 5 – (A) hMT+ BOLD-contrast responses for the adjusted performance experiment, (B) hMT+ responses for the N-back task, and (C) the shape defined by motion (SFM). For comparison, panel C includes data from the original experiment (also shown in Fig. 2). (D–F) The same conditions, except for STSp. Signal change calculated as the best-fit beta estimate with baseline normalization. Error bars indicate +/−1 standard error of the mean.

the shallow responses for the simple motion conditions in hMT+, coherent motion and collinear triads elicited shallow responses in STSp while subjects performed a 1-back task. Though the conditions elicited significant contrast-dependence ($p<.001$), this was still more shallow than the biological motion condition. Thus we conclude that working memory load alone is insufficient to generate contrast-dependent BOLD responses in the hMT+ and STSp.

2.4. *Generalization to non-biological structure-from-motion?*

The previous experiments leave us with the question of whether the steep contrast-dependency we observed is specific to biological motion, or is it also observed in other forms of structure-from-motion? To test this, we collected contrast response functions from two subjects using a new stimulus: a translating rectangle that is defined purely by motion (incoherent motion embedded in coherent motion; Fig. 1D). Like biological motion conditions, subjects performed a 1-back task on the translating direction of the virtual shape. Results from these SFM measurements are shown in Fig. 5B (with individual subject data in Supplemental Fig. 3C). For comparison, this panel includes data from the previous three motion conditions obtained from the original experiment.

In hMT+, the BOLD-contrast response functions we measured for the SFM were dependent on contrast, with slopes significantly different from zero ($p<.001$, corrected). Overall, the slopes estimated from this SFM condition were shallow in comparison to that estimated from biological motion (.012% BOLD signal change per unit contrast, as compared to .049 for biological motion), much like our previous coherent and collinear motion measurements. For comparison, STSp shows BOLD-contrast response functions also significantly different from zero ($p<.001$), but substantially more steep than for the coherent motion and collinear triad conditions. These findings suggest that the BOLD-contrast dependent response pattern reflects the influence of shape processing (presumably computed outside the hMT) on these early visual signals.

2.5. *MT versus MST*

In a final analysis, we considered whether the BOLD responses we observed during the biological motion condition originated from some subdivision within the hMT complex, as opposed to from within the human MT itself. Within the typical resolution of most neuroimaging experiments (including ours), the hMT complex includes both the MST complex and MT proper brain regions. MST neurons, in particular, have preferred tuning to more complex motion patterns (e.g., Duffy and Wurtz, 1991) and computational models have suggested these computations to facilitate biological motion perception (Giese and Poggio, 2003). It is therefore possible that our contrast-dependent biological motion responses reflect the contribution of MST to the hMT+ BOLD response.

To test this hypothesis, we acquired additional localizer scans on two subjects that delineate the hMT proper from the remainder of the motion-sensitive satellite brain areas, including the human MST (see Methods). We then functionally verified our mapping by measuring the response for optic flow patterns, which are known to activate the hMST region more strongly than the hMT proper (Smith et al., 2006).

From these measurements we were able to determine that both the hMT and hMST+ have contrast-dependent neural signals during biological motion perception (both have non-zero slopes, $p<.001$, corrected). Notably, the hMST+ responded more strongly during the optic flow patterns as compared to the coherent or collinear motion, replicating previous reports of optic flow selectivity over coherent motion in the hMST+ (Smith et al., 2006), and demonstrates that these responses are also contrast invariant. We conclude that neural activity in the hMST+ alone is insufficient to explain the contrast dependencies we observe for our complex motion patterns.

3. Discussion

Brain areas within visual cortex do not analyze perceptual information in isolation. There is extensive communication between all regions of visual cortex, with much of this engaged depending on task demands. Researchers have revealed many features of the cortical response in the hMT+ that link this brain area to awareness of visual motion

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(Moutoussis et al., 2005; Rees et al., 2000; Sunaert et al., 2000; Tootell et al., 1995a). In particular, MT neurons appear to be well suited to extract directional signals from complex visual scenes across a wide range of patterns and viewing conditions (Albright and Stoner, 2002; Bisley et al., 2004).

Here we report on contrast dependence in the human MT complex during a range of motion conditions that vary in visual complexity. We find the hMT+ BOLD response to be contrast invariant for translating coherent and collinear motion, meaning that the intensity of the population response did not increase significantly with increasing contrast. We found a contrast-dependent response, however, when subjects viewed point-light biological motion. This means that increases in the luminance contrast in the tokens that depict biological motion are accompanied by increases in the hMT+ BOLD response. We also found contrast-dependencies when task demands incur an attentional load, which in the case of our biological motion, likely reflects the spatio-temporal integration required to recognize these sequences.

The findings in this study both replicate and expand upon previous physiological and neuroimaging investigations, which have revealed hMT+ to be largely insensitive to contrast (e.g., Buracas et al., 2005; Tootell et al., 1995b; Wandell et al., 1999). Those previous studies used simple stimuli such as sine wave gratings and random dot patterns, typically with fixed signal to noise levels. When we expand those measurements to more complex stimuli, we find a different pattern of brain responses.

We do not attribute our findings to low-level differences in stimulus size, dot number or speeds between our conditions. We know that the hMT+ is retinotopically organized (Huk et al., 2002) and is speed-tuned (Chawla et al., 1998), therefore one could hypothesize that differences in BOLD responses for our conditions may be due to differences in stimulus size, dot number, or dot speeds across our conditions. The biological motion (with an average stimulus size of 3×1.5°) and the collinear motion (0.17×1.35°) conditions both subtended far less visual angle than patches of the coherent and SFM motion (both 8.7°^{2}). On the basis of size alone one would anticipate the strongest BOLD response from the coherent and SFM motion conditions. Instead we found, on average, that the hMT+ response was stronger for the larger coherent motion than for the small collinear motion, but the biological motion response at the highest contrast level was significantly greater than both. Similarly, the biological motion animations elicited a stronger response despite consisting of relatively few dots (12 dots, versus 100 in the coherent motion). The average speeds of the dots in each of our conditions varied slightly, in part because the biological motion conditions have a range of speeds. On average the dot speeds in our stimuli ranged from 6.8°/s to 8.5°/s, with differences in speeds across the three conditions was less than 2.3°/s. All of these speeds are within the range known to optimally drive hMT+ (Chawla et al., 1998) and are within the FWHM tuning of the majority of MT neurons in monkey (Lagae et al., 1993).

3.1. *The hMT+ BOLD response and attention*

Our findings may reflect, to some extent, an interaction with attention on the hMT+ BOLD response. We know from previous studies that when attention is directed to moving features in the visual field, the BOLD response in the hMT+ increases (O'Craven et al., 1999; Schoenfeld et al., 2007). When the biological motion targets were unmasked, the BOLD-contrast response was the highest among our conditions, perhaps evidence for increased attention to key features in biological motion that are more evident at higher contrasts. Calibrating task demands to equate attention demands across tasks and contrast levels had little effect on this overall pattern of results. Masking biological motion with dynamic noise dots attenuated slightly the slope of the response (as a function of contrast) and flattened the contrast response functions for the coherent motion and collinear triad conditions, but left the across condition differences intact. Thus, differential attention demands are only a partial explanation of our findings. Likewise, we found an influence of task constraints on our measures of the hMT+ BOLD response. For the non-biological conditions, the slopes of the BOLD-contrast response function increased slightly during the 1-back task as compared to when subjects made direction discriminations. These results may reflect the maintenance of task relevant information during the brief inter-stimulus interval that would be needed to complete the 1-back task. There is evidence from single-unit studies that MT neurons are actively involved in this maintenance stage when the pertinent information has a velocity component (Bisley et al., 2004). Adding a working memory load, however, did not increase the slope of the contrast responses for the coherent or collinear motion stimuli to nearly the levels found in the biological motion condition.

One could argue that even by calibrating the task demands, the contrast-dependent responses we measure for biological motion may be the result of maximally representing each individual dot in the biological motion condition, to take the most advantage of the available contrast. We know from previous reports that each dot in a biological motion sequence is more critical to behavioral decisions than any given dot in a coherent motion sequence (e.g., Neri et al., 1998). We also know that behavioral decisions on biological motion, much more than translating motion, benefit from additional information, either through higher contrast or longer temporal integration windows (Garcia and Grossman, 2008; Neri et al., 1998). The behavioral evidence, together with these neuroimaging findings, suggests that the attentional boost associated with each increase in information unit in biological motion more readily boosts the response in early visual cortex.

3.2. *Object selective responses in the hMT+*

One interpretation of our findings is that the contrast-dependent BOLD response reflects the influence of form-selective neural populations on the hMT+ BOLD response. A handful of studies have reported strong hMT+ responses when subjects view stationary images that imply motion (Kim and Blake, 2007; Kourtzi and Kanwisher, 2000), and in some instances stronger BOLD response for objects (stationary or moving) as compared to scrambled objects (Kourtzi et al., 2002). Most importantly for our experiments, Downing et al. (2001) showed significant overlap between the hMT+ and the human extrastriate body area (EBA), which is functionally

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defined as the brain region with stronger responses to stationary images of headless bodies are compared to snapshots of common household objects. In a follow-up study, Peelen et al. (2006) demonstrated that the largely overlapping region of interest identified by the hMT+ and EBA localizers could be separated into motion-selective voxels and form-selective voxels by investigating the response preference of individual voxels (a multivariate approach), but not through standard imaging analyses (univariate analyses). The implication is that the coarse resolution of fMRI combines these two populations of neurons.

One could speculate as to the broader implications of having a neural population tuned to form properties of visual stimuli within the human MT complex. Among the hMT+ satellite areas in monkey are two additional brain areas, the dorsal and ventral fundal areas of the superior temporal sulcus (FSTd; FSTv). The FSTd is associated with spatial vision and has many connections to the dorsal visual pathway (Desimone and Ungerleider, 1986), while the FSTv is highly interconnected with inferior temporal lobe (Kaas and Morel, 1993). To date the human homologue to the FST (dorsal or ventral) has yet to be identified, but it is worth noting that at least one study (Nelissen et al., 2006) reported fMRI responses within FSTv in the macaque to action hand movements that were four times the response to simple translating motion. With the spatial resolution of our current neuroimaging technique (3 mm^3 voxels), it is a reasonable conjecture that wherever the FSTv exists in human cortex, it is likely within the region that we have designated the hMT+. Our attempts to narrow this region by constraining our analysis based on retinotopy, or by preference for optic flow patterns versus translating motion (MST localizer), failed to isolate this contrast dependent response to a single ROI within hMT+. Thus we are not able to conclusively link this signature to a single mechanism within the motion sensitive complex.

One could conclude, however, that our contrast dependent responses measured in the hMT+ may reflect the pooled populations of motion-selective (velocity tuned) and form-selective neurons. On the basis of previous studies, and our own findings with the unstructured motion sequences, we could hypothesize that the motion-selective neurons retain their contrast-invariant properties even for complex stimuli such as biological motion. In such a scenario, the contrast-dependent responses would be the signature of the form-selective population of neurons. Such a scenario would be intriguing because it would present an approach for isolating these two populations, without the use of multivariate statistical techniques.

3.3. *Relevance to the biological motion literature*

Recognizing actions from point-light biological motion is a complex process believed to recruit motion-based and form-based perceptual analyses, presumably instantiated in the motion and form pathways, respectively. Some computational models have proposed form-based template analyses (Lange and Lappe, 2006), and these models have been bolstered by neuroimaging findings of brain responses correlated to biological motion perception in ventral temporal cortex (Grossman and Blake, 2002; Michels et al., 2005; Vaina et al., 2001). In particular, both the fusiform body area (FBA) and extrastriate body area (EBA) have been proposed as candidate brain sites responsible for analyzing stationary snapshots of body postures extracted from the action sequences (Giese and Poggio, 2003; Lange and Lappe, 2006; Lange et al., 2006).

More recent studies, however, have argued that the critical features in biological motion perception to be inherently dynamic (Casile and Giese, 2005; Thurman and Grossman, 2008). The MST subdivision, in particular, has been suggested to play a role in computing the relative motion of the pendular and hierarchical limbs moving during human actions (Giese and Poggio, 2003). Critically, the STS is thought to be a convergence zone that receives inputs from the motion and form pathways (Cusick et al., 1995). Because we observed the contrast-dependent BOLD responses in both the hMT complex and the STS, it is possible that this is the signature of the interaction of these pathways.

So although the relative importance of form and motion analyses in biological motion perception is yet unclear, there is no question that they both can play a critical role (e.g., Giese and Lappe, 2002). It is undoubtedly true that the unique demands of analyzing these point-light animations engages mechanisms within the hMT+ that translating motion does not, and it is theoretically possible that these mechanisms (even without the outside influence of additional brain areas) are inherently contrast-dependent. Because there have been no reported investigations of single-unit MT responses to biological motion, and because of limitations in current fMRI techniques for isolating MT proper, this is a possibility that cannot be ruled out.

3.4. *Relevance to neurophysiology literature*

There have been no reports (to our knowledge) of single-unit studies of hMT neuron responses to biological motion, and without these measures we can only infer that our fMRI findings would reflect similar neural population responses in the monkey. There are, however, some key differences between the human and non-human primate perceptual analyses of point-light biological motion, and the non-human primate MT and hMT. For instance, although rhesus monkeys require more extensive training to discriminate some viewpoints of biological motion as compared to others and the training did not generalize to the same actions portrayed by different actors (Vangeneugden et al., 2009), a finding that has not been documented in the human literature. And in general, the neural specificity for actions in these trained monkeys is far more specific than would be expected on the basis of human behavior (Vangeneugden et al., 2011).

There have also been several documented differences between the non-human primate functional specialization in the MT region and the putative homologies in the human (Orban et al., 2003). For example, in an fMRI study in the monkey, biological actions (a moving hand) elicited higher BOLD activity than non-biological motion (a moving inanimate object) in the macaque MT (Nelissen et al., 2006). This study also reported four times the BOLD response for action

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hand movements compared to simple translating motion of dots (similar to the stimuli used in our manuscript) in the monkey FSTv. Thus it seems that there is much to be learned about the complex biological motion response in these early visual areas.

3.5. *General discussion*

Overall, our findings depart from the traditional depiction of hMT+, as cue-invariant, non-discriminately activating for motion stimuli and with poor sensitivity to contrast. Our results instead are evidence for a more interesting response profile, with contrast-dependencies varying as a function of stimulus complexity.

4. Experimental procedures

4.1. *Participants*

Four individuals (2 males, 19–33 years old) with normal or corrected to normal visual acuity participated in these experiments. All subjects were right-handed (self-report) and were verified to have normal color vision as measured by 22/24 correct on the Ishihara color test. Two observers (S2, S3) were naïve to the experimental manipulations, but all were experienced psychophysical observers. Observers gave informed, written consent as approved by the University of California, Irvine Institutional Review Board, and were paid for their participation.

4.2. *Stimuli and procedure*

In these experiments, the neural response was measured as a function of luminance contrast, from 0 to 20% contrast. To establish the luminance levels required to achieve 0% perceptual contrast (psychophysical isoluminance), we used the minimum flicker procedure. For each subject, we found the intensity at which two wavelengths (for this study, yellow and gray) were perceived to have equal luminance (Anstis and Cavanagh, 1983). Briefly, observers monocularly viewed a stationary random dot image (a single frame of the coherence stimulus), contrast reversing between yellow and gray. Subjects pressed keys to adjust the brightness of the yellow until the perceived flicker of the 23 Hz display was minimized. This procedure was repeated 10 times, and the mean yellow intensity adjustment was calculated. Because perceptual isoluminance is rarely equivalent to 0% physical luminance contrast, and the ratio of luminance required to achieve this point varies from individual to individual (and even between the eyes of the same individual, Cavanagh and Anstis, 1991), all displays throughout the experiment were positioned parafoveally and viewed monocularly. Subjects repeated the minimum flicker procedure prior to starting each session (different days) and were able to return to the same contrast levels from day to day.

All animations were constructed from dot displays using Matlab (Mathworks, Inc.) in conjunction with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Examples of the four stimuli are shown in Figs. 1A–E, with Fig. 1F displaying where on the stimulus screen each stimulus was shown. All animations were viewed within an 8.7° aperture centered 6.5° parafoveally. Subjects monocularly fixated on a central (.44°) fixation cross and attended to the displays, which were positioned either in the right visual field (S3, S4) or left visual field (S1, S2). Dots were depicted as yellow circles (.17° of visual angle, mean CIE: x=.412, y=.500) against a gray background (mean intensity 10.1 cd/m^2). Yellow and gray were used to investigate the isoluminant responses within the regions of interest.

4.2.1. *Biological motion (BIO)*

Point-light biological motion animations were created from digitized video of an actor performing various activities (e.g. running, walking, kicking, throwing) with reflective tape on the joints. The joints on the actor were replaced with small dots, and the overall figure scaled to approximately 3×1.5° visual angle. Brief segments of the actions were displayed for 500 ms (30 frames displayed at 60 Hz, the speed at which the recordings of the actions were originally acquired). Scrambled motion (used in the localizer scans) was created by randomizing the starting positions of the biological motion dots (within a 3×1.5° virtual window, matched to the size of the biological figure) but retained the motion trajectories (e.g., Grossman and Blake, 1999). The location of the target figure within the stimulus aperture jittered 1.5° from trial-to-trial to prevent single dots or small clusters of dots from being predictive of the target identity. During scanning, observers were asked to report whether each short animation was the same or different from the animation immediately preceding it (1-back task, as used in Grossman et al., 2000; Peelen et al., 2006).

Because biological motion perception varies in difficulty with contrast (Garcia and Grossman, 2008), we conducted a control experiment in which task demands were adjusted psychophysically to approximately threshold performance levels (79.4% accuracy). This experimental manipulation tested whether our measured BOLD-contrast response functions in the previous experiment were confounded by attentional load. To adjust performance we embedded the biological animations in masking noise dots, with few masking noise dots in the low contrast conditions and more masking noise dots in the higher contrast conditions. The number of masking noise dots was determined individually for each subject at each contrast level (Table 1) as measured in 3–1 double interleaved staircase psychophysical procedure prior to scanning. To optimally mask the target figures, the noise dots (spatially randomized within the 8.7° aperture) had motion trajectories matched to the point-light biological animations. Using this method, a biological or scrambled 'walker' figure was masked by 'walker' noise dots, a 'kicker' masked by 'kicker' noise dots, and so forth.

4.2.2. *Coherent motion (COH)*

Observers viewed 500 ms random-dot kinematograms (RDKs) consisting of 100 dots distributed across the 8.7° stimulus aperture. In the initial experiment, all dots moved coherently in the same direction (either left or right) with a speed of 8.5°/s. Subjects were asked to report the direction of the dots (left or right).

This is a trivially easy task at all but the lowest contrast levels, and because all dots are moving entirely coherently,

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observers can make this discrimination on the basis of a single dot. Therefore, to adjust task difficulty and to force the observers to spatially and temporally integrate the coherent motion signal, we conducted a control experiment in which the coherence levels of the RDKs were varied to adjust performance at approximately threshold levels (79.4% accuracy). To achieve this, some percentage of dots on each frame moved coherently in one direction, while the remaining dots moved in randomly selected directions. In these non-fixed path motion displays, it is highly unlikely that a single dot may be diagnostic as to the overall coherent direction of motion. The percentage of coherently moving dots was determined individually, for each contrast level, from the method of constant stimuli procedure using the same stimuli, completed in the laboratory prior to scanning (Table 1). In these task-difficulty matched displays, observers generally required coherence levels of approximately 22% at all but the lowest contrast levels to achieve threshold accuracy.

In a second control experiment measuring the effects of task demands, we measured BOLD-contrast response functions for the coherent motion while subjects engaged in a 1-back direction task (subjects indicated whether the current animation depicted motion in the same direction as the previous animation). In this control experiment, all the dots moved completely coherently and the remaining experimental parameters for coherent motion conditions were unchanged.

4.2.3. *Collinear triads (3DOT)*

Observers viewed 500 ms animations of three horizontally aligned collinear dots moving left or right. These animations were matched, in part, to parameters extracted from the point-light biological motion animations. The horizontal extent of the dots subtended 1.35° visual angle with .43° separating each dot, which approximated the size of a biological motion limb. The speed of the dot movement was fixed at 6.8°/s, which approximated the average speed of the biological figure. The position of the triad was randomly spatially jittered 2.2° around the center of the aperture on each trial (within the region subtended by a full biological motion figure), and observers were asked to report the motion direction of the target dots (left or right).

Like the coherent motion task, discriminating leftward from rightward dot motion for these collinear triads is trivially easy at all but the lowest contrast levels. Therefore, to adjust task difficulty across all contrast conditions, in a second set of experiments the collinear triads were embedded in motion matched masking noise dots. Noise dots were randomly distributed across the stimulus aperture, and moved incoherently on each frame. As for the other experiments, the number of noise dots for each contrast level was determined prior to scanning in the laboratory.

In a second control experiment measuring the effects of task demands, we measured BOLD-contrast response functions for the collinear motion while subjects engaged in a 1-back direction task. The collinear triad was viewed without any masking noise dots, and all other experimental parameters were unchanged.

4.2.4. *Structure from motion (SFM)*

Observers viewed 500 ms animations of RDK animations modified so as to depict a 3×1.5° rectangle translating within the 8.7° noise array. The stimulus consisted of 600 dots randomly distributed within the stimulus aperture translating coherently (in the same direction) at a speed of 8.5°/s. On each frame a subset of the dots located within a virtual rectangle had their direction of motion randomized so that they moved incoherently, forming a region of incoherent motion embedded within the coherent motion. The virtual rectangle translated 8.5°/s on each frame either leftward or rightward. From these displays, observers readily reported the impression of a rectangle sliding across the stimulus aperture, either to the left or right. Subjects were asked to make a 1-back judgment on the direction of translation of the virtual rectangle.

4.2.5. *Optic flow (FLOW)*

The optic flow stimulus was used both in a localizer scan and as condition served as a test for functional specialization of the hMST+ subdivision of the hMT+. In the hMT+ localizer scan, observers passively viewed 14 s animations of 500 dots that moved inward or outwards from the center of the 8.7° stimulus aperture, centered 6.5° into the periphery. Observers passively viewed the same parafoveal stimulus for 18 s blocks in the experimental scans. The movements of the dots yielded the impression of expansion or contraction. Dots moved with an average speed of 8.5°/s.

4.3. *Neuroimaging*

Neuroimaging data was collected on a 3 T Siemens Trio MR scanner at the Dana and David Dornsife Cognitive Neuroscience Imaging Center at the University of Southern California. Subjects lay supine in the scanner and viewed the animations through a periscope mirror. Animations were projected with a Christie DLV 1280-DV DLP projector controlled by Matlab running on a Macintosh computer. Additional measures (the coherent motion and collinear motion 1-back task, and the SFM measurements) were conducted on a Philips Achieva 3T Magnetic Resonance system located at the University of California Irvine. Parameters for the visual displays and scanning acquisitions were unchanged between the experiments.

Anatomical and functional brain images were collected via a standard, single channel birdcage headcoil. We collected high-resolution (T1, MPRAGE, TE=4.1 ms, flip angle=12°, 192 sagittal slices, 256×256 matrix, 1×1×1 mm^3 voxels) whole-brain anatomical images from each individual to be used for co-registration of the functional data. Functional data were collected using a single-shot T2*-weighted imaging sequence (gradient EPI, TE=32 ms, flip angle=90°, A–P phase encoding) with slices that covered the entire brain (28 axial slices, 3.5×3.5×4 mm^3 voxels, 0 mm gap between slices, TR=2000 ms). For all functional scans, the first 4 s of each scan was discarded to allow for saturation of the BOLD response, and 4 s of passive fixation was included at the end to allow for complete measurement of the hemodynamic response.

4.3.1. *Localizer scans*

Subjects participated in a number of localizer scans designed using standard techniques established in the literature. The goal of these localizers was to independently identify targeted regions of interest (ROI) shown to be involved in motion perception and biological motion perception, within which we

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can measure BOLD-contrast response functions. The use of independent localizers circumvents issues of statistical circularity inherent to many fMRI study designs (for discussion, see Kriegeskorte et al., 2009). Localizers were analyzed in the native brain space for each individual subject to account for variability in anatomy, particularly within brain areas known to be organized retinotopically. Talairach coordinates for these ROIs are shown in Table 2, and the ROIs from a representative subject are shown in Fig. 4. Each localizer scan proceeded as follows:

The hMT+ ROI was identified in using two standard localizers. In the first, subjects viewed 14 s blocks of expanding and contracting dot motion (optic flow) alternating with 14 s blocks of stationary dots. Because hMT+ has been identified as having retinotopic organization (Huk et al., 2002), the stimulus was constrained to an 8.7° aperture centered 6.5° in the periphery, the same size and position as the experimental stimuli. Each block was repeated seven times for a total of 106 volumes acquired in each scan. This scan was repeated 1–2 times for each subject. The hMT+ was identified as that region on the ascending branch of the inferior occipital sulcus that responded significantly more during the optic flow blocks as compared to the stationary blocks (FDR<.05).

The hMT+ is a relatively large region of interest, and is believed to encompass a number of MT satellite brain areas, including the MST, FSTd and FSTv. Therefore two subjects participated in a second localizer scan designed to isolate the MT proper from the MST subregion, following the protocol of previously published studies (Dukelow et al., 2001; Huk et al., 2002). Participants viewed 14 s blocks of ipsilateral or contralateral optic flow (randomly switching between inwards and outward motion) subtending 10° of visual angle and centered 11° in the periphery. These motion blocks alternated with 14 s of a stationary dot pattern, and were repeated five times within each 154 volume run. This scan was repeated 4–6 times. From this localizer, MT proper was identified as the region of the hMT+ complex activated only by contralateral motion, with the remainder of the hMT+ assigned as hMST+ (Fig. 6).

All subjects participated in three other localizer scans to define regions of interest in primary visual cortex (V1), the superior temporal sulcus (STS) and the fusiform face area (FFA). To define the V1, subjects viewed 14 s blocks of a flickering checkerboard, alternated with 14 s blocks of fixation, with the checkerboards confined to an 8.7° aperture positioned 2.2° parafoveally, the same size and position as the experimental stimuli. Each block was repeated 7 times for a 106-volume scan. V1 was identified as that region on the calcarine sulcus that responded significantly more during the flickering checkerboard blocks as compared to the fixation blocks (FDR<.001).

The human STS was identified using a biological motion localizer that is standard in the literature (e.g., Pyles et al., 2007; Saygin, 2007). The localizer consisted of 18 s blocks of point-light biological motion performing various actions (e.g., running, jumping, kicking, etc.), alternated with 18 s blocks of scrambled biological motion. Scrambled animations were created by randomizing the starting positions of the dots while leaving the biological motion vectors intact. Animations within the block were shown for 1 s, with a 1 s interstimulus interval (ISI). Each block was followed by a 4 s fixation (to allow for the fall-off of the hemodynamic response) and was repeated 7 times within the 140-volume scan. Two regions were defined from the biological motion localizer, an STSp region and an inferior temporal sulcus (ITS) region, both of which have been previously implicated in biological motion perception (Thompson et al., 2005).

Subjects also participated in a localizer designed to reveal the human fusiform face area (FFA). Spatially overlapping with

Table 2 – Talairach coordinates for the regions of interest (ROIs). ROIs were identified through independent localizer scans or through the GLM analysis (as reported in the text). Table includes the number of subjects for each hemisphere, the Talairach coordinates for the mean center of mass (with standard deviations across individuals), and the mean number of voxels included in each ROI. DLPFC: dorsolateral prefrontal cortex. IPL: intraparietal sulcus. ITS: inferior temporal sulcus. SF: Sylvian fissure. *Due to the retinotopic nature of MT, only contralateral hMT, hMT+, and hMST+ were defined with the independent locations.

Localizers	Left hemisphere					Right hemisphere				
	Num	X	Y	Z	Voxels	Num	X	Y	Z	Voxels
hMT+	2/2	−50 (2.5)	−62 (0.5)	−3 (3.5)	1070	2/2	45 (4.5)	−67 (4.5)	−1 (.35)	943
STSp	2/2	−53 (0.7)	−61 (4.9)	6 (4.6)	971	2/2	48 (4.2)	−56 (0.5)	8 (0.5)	343
ITS	2/2	−52 (2.0)	−63 (1.0)	−5 (3.0)	620	2/2	43 (7.0)	−63 (3.0)	−11 (1.3)	756
FFA/FBA	3/4	−41 (0.8)	−48 (4.5)	−21 (0.9)	487	4/4	36 (3.0)	−49 (1.5)	−19 (1.3)	774
V1/V2	2/2	−12 (8.0)	−82 (5.5)	−5 (1.7)	884	2/2	7 (4.8)	−83 (0.5)	−6 (0.1)	876
hMT	2/2	−45 (3.0)	−73 (3.5)	−3 (1.5)	579	2/2	49 (6.5)	−69 (7.0)	−2 (1.1)	463
hMST+	2/2	−44 (0.5)	−68 (0.5)	−1 (0.0)	623	2/2	42 (3.5)	−63 (0.2)	−1 (0.2)	480
Linear contrast										
ITS	4/4	−42 (1.0)	−48 (2.7)	−14 (1.7)	783	4/4	42 (2.6)	−55 (3.6)	−14 (1.5)	890
MT+	4/4	−45 (4.0)	−67 (3.6)	−1 (3.5)	964	4/4	43 (3.3)	−63 (5.2)	−1 (2.4)	930
STS	0/4					2/4	61 (2.5)	−29 (6.5)	2 (2.3)	763
STSp	4/4	−46 (4.0)	−55 (6.9)	9 (2.9)	848	4/4	47 (2.7)	−52 (5.1)	12 (1.2)	847
IPL	0/4					2/4	52 (4.0)	−34 (2.5)	21 (1.0)	831
SF	0/4					2/4	4 (1.8)	−64 (15)	32 (1.5)	813
DLPFC	2/4	−45 (0.0)	28 (0.5)	21 (6.5)	497	0/4				

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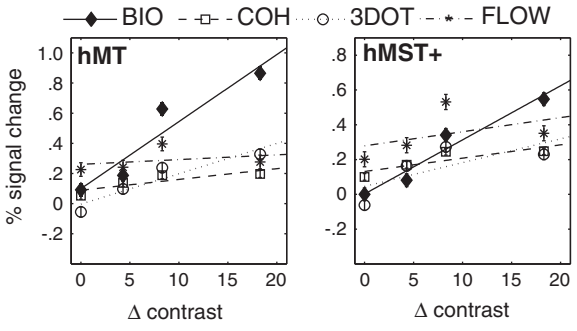

Fig. 6 – BOLD-contrast response functions for the hMT proper and hMST+ subdivisions of the original hMT+ ROI. Signal change calculated as the best-fit beta estimate with baseline normalization. Error bars indicate +/−1 standard error of the mean.

the FFA, the FBA is a ventral temporal brain area involved in the perception of static bodies as compared to common household items (Peelen and Downing, 2005), but also has brain signals correlated with biological motion perception (Grossman et al., 2004; Michels et al., 2005). There are three means by which the FBA has been identified, including using a stationary body localizer, using a traditional biological motion localizer (such as the one we used to identify the STSp), or using a standard FFA localizer. All three of these localizers reveal, with variable efficacy, the same cluster of activity on the fusiform gyrus that is indistinguishable within subjects (Peelen and Downing, 2005). We localized the FFA by showing subjects 18 s blocks of stationary face images, alternated with 18 s blocks of common household objects. Each image subtended 6.6° of visual angle, and was presented for 1 s with a 1 s ISI. Each block was separated by 4 s, and repeated 7 times within the 140-volume scan. The FFA was identified as that region on the fusiform gyrus that responded significantly more strongly to faces than objects (FDR < .05).

4.3.2. *BOLD-contrast response functions*

In addition to the localizer scans, subjects participated in a number of experimental scans designed to estimate the BOLD amplitude, as a function of contrast, for each of our experimental conditions. These scans were independent from those used to generate regions of interest, but were acquired within the same scanning sessions.

The experimental scans proceeded as blocked fMRI experiments with the stimulus conditions blocked by contrast. Measurements were taken at four contrast levels, corresponding to perceptual isoluminance, and 4.3%, 8.3%, and 18.3% contrast increments from isoluminance. Blocks within each run were separated by 4 s fixation intervals, and all scans ended with a 4 s fixation interval to measure the hemodynamic response function associated with the final block. All scans were repeated at least four times.

4.3.3. *Preprocessing and analysis*

For all functional scans, the first four volumes of each scan were discarded to allow for stabilization of the MR signal and the remaining volumes were corrected for within-scan motion in k-space (prospective acquisition correction, Thesen et al., 2000). All subsequent analysis was conducted with Brain Voyager QX (Brain Innovations, Inc.) and with functions written in Matlab (Mathworks). Functional data was corrected for across-scan motion and linear signal drift, then co-registered to each individual's high-resolution anatomical in native brain space.

For the localizer scans, ROIs were defined by correlating the BOLD response to a standard boxcar function shifted in time 4–8 s to compensate for the lag in the hemodynamic response, which varies across subjects and brain areas (e.g., Aguirre et al., 1998; Huettel and McCarthy, 2001). Significance was assessed using the false discovery rate (FDR < .05), which controls the expected proportion of false positives among voxels in which the null hypothesis is rejected (Genovese et al., 2002).

Within each ROI, a within-subject general linear model was applied to the experimental scans to estimate the BOLD amplitude for each stimulus condition, at each contrast level. Regressors were designed from boxcar protocols, convolved with a difference-gamma hemodynamic response function. Signal change was computed as the best-fit beta estimate, with baseline normalization. The BOLD-contrast response functions were fitted with linear regression lines, and to test for contrast-dependence, we computed a statistical contrast for each ROI, and each condition, that linearly weighted each contrast level. The resulting t-scores are shown in Supplemental Tables 1 and 2, with the corresponding p-values, Bonferroni corrected for family-wise false-positive error rates. For all tasks, perceptual isoluminance (0% contrast) renders motion extremely difficult to perceive, and thus subjects were not able to maintain threshold task performance. This is to be expected based on previous findings (Bilodeau and Faubert, 1999; Wuerger and Landy, 1993) and therefore all statistical tests of the BOLD-contrast response slopes were computed using 5%, 10% and 20% contrast only.

Because the ROI analysis is 'blind' to activity outside of the predefined regions of cortex, we conducted a second (though not statistically independent) analysis on the entire brain using the same linear model (with equal weights on each condition). This analysis was computed for the biological motion condition (Fig. 4) and for the coherent and collinear triad conditions (Supplemental Fig. 2). These statistical maps reveal those voxels that significantly increase in amplitude for each of our conditions.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.brainres.2012.05.034.

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