

Neuronal Basis of the Motion Aftereffect Reconsidered

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Summary

Several fMRI studies have reported MT+ response increases correlated with perception of the motion aftereffect (MAE). However, attention can strongly affect MT+ responses, and subjects may naturally attend more to the MAE than control trials without MAE. We found that requiring subjects to attend to motion on both MAE and control trials produced equal levels of MT+ response, suggesting that attention may have confounded the interpretation of previous experiments; in our data, attention accounts for the entire effect. After eliminating this confound, we observed that direction-selective motion adaptation produced a direction-selective imbalance in MT+ responses (and earlier visual areas), and yielded a corresponding asymmetry in speed discrimination thresholds. These findings provide physiological evidence that population level response imbalances underlie the MAE, and quantify the relative proportions of direction-selective neurons across human visual areas.

Introduction

The motion aftereffect (MAE) occurs when prolonged viewing of motion in one direction makes subsequently viewed stationary stimuli appear to move in the opposite direction. This well-known, engaging illusion is believed to reflect the adaptation of direction-selective neurons in visual cortex. Models of the MAE hypothesize that the direction specificity of the MAE percept (e.g., rightward adaptation yields a leftward MAE) results from an imbalance in the post-adaptation responsiveness of different subpopulations of direction-selective neurons (Mather, 1980; Mather and Harris, 1998; Sutherland, 1961). For example, rightward adaptation decreases the responsiveness of rightward-selective neurons, with little or no effect on the responsiveness of leftward-selective neurons. Following adaptation, a stationary test pattern will evoke larger responses in the unadapted leftward-selective neurons than in the adapted rightward-selective neurons, yielding a percept of leftward motion.

Single-unit electrophysiology experiments suggest that the responses of some direction-selective neurons are affected in direction-specific ways by motion adaptation. Responses of direction-selective neurons are depressed by unidirectional motion in their preferred direction, with little or no effect of prolonged motion in the

opposite direction. This has been observed in rabbit retina (Barlow and Hill, 1963), cat primary visual cortex (Giaschi et al., 1993; Hammond et al., 1985, 1986, 1988; Marlin et al., 1988; Saul and Cynader, 1989; Vautin and Berkley, 1977; von der Heydt et al., 1973), owl monkey MT (Petersen et al., 1985), and macaque MT (van Wezel and Britten, 2001) an extrastriate area widely believed to play a central role in motion perception (Albright, 1993).

Several recent neuroimaging experiments have reported response increases during the MAE (Culham et al., 1999; Hautzel et al., 2001; He et al., 1998; Taylor et al., 2000; Tootell et al., 1995a). In these experiments, activity was measured in human MT+ (also known as V5), believed to be homologous to macaque areas MT and MST. Responses were larger during the MAE (e.g., after prolonged unidirectional motion) than during a control condition without MAE (e.g., after alternating direction motion). Furthermore, the response time course was correlated with the time course of the perceptual aftereffect (Culham et al., 1999; He et al., 1998; Tootell et al., 1995a).

However, the response increases previously observed in MT+ cannot unambiguously be interpreted as the effects of adaptation per se, and may instead reflect attention to the aftereffect (in this paper, we use the term “attention” to encompass both selective attention and nonspecific effects of arousal). Our reasoning is as follows. First, the MAE is an engaging illusion; when subjects perceive illusory motion (e.g., MAE trials), they may attend to the stimulus more strongly than when no motion is perceived (e.g., control trials). Second, previous fMRI MAE experiments were performed under viewing conditions without explicit attentional control, so subjects were free to allocate attention differentially between MAE and control trials. Third, attention can increase MT/MT+ responses.

To separate the effects of attention from adaptation, we measured fMRI responses during the MAE under conditions of both passive viewing and directed attention. Under passive viewing conditions (similar to those used in previous fMRI studies), MT+ responses were larger during the MAE. However, under conditions of directed attention (when subjects were required to perform a threshold-level task on the motion of the stimulus), MT+ responses were equally large on MAE and control trials. This result suggests that the response increases observed in previous fMRI experiments may have been due to attention to the aftereffect.

After identifying and eliminating this attentional confound, we performed two complementary tests for direction-selective adaptation. In the first experiment, subjects were adapted to one direction of motion, and then viewed test stimuli moving in either the adapted direction or the direction opposite that of adaptation. Direction-selective adaptation was observed in MT+, V1, and V2, and simultaneously collected psychophysical data revealed a complementary direction-selective asymmetry in perceptual speed sensitivity. In the second experiment, fMRI responses were measured during repeated

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presentations of a stimulus moving in a single direction, and compared to responses when the direction of stimulus motion varied from trial to trial. Robust direction-selective adaptation was observed in MT+ as well as in earlier visual cortical areas.

We interpret our results as evidence that (1) motion adaptation yields a direction-selective decrease in the responses of neurons selective for the adapted direction of motion; and (2) previous neuroimaging MAE experiments confounded this adaptation-induced response decrease with a response increase caused by attention to the illusory percept of motion during the MAE. These findings challenge the notion that the perception of motion is necessarily correlated with a net increase in MT+ activity. Instead, our results confirm that the MAE reflects an imbalance in the relative responses of subpopulations of neurons with different direction preferences. In addition, our results suggest that a particularly high proportion of neurons in human MT+ are direction selective, the defining characteristic of neurons in macaque MT and MST.

Results

Separating Attention from Adaptation

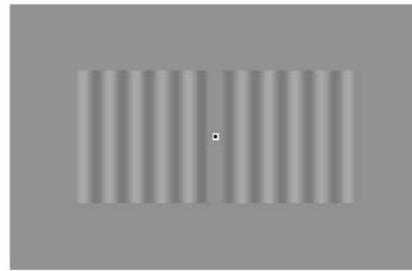
We begin by demonstrating the confounding effects of attention on the interpretation of fMRI measurements of motion adaptation and the MAE.

Passive Viewing versus Directed Attention

Under conditions of passive viewing, we replicated previous fMRI reports of MAE-related MT+ increases. Each trial in this experiment consisted of four periods: adapting motion, blank storage, stationary test, and blank rest (Figure 1). This storage protocol (similar to that used by He et al., 1998) with long blank periods allowed us to separate responses to the stationary test stimulus from responses to the moving adaptor because the blank periods were long enough to allow the hemodynamic response to return close to baseline. In each fMRI scan, subjects viewed a counterbalanced sequence of MAE and control trials. On MAE trials, both the left and right gratings moved inward toward the fixation point for the duration of the adapting motion period. On control trials, the gratings alternated their direction of motion (inward/outward) every 0.5 s to avoid direction-specific adaptation. After the storage period, the stationary test gratings appeared to move (drifting outward, exhibiting a MAE) on MAE trials but were veridically perceived as stationary (no MAE) on control trials.

In accord with the results of previous fMRI studies, MT+ responses during the test period were larger on MAE trials than on control trials. Figure 2 shows a representative MT+ time series during the test period from subject ACH, as well as MT+ response amplitudes for all three subjects. The response amplitudes demonstrated a significantly larger MT+ response during the MAE for all subjects (ACH, $p < .00005$; ARW, $p < .01$; BTB, $p < .05$; 2-tailed t test). On average, MT+ amplitudes were 42% larger on MAE than control trials. We were therefore able to replicate the pattern of results described in previous MAE experiments in every subject. Although some other visual areas in some subjects exhibited similar trends, no area other than MT+ showed

A



B



Figure 1. Stimulus and Protocol for Passive Viewing versus Directed Attention Experiment

(A) Stimulus. Pair of 10° square patches to the left and right of a central fixation square, separated by 1°. (B) Trial structure. Each trial consisted of 25.5 s of adapting motion, 18 s blank, 5 s test stimulus, and 19 s blank. On MAE trials, the adapting gratings drifted inward toward fixation for the entire 25.5 s motion period; thus, the test stimulus appeared to drift outward (“out”). On control trials, the adapting gratings reversed their direction of motion at 2 Hz, so the test stimulus appeared stationary (“stat”). During directed attention scans, a very slight (~0.06°/s) speed increment was added to one of the gratings.

a statistically reliable difference in at least two of the three subjects. We emphasize our efforts to maximize the strength of the perceptual aftereffect: stimulus parameters were optimized based on extensive psychophysical pilot studies, the adaptation direction was the same throughout each scanning session, subjects were instructed to attend carefully to the adaptation stimulus, and subjects confirmed that they had experienced a strong perceptual MAE.

We then repeated our measurements under conditions of directed attention. If increased attention during the MAE trials was actually driving the observed increase in response, then forcing subjects to pay equal attention to MAE and control trials should reduce or eliminate the response difference. To equate attention during the corresponding test periods of MAE and control trials, we instructed subjects to perform a sequence of 2-alternative forced-choice speed discriminations during the 5 s test period of all trials. During MAE trials, both gratings appeared to drift outward (due to the MAE); the grating with the threshold-level physical motion added to it appeared to move very slightly faster. During control trials, both gratings appeared approximately stationary (because there was no MAE), but the grating with the slight motion increment sometimes appeared to move very slightly outward.

Requiring subjects to perform this task on both MAE and control trials allowed us to dissociate the effects of attention from those of adaptation by (1) equating

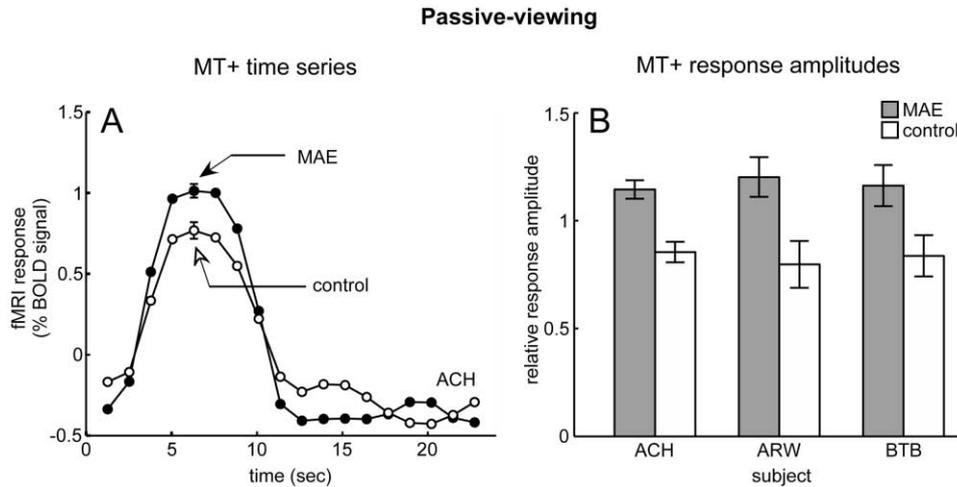


Figure 2. MT+ Responses during Passive Viewing Were Larger for MAE than for Control Trials

(A) Sample time series from MT+ of one subject. Responses during MAE trials (filled symbols) and control trials (open symbols), subject ACH. Error bars represent ± 1 SEM of a single time point across repeated trials; SEMs were similar for all time points. Note that data are plotted in terms of percent change about the mean, so it is necessary to consider the peak-to-trough amplitudes corresponding to MAE and control trials; simply comparing the heights of only the peaks will underestimate the difference between the two conditions. (B) Response amplitudes for all subjects. Dark bars, MAE trials; light bars, control trials. Error bars represent ± 1 SEM across repeated trials. Note that amplitudes are normalized within each subject to have mean = 1 (see Experimental Procedures).

psychophysical performance (as a proxy for equating attention) between MAE and control trials, while (2) retaining the perceptual difference between MAE trials (compelling percept of illusory motion) and control trials (no clear percept of motion). Behavioral responses were collected in the scanner to confirm that subjects were performing the task at threshold difficulty levels on both MAE and control trials (Table 1). The physical motion of the gratings was extremely slow (speed increments of $\sim 0.06^\circ/\text{s}$). Because subjects were at psychophysical threshold ($\sim 75\%$ correct), they reported that it was often difficult to discern the presence of motion on control trials and the speed difference on MAE trials, and that they often felt that they were guessing to perform the task.

Directing attention by requiring subjects to perform this task removed all significant differences in MT+ responses (Figure 3); when subjects were required to attend equally to MAE and control trials (as opposed to being allowed to naturally attend more strongly to the MAE), MT+ responses were not significantly different (ACH, $p = .48$; ARW, $p = .21$; BTB, $p = .99$, 2-tailed t test). A repeated measures ANOVA confirmed that the pattern of MT+ responses was significantly different for passive viewing and directed attention: that the large

difference between MAE and control responses observed during passive viewing was smaller during directed attention ($F_{1,105} = 11.681, p = .001$; i.e., significant trial type \times viewing condition interaction), and that there were no significant individual differences in this pattern of results ($F_{2,105} = .392, p = .68$; ns subject \times trial type \times viewing condition).

The observed similarity of responses on MAE and control trials under conditions of directed attention does not simply reflect low statistical power. In an effort to optimize our ability to detect a small difference between MAE and control trials, we collected a large number of repeated measures (30–60) of each trial type within each of three subjects, as compared to previous neuroimaging experiments which comprised ~ 2 –8 repetitions of each trial type in each of ~ 5 –12 subjects. We emphasize that our design was powerful enough to clearly replicate the passive viewing difference between MAE and control trials in every subject. Yet, under directed attention, no subjects showed a marginally significant difference between MAE and control trials. Furthermore, no significant individual differences were observed between subjects (see above).

We piloted several variants of these experiments and each time observed a similar pattern of results: MT+

Table 1. Psychophysical Performance during the Directed Attention fMRI Experiment

Subject	Trial Type			
	MAE		Control	
	Speed ($^\circ/\text{s}$)	% Correct	Speed ($^\circ/\text{s}$)	% Correct
ACH	0.058	67	0.060	75
ARW	0.066	87	0.064	61
BTB	0.058	75	0.054	82

Speed increment ($^\circ/\text{s}$) and % correct performance for each subject.

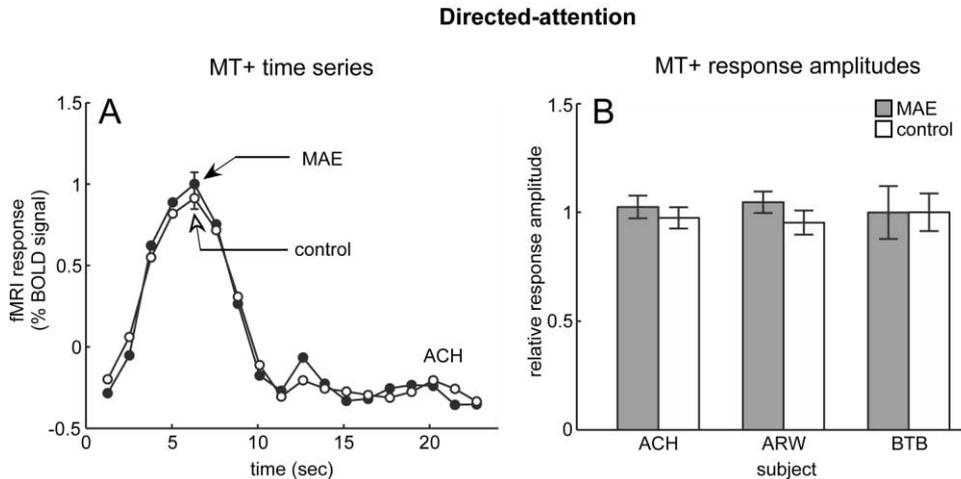


Figure 3. MT+ Responses during Directed Attention Did Not Differ Significantly on MAE and Control Trials Same format as Figure 2. (A) Sample time series (subject ACH). (B) Response amplitudes (all subjects).

responses were not significantly different on MAE and control trials. First, we instructed the subject to perform the same speed discrimination task but on a brief (0.5 s) test stimulus. Second, we instructed the subject to perform a threshold-level contrast discrimination task on the brief (0.5 s) test stimulus. Third, we instructed subjects to perform a speed discrimination task on a moving test stimulus ($\sim 8^\circ/\text{s}$ presented for 5 s). In each variant, results were comparable to those in the main experiment.

fMRI Saturation Control

The interpretation of our results is not confounded by saturation of the fMRI responses. Response amplitudes were larger during directed attention than during passive viewing. In fact, the main effect of directed attention was to increase the responses on control trials (compare Figures 2A and 3A, open symbols). If task performance had increased the hemodynamic responses to the point of saturation, it would not have been possible to observe a difference between MAE and control trials. This was unlikely because our test stimulus (stationary low contrast gratings) was not as effective at evoking responses in human MT+ as compared, for example, to full contrast moving dot fields (Chawla et al., 1998, 1999a; Huk and Heeger, 2000). Even so, we performed an additional control experiment to test for response saturation by interspersing two types of test trials: (1) moving (alternating inward/outward) 100% contrast gratings; and (2) stationary 20% contrast gratings (exactly like those in the main directed attention experiment). For both trial types, subjects performed threshold speed discrimination judgments. MT+ responses to the high contrast moving test stimuli were $\sim 70\%$ larger than responses to the low contrast stationary test stimuli ($p \approx 0$, 2-tailed t test). Thus, while directing attention caused an increase in the MT+ responses on control trials, there was still ample headroom in the fMRI signal to observe a further response increase induced by the MAE, if there had been one.

The results of this saturation control experiment also demonstrate that the addition of the slight speed incre-

ments cannot by themselves account for the differences between the directed attention and passive viewing results. The speed increments were added to both MAE and control trials. Given that MT+ activity was not saturated, responses could have increased due to the added speed increments on both MAE and control trials.

One might be concerned, nonetheless, that there was a slight physical motion in our directed attention experiment. There would indeed be cause for concern if MT+ responses were equally large whenever motion was perceived, be it caused by illusory motion of a stationary stimulus or by physical motion of a slowly moving stimulus. However, this proposition assumes that net MT+ activity is essentially binary, indicating the presence or absence of perceived motion. Such a characterization of MT+ activity is clearly inconsistent with the known (graded) responses of both macaque MT and human MT+ (Britten et al., 1993; Rees et al., 2000; Tootell et al., 1995b).

MAE Speed-Matching Psychophysical Experiment

In addition to the psychophysical data collected during the directed attention fMRI experiments, we performed a separate psychophysical experiment outside the scanner to confirm subjects' subjective reports of strong perceptual MAEs during our fMRI experiments. The strength of the MAE was measured under viewing conditions matched to those in the scanner, using a speed matching protocol with various storage period durations (see Experimental Procedures). Subjects perceived a strong MAE for all storage durations. After a 0.5 s storage period, perceived MAE speed was $0.63^\circ/\text{s}$, after 18 s of storage, the perceived speed was $0.44^\circ/\text{s}$, and after 30 s of storage, the perceived speed fell to $0.29^\circ/\text{s}$. These robust MAE speeds after 18 s of storage are consistent with previous measurements of MAE duration after considerable storage periods (Thompson and Wright, 1994; Verstraten et al., 1994).

Direction-Selective Adaptation

Having demonstrated that it is necessary to separate attentional effects from the effects of adaptation, we

performed a pair of experiments to test for direction-selective adaptation using two complementary adaptation protocols, both performed under conditions of directed attention.

Adapted versus Opposite Direction Experiment

To test for direction-selective adaptation, we compared responses to a brief test stimulus that moved in either the same direction as an adaptation stimulus or opposite the direction of adaptation. A test stimulus that moves in the same direction as adaptation will elicit a response primarily in neurons that have just been adapted, while a test stimulus moving in the opposite direction will elicit a response primarily in neurons that have not been adapted. Therefore, if adaptation is direction selective, we should observe a stronger response to an opposite direction test than to an adapted direction test.

We employed a block alternation protocol to compare responses to opposite direction and adapted direction test stimuli. After an initial 30 s adaptation period, subjects viewed an alternating sequence of three opposite direction trials followed by three adapted direction trials (Figure 4A). Each trial consisted of 4 s of top-up adaptation followed by a 0.5 s moving test stimulus. On opposite direction trials, the test stimulus moved in the direction opposite that of adaptation; on adapted direction trials, the test stimulus moved in the same direction as adaptation. This repeated sequence of top-up adaptation followed by a brief test trial allowed us to keep the adaptation state relatively constant during each scan. To control attention and to test for a perceptual effect of adaptation, subjects performed a speed discrimination task on each trial during the course of each fMRI experiment.

Direction-selective adaptation in MT+ was evident in all three subjects, with responses to opposite direction test blocks significantly larger than adapted direction blocks (ACH, $p < .005$; ARW, $p < .01$; DJH, $p < .01$; 2-tailed t test, Figure 4B). Additionally, direction-selective adaptation was observed for two of the three subjects in V1 (ACH, $p < .0001$; ARW, $p < .00005$) and V2 (ACH, $p < .05$; ARW, $p < .0005$). These results provide evidence that neurons in human MT+, as well as in V1 and V2, are direction selective, and imply that the subset of direction-selective neurons that had responded most strongly to the adapting motion showed relatively smaller responses after adaptation than neurons with the opposite direction preference.

To properly interpret the absolute magnitude of the mean amplitudes (which ranged from 0.035 to 0.081), it is important to recognize that adapted and opposite direction trials were identical except for the direction of motion of the test stimulus. The duration of the test stimulus (0.5 s) was short relative to the trial duration (6 s), so that the effective duty cycle was only 1/12th of the block alternation period. After scaling the responses by 12 to compensate for the small duty cycle, the average response amplitudes in MT+ ranged from 0.41 to 0.97 across the three subjects. Although this correction assumes linearity of the hemodynamic response (scaling the duty cycle scales the response by the same factor), the resulting scaled response amplitudes are within a factor of two of those observed in our second direction-selective adaptation experiment (see Table 3).

Adaptation improved psychophysical performance in

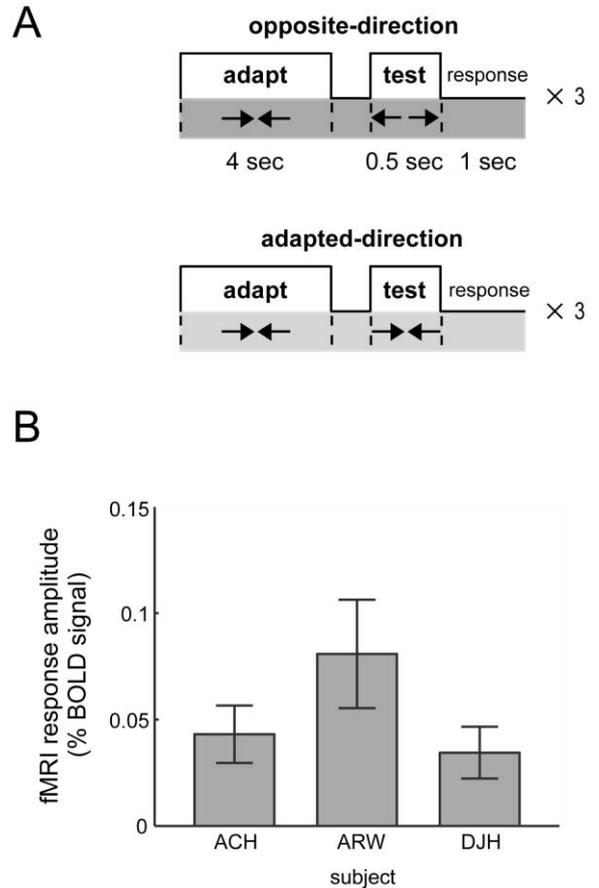


Figure 4. Adapted versus Opposite Direction Experiment (A) Trial and scan design. Each trial consisted of 4 s of adaptation, 0.5 s blank interstimulus interval, 0.5 s moving test stimulus, and 1 s response period. On opposite direction trials, the test stimulus drifted in the direction opposite that of adaptation (e.g., inward adaptation, outward test). On adapted direction trials, the test stimulus drifted in the same direction as the adapting motion (e.g., inward adaptation, inward test). Equal numbers of inward and outward adaptation scans were performed for each subject in separate scanning sessions. (B) Direction-selective adaptation produces a response asymmetry in MT+. Responses were larger to opposite direction blocks than to adapted direction blocks. Height of bar indicates magnitude of fMRI response difference in MT+ for each subject. Error bars correspond to ± 1 SEM across repeated scans.

a direction-selective manner (Table 2); speed-discrimination thresholds (measured during the fMRI scans) were lower for adapted direction than for opposite direction test stimuli (ACH, $p < .005$; ARW, $p < .05$; DJH, $p < .05$; bootstrapped comparison of same and opposite direction trials). This direction-selective psychophysical effect is a behavioral correlate of our finding of direction-selective adaptation in cortical activity, as well as confirmation that our stimulus conditions elicited strong perceptual adaptation effects. This finding complements recent reports of enhanced speed sensitivity following motion adaptation (Bex et al., 1999; Clifford and Wenderoth, 1999), demonstrating the direction selectivity of these sensitivity changes.

Adapted versus Mixed Direction Experiment

As a complementary test for direction selectivity, we adopted a protocol developed by Grill-Spector et al.

Table 2. Psychophysical Thresholds Measured during the Adapted versus Opposite Direction fMRI Experiment

Subject	Trial Type	
	Adapted Direction	Opposite Direction
	Speed Increment (%)	Speed Increment (%)
ACH	4.3	6.9
ARW	7.3	9.1
DJH	6.6	9.3

Threshold (% speed increment) estimated from an adaptive staircase run during the fMRI experiment. Note that speed thresholds are lower on adapted direction than on opposite direction trials for all subjects.

(1999) for measuring the effects of adaptation with fMRI. Under conditions of directed attention, we compared fMRI responses during blocks of trials in which the stimulus repeatedly moved in a single direction with blocks in which the stimulus direction varied from trial to trial. When a stimulus moves rightward, for example, the net population response is driven primarily by the strong responses of the subpopulation of rightward-selective neurons. After continued rightward motion, the responses of these rightward-selective neurons would be expected to decrease due to direction-selective adaptation, and thus the population response would also decrease. If the stimulus then changed direction, perhaps moving upward, the population response would then be driven by upward-selective neurons that were not adapted, and so the population response would rebound, rising back to a pre-adapted level.

We applied this logic to test for direction selectivity. After an initial adaptation period (39 s), subjects viewed alternating adapted direction and mixed direction blocks of trials (Figure 5A). During adapted direction blocks, the stimulus moved in the same direction on each trial; during mixed direction blocks, the direction of stimulus motion was randomly selected on each trial from a set of six possible directions ($\pm 45^\circ$, 90° , and 135° away from the direction of motion in adapted direction blocks). Subjects again performed a speed discrimination task on each trial to control attention.

Strong direction-selective adaptation was evident in MT+ for all subjects, with larger responses during mixed direction blocks than adapted direction blocks ($p < 10^{-5}$, Figure 5B). Direction-selective adaptation was also present in earlier visual areas including V1 (e.g., $p \leq .05$ for V1 across subjects), although the absolute magnitudes of these effects were considerably smaller than in MT+ (Table 3). To properly compare the strength of these adaptation effects, it is necessary to take into account possible differences in baseline responsivity across different individuals and across visual areas. We therefore defined a "direction selectivity index," which we computed as the ratio of the mean response from the adaptation scans to the mean response elicited during a separate series of baseline scans (Figure 5C). In these baseline scans, the stimulus alternated between 18 s of moving dots (alternating direction every 1 s, displayed in apertures identical to those in the adaptation scans) and 18 s of a blank screen.

The direction selectivity index was much larger in

MT+ than in any other visual area (Figure 5D). V3A showed the next strongest effect of direction-selective adaptation, consistent with previous reports of strong motion responsivity (Smith et al., 1998; Tootell et al., 1997). Area V4v showed strong direction selectivity, contrary to some theories of the functional specialization of this area. Other early visual areas (V1, V2, V3) exhibited smaller direction-selective adaptation effects, despite responding robustly during the baseline scans. Thus, direction-selective adaptation was strongest in MT+, consistent with the high proportion of direction-selective neurons in macaque MT (Maunsell and Van Essen, 1983; Zeki, 1974).

Discussion

Taken together, our results suggest that (1) motion adaptation decreases the responses of direction-selective neurons selective for the adapted direction of motion; and (2) previous neuroimaging MAE experiments have confounded the direction-selective response decrease caused by adaptation with a response increase caused by attention to the MAE percept.

Reinterpretation of Previous Neuroimaging MAE Experiments

Previous neuroimaging experiments did not attempt to control attention. Tootell et al. (1995a) showed that the time course of the fMRI responses in MT+ correlated with the time course of the nulling speed of the MAE. Culham et al. (1999) observed that MT+ responses increased even when a storage period was inserted between the adaptation and test periods. He et al. (1998) demonstrated that MT+ responses rose and fell as the test stimulus was placed inside or outside an adapted subportion of the visual field. Tootell et al. (1995a) and He et al. (1998) performed measurements under passive viewing conditions, while Culham et al. (1999) and Taylor et al. (2000) had subjects indicate when the perceptual MAE ended; similarly, Hautzel et al. (2001) instructed subjects to indicate when a perceptual MAE was present. Note that these duration estimation or aftereffect detection tasks, if anything, could exaggerate the attentional difference between MAE and control trials. On MAE trials, subjects needed to attend for several seconds to judge the end of the aftereffect. On control trials, no MAE occurred, so there was less time devoted to making the judgment.

The MAE is a compelling perceptual experience that draws attention. As the MAE weakens over time, returns after storage, or alternately appears and disappears based on the location of the test stimulus, subjects not under attentional control would likely attend more strongly when the MAE was perceived than when it was absent or weak. We observed MT+ response increases only when subjects were not performing a threshold-level task, and hence were free to attend more strongly during MAE than control trials. The attention that an unconstrained observer may direct toward the stimulus during the MAE does not cause the illusory percept of motion; rather, attention is increased given that the MAE percept is already occurring.

When Tootell et al. (1995a) first reported MAE-related

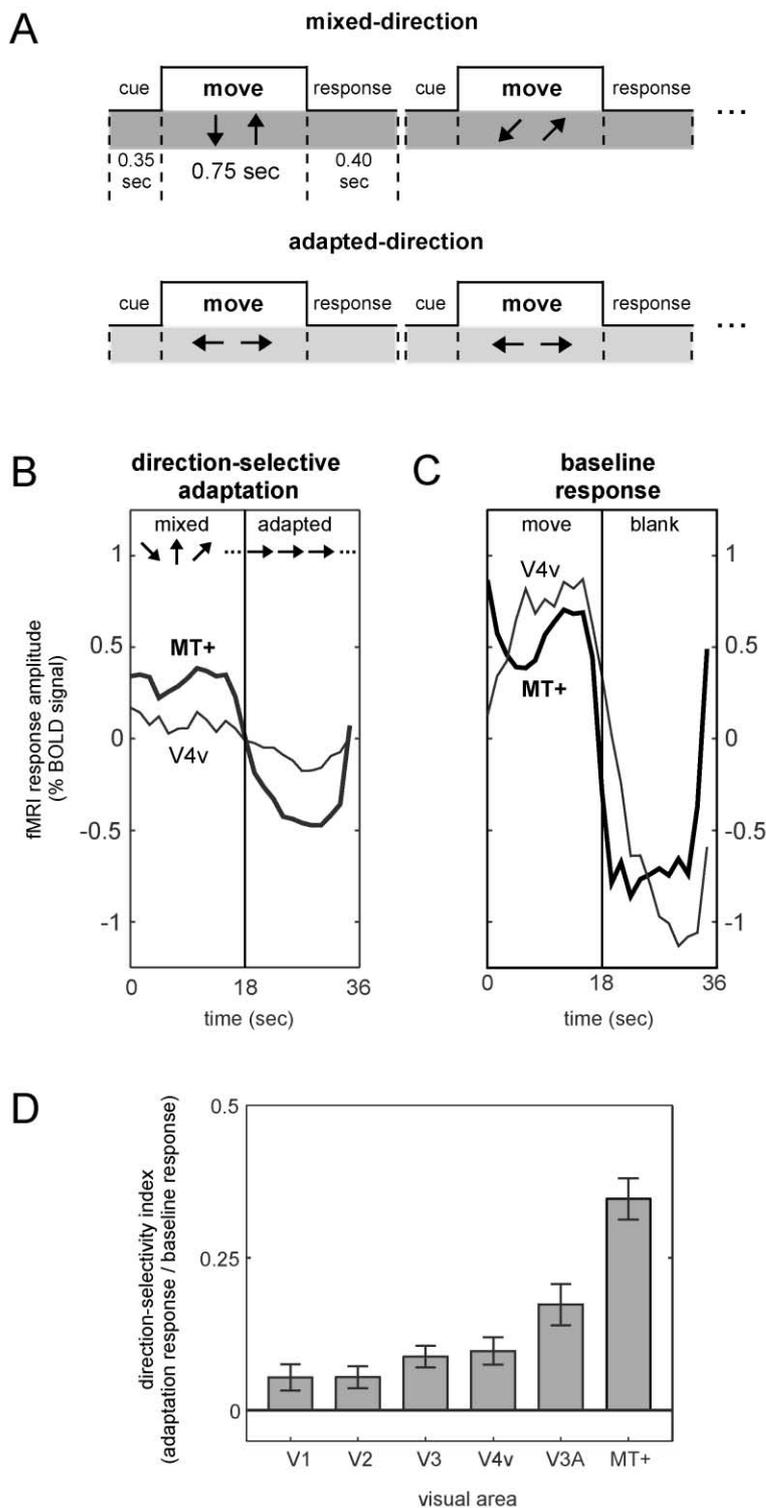


Figure 5. Adapted versus Mixed Direction Experiment

(A) Trial and scan design. Each trial consisted of a 0.35 s cue period (arrows, indicating the upcoming direction of motion of the corresponding dot patch), 0.75 s moving stimulus, and 0.40 s response period. Each scan consisted of 7 alternating blocks of 12 adapted direction trials followed by 12 mixed direction trials. The directions of the dots on each mixed direction trial were chosen pseudorandomly (possible directions were $\pm 45^\circ$, $\pm 90^\circ$, and $\pm 135^\circ$ from direction of motion in the adapted direction block). (B) Direction-selective adaptation. Average time series during adapted versus mixed direction experiment (subject ACH). MT+ responses (thick line) were much larger during mixed than during adapted direction blocks, suggesting strong direction-selective adaptation. V4v responses (thin line) modulated only slightly, in comparison to MT+. (C) Baseline responses. Average time series during baseline experiment (subject ACH). Responses in both MT+ and V4v modulated strongly as stimulus alternated between moving dots and a blank field. (D) Direction selectivity index. Direction-selective adaptation was strongest in MT+, but evident to a lesser degree across other visual areas. Index was computed as the mean response amplitude during adapted versus mixed direction scans divided by the mean response amplitude during baseline scans. Height of bars indicates the average direction selectivity index for each visual area (geometric mean across subjects). Error bars indicate ± 1 SEM across subjects.

responses in MT+, the effects of attention on human MT+ responses were not well established. In fact, the large attentional effects demonstrated in the following years came as a surprise to the field. Single-unit and neuroimaging experiments since 1995 have shown that that directed spatial attention can increase responses in human MT+ and monkey MT (Brefczynski and DeYoe,

1999; Gandhi et al., 1999; Somers et al., 1999; Treue and Maunsell, 1996, 1999), and featural attention to motion (as compared to contrast, shape, or color) can selectively increase responses in MT+ and monkey MT (Beauchamp et al., 1997; Buchel et al., 1998; Chawla et al., 1999b; Corbetta et al., 1990, 1991; Huk and Heeger, 2000; O'Craven et al., 1997; Treue and Martinez Trujillo,

Table 3. Response Amplitudes in Adapted versus Mixed Direction Experiment

Subject	Visual Area					
	MT+	V1	V2	V3	V4v	V3A
ACH	0.44	0.11	0.08	0.15	0.11	0.23
ARW	0.33	0.14	0.13	0.13	0.12	0.23
DJH	0.26	0.11	0.08	0.12	0.11	0.15

Average fMRI response (% BOLD signal change) in each visual area for each subject.

1999). The attentional effects, as measured with fMRI, can be quite substantial compared to stimulus-evoked responses (Huk and Heeger, 2000; Kastner et al., 1999; Ress et al., 2000; Scannell and Young, 1999; Somers et al., 1999); in our data, attention appears to account for the entire difference between MAE and control trials.

It is difficult to directly interpret the previous neuroimaging results in terms of the responses of direction-selective neurons. These experiments employed “control” trials with alternating direction motion during the adaptation period (no single-unit studies have used a comparable control condition). Although alternating direction motion did not produce a perceptual MAE with a stationary test stimulus, it may nonetheless have adapted two subpopulations of neurons. Indeed, the results of a psychophysical study using transparent motion adaptation and dynamic test patterns suggest that bidirectional motion can adapt multiple pools of direction-selective neurons (Grunewald and Lankheet, 1996). Instead of comparing adaptation with no adaptation, the fMRI experiments may have compared unidirectional adaptation with bidirectional adaptation.

Importance of Controlling Attention in fMRI Experiments

Our findings underscore the importance of performing fMRI experiments under conditions of controlled attention. Because increases in attention may reflect small changes in the baseline firing rates of a large number of neurons, fMRI measurements can potentially be dominated by attention and/or nonspecific arousal effects, instead of stimulus or adaptation-related activity (Chawla et al., 1999b; Huk and Heeger, 2000; Kastner et al., 1999; Ress et al., 2000; Scannell and Young, 1999). We suggest that neuroimaging experiments employ designs in which subjects continuously perform an attentionally demanding task throughout the experiment. Different blocks or trial types should employ the most similar tasks possible, at matched threshold-level difficulty.

Models of Direction-Selective Adaptation

Our results demonstrate that motion adaptation decreases the responses of the subpopulation of direction-selective neurons that respond strongly to the direction of adapting motion. Models of the motion aftereffect (Mather, 1980; Mather and Harris, 1998; Sutherland, 1961) posit that the illusion reflects an adaptation-induced anisotropy (or “distribution shift”) of the population response, caused primarily by a decrease in the

Table 4. fMRI Pulse Sequence Parameters

Passive Viewing versus Directed Attention						
Subject	T	TR	NA	TE	FA	FOV
ACH	1.5	750	2	40	65	240
BTB	1.5	750	2	40	65	240
ARW	3	750	2	30	55	220
Direction-Selective Adaptation						
Subject	T	TR	NA	TE	FA	FOV
ACH	3	750	2	30	65	220
ARW	3	750	2	30	65	220
DJH	3	750	2	30	65	220

T = field strength (Tesla), TR = repetition time (ms), NA = number of interleaved acquisitions per image, TE = echo time (ms), FA = flip angle (deg), FOV = field of view (mm). Slice orientation was axial for passive viewing versus directed attention and adapted versus opposite direction experiments. Slice orientation was coronal for adapted versus mixed direction and baseline responsivity experiments. In all experiments, the effective inplane pixel size was 3.2×3.2 mm and the slice thickness was 4 mm.

responses of neurons with preferred directions similar to that of adaptation. Given recent evidence that fMRI signals are linked to the average neural activity within a cortical region (Heeger et al., 2000; Logothetis et al., 2001; Rees et al., 2000), our measurements serve as a population-level confirmation of these theoretical models. Direction-selective adaptation was strongest in MT+ but was also evident to varying degrees in earlier visual areas, including V1. Such a distributed pattern of response changes is consistent with psychophysical evidence suggesting multiple (striate and extrastriate) loci of adaptation (Wenderoth et al., 1988), as well as with the adaptation effects observed in single-unit measurements in primary visual cortex (Giaschi et al., 1993; Hammond et al., 1985, 1986, 1988; Marlin et al., 1988; Saul and Cynader, 1989; Vautin and Berkley, 1977; von der Heydt et al., 1973), owl monkey MT (Petersen et al., 1985), and macaque MT (van Wezel and Britten, 2001).

In summary, previous neuroimaging demonstrations of a population-level increase in MT+ responses are unlikely to provide a characterization of the specific neuronal signals related to the MAE. Instead, the direction selectivity of the aftereffect requires an explanation in terms of relative changes in responsiveness between subpopulations of neurons with different direction tunings. Our measurements using moving test stimuli confirm that adaptation causes a directional imbalance in the population response of several visual cortical areas.

Linking MT Responses and the Perception of Motion

There are many lines of evidence linking neuronal signals in macaque MT/human MT+ with various aspects of motion perception (e.g., Beckers and Zeki, 1995; Goebel et al., 1998; Hotson et al., 1994; Parker and Newsome, 1998; Smith et al., 1998; Vaina et al., 1999; Zeki et al., 1993; Zihl et al., 1983). Changes in the population response in MT/MT+ should have implications for motion perception, but a net increase in activity is only one such possible change (e.g., Treue et al., 2000). None of the computational models of motion perception require

that every percept of motion be accompanied by a net increase in MT/MT+ response. Rather, most models hypothesize that a percept of motion is encoded by a relative difference between the responses of neurons with different direction preferences (Mather, 1980; Mather and Harris, 1998; Simoncelli and Heeger, 1998).

Direction Selectivity and MT/MT+ Homology

The case for homology between monkey MT and human MT+ rests upon its general location with respect to other identified visual areas in both species, its cytoarchitecture, and its heightened sensitivity to visual motion in comparison to other visual areas (Demb et al., 1998; Tootell et al., 1995b; Tootell and Taylor, 1995; Watson et al., 1993; Zeki et al., 1991). In the monkey, however, the primary physiological signature of MT is direction selectivity measured at the single neuron and columnar level (Albright et al., 1984; Maunsell and Van Essen, 1983; Zeki, 1974). No single neuron or columnar level observations have yet been made for human MT+. One previous neuroimaging study has provided evidence for direction-selective interactions in MT+ based on fMRI measurements of motion opponency (Heeger et al., 1999). Our finding of direction-selective adaptation provides clear evidence that MT+, like monkey MT, processes direction-selective signals. Additionally, our results suggest that direction-selective neurons are present in other visual areas to varying degrees: V3A is strongly direction-selective, while V1, V2, V3, and V4v appear to have smaller subpopulations of direction-selective neurons. We emphasize that fMRI adaptation studies (Grill-Spector et al., 1999), performed under conditions of controlled attention, can reveal the selectivities of subpopulations of neurons in the human brain, even when those neurons are intermingled at a spatial scale that is finer than the spatial sampling resolution (voxel size) of the fMRI measurements.

Experimental Procedures

General

Subjects

fMRI and psychophysical data were collected in four subjects, males, ages 25–39, all with normal or corrected-to-normal vision. All were experienced psychophysical observers, subject ARW was naïve as to the hypothesis of the passive viewing versus directed attention experiment. The experiments were undertaken with the written consent of each subject, and in compliance with the safety guidelines for MR research.

Data Acquisition

Each subject participated in several scanning sessions: one to obtain a high-resolution anatomical volume, one to identify MT+, one to identify the retinotopically organized cortical visual areas, several to measure motion adaptation, and one to measure baseline responses.

MR imaging was performed using either a clinical 1.5T GE or 3T GE scanner, using a custom-designed dual surface coil. A bite bar stabilized subjects' heads. Subjects viewed the stimuli while a time series of fMRI volumes were acquired every 1.5 s using a T2*-sensitive, spiral-trajectory, gradient-echo pulse sequence (Glover, 1999; Glover and Lai, 1998; Sawyer-Glover and Glover, 1998). Pulse sequence parameters for each experiment are shown in Table 4. The slice prescription was selected to cover the retinotopic visual areas and to extend rostrally to include MT+.

Each MR scanning session began by acquiring a set of T1-weighted anatomical images in the same slices as the functional

images (1.5T: fast spin-echo, FOV = 220 mm, TR = 500 ms, TE = 15 ms, echo-train length = 2; 3T: SPGR, FOV = 220 mm, TR = 68 ms, minimum TE). The inplane anatomical images were aligned to a high-resolution anatomical volume of each subject's brain so that all MR images (across multiple scanning sessions) from a given subject were coregistered with an accuracy of ~1 mm (Nestares and Heeger, 2000).

Defining the Visual Areas

The fMRI data were analyzed in each of several visual cortical areas, defined separately in each subject. MT+ was identified as a contiguous region of gray matter that responded more strongly to full-field moving dots than to a stationary dot pattern (Tootell et al., 1995b; Watson et al., 1993; Zeki et al., 1991), typically within or near the occipital continuation of the inferior temporal sulcus (Dumoulin et al., 2000). Retinotopically organized visual areas (V1, V2, V3, V3A, V4v) were defined by measuring the polar angle component of the cortical retinotopic map (DeYoe et al., 1996; Engel et al., 1994, 1997; Schneider et al., 1993; Sereno et al., 1995; Wandell, 1999).

The gray matter regions corresponding to MT+ and the retinotopic areas were further delimited based on the responses to a reference scan. The reference scan responses were used to exclude unresponsive voxels, e.g., gray matter regions that would have responded to visual field locations outside the stimulus apertures, or voxels that had too little overlap with gray matter. A reference scan was run during each scanning session. During the reference scan, subjects fixated while the display alternated between 18 s of moving dots and 18 s of stationary dots (presented in patches in the same positions as the stimulus used in the corresponding adaptation experiment). Voxels that were not strongly correlated with the stimulus alternations ($r > .40$, 0–9 s time lag) were discarded from further analysis. Thresholds ranging from .23 to .70 yielded similar results.

Separating Attention from Adaptation

Passive Viewing versus Directed Attention experiment

Stimulus and Protocol. Subjects viewed a pair of sinusoidal gratings, $10^\circ \times 10^\circ$ square (contrast = 20%, spatial frequency = 0.5 cyc/°; Figure 1A), separated by 1° , to the left and right of a central fixation point (full contrast, 0.5°). When the gratings moved, they drifted at $8^\circ/s$ (4 Hz). Stimuli were presented on a flat-panel display (NEC, multisynch LCD 2000) in a Faraday box with a conducting glass front, positioned near the subjects' feet. Subjects lay on their backs in the MR scanner and viewed the display through binoculars. Resulting percepts were virtually identical in all respects to viewing the display without binoculars from a distance of 50 cm.

Each subject participated in 4–5 sessions to measure MAE-related activity. Passive viewing scans were performed during the first two sessions. Then subjects spent several days practicing the task before the directed attention scans, performed during the next two or three scanning sessions. We collected 30–60 repeats of each trial type in each subject.

In each scan, subjects viewed a counterbalanced series of MAE and control trials (Figure 1B). On MAE trials, the adapting gratings drifted inward toward fixation for the full 25.5 s motion period. On control trials, the adapting gratings alternated their direction of motion (inward/outward) every 0.5 s. A uniform gray field (equal mean luminance) replaced the gratings during blank periods.

Stimulus parameters (size, spatial frequency, speed) were selected to produce the strongest perceptual MAE, based on previous psychophysical measurements of the MAE (Pantle, 1974; Wright and Johnston, 1985) and extensive psychophysical pilot experiments. Subjects were instructed to fixate while attending to the stimulus throughout the scan, as attending to the adaptor produces a stronger aftereffect (Buchel et al., 1998; Chaudhuri, 1990; Rees et al., 1997; Shulman, 1993).

Psychophysical Task during fMRI Scans. During directed attention scans, the 5 s test period was divided into three equal duration (1.67 s) subtrials. On each subtrial, one grating (left or right) moved very slowly outward, while the other was stationary. Subjects viewed the three consecutive subtrials and then indicated which grating appeared to move faster more often. No (correct/incorrect) feedback was provided. Speeds (on average ~0.06°/s) were determined separately for each subject, based on asymptotic performance during practice sessions, to yield ~80% correct performance (Table 1).

fMRI Data Analysis. Data from the first 6 s of each fMRI scan were discarded to minimize transient effects of magnetic saturation. The fMRI time series were preprocessed by (1) highpass filtering the time series at each voxel to compensate for the slow signal drift typical in fMRI signals (Smith et al., 1999), and (2) dividing each voxel's time series by its mean intensity to convert the data from arbitrary image intensity units to units of percent signal modulation and to compensate for the decrease in mean image intensity with distance from the surface coil. The resulting time series were averaged throughout the gray matter corresponding to each visual area's representation of the stimulus.

The relative fMRI response amplitudes (Figures 2B and 3B) were computed as follows. The time series for each trial was extracted beginning when the test stimulus appeared and ending at the end of the blank rest period following the test period. Each trial's time series can be regarded as a vector of time samples, R_i , where i is the trial index. All N trials of a particular fMRI scanning session were averaged together, regardless of trial type, to create a session-mean time series:

$$\bar{R} = \frac{1}{N} \sum_{i=1}^N R_i$$

Next, we computed a normalized relative amplitude for each trial, A_i , by projecting (inner product) the time series from each individual trial onto the session-mean time series and dividing by the squared norm of the session-mean time series:

$$A_i = \frac{R_i \cdot \bar{R}}{\|\bar{R}\|^2}$$

These calculations were done separately for each scanning session because of substantial session-to-session variations in the hemodynamic response. Statistics were computed on the resulting relative response amplitudes.

MAE Speed-Matching Psychophysical Experiment

Perceived MAE speed was determined outside the scanner using a speed-matching protocol, to quantitatively assess the strength of the perceptual MAE during our fMRI experiments. Stimuli were as similar as possible to the fMRI experiments (identical monitor calibrated to have the same mean intensity and contrast, matched virtual viewing distance).

Subjects viewed a pair of gratings to the left and right of a central fixation square. For 25.5 s, one grating drifted inward (speed = 8°/s, as on MAE trials in the fMRI experiment) while the other alternated between moving inward and outward every 0.5 s (as on control trials). Thus, one grating yielded a MAE following adaptation while the other did not. The gratings were then replaced with a uniform gray field (of equal mean luminance) for one of three storage durations: 1, 18, or 30 s. Finally, the gratings reappeared for 0.35 s: the grating on the adapted side was physically stationary but appeared to drift outward (due to MAE), and the grating on the unadapted side drifted outward (due to physical motion). Subjects indicated which grating appeared to move faster. The physical speed of the unadapted grating was adjusted, using a one-up, one-down adaptive staircase procedure, to estimate the perceived (matching) speed of the MAE.

Direction-Selective Adaptation

Adapted versus Opposite Direction Experiment

Stimulus and Protocol. Subjects viewed a pair of sinusoidal gratings, 10° × 10° square (contrast = 20%, spatial frequency = 0.5 cyc/°, temporal frequency = 4 Hz, speed = 8°/s), separated by 5°, to the left and right of a central fixation point.

Each scan consisted of a 30 s adaptation period followed by 7 alternating (36 s) cycles; each cycle consisted of alternating blocks of 3 adapted direction trials followed by 3 opposite direction trials (Figure 4A). In half the scanning sessions for each subject, the adaptation stimulus always moved inward; in the other half, it moved outward. Responses were averaged across sessions, and hence across adapting direction, to ensure that our measurements of direction selectivity were not confounded with an inherently stronger

response to either inward or outward motion unrelated to adaptation.

Psychophysical Task during fMRI Scans. Subjects performed a speed discrimination task on the test gratings. Both gratings moved either inward or outward, but one moved slightly faster than the other. The speed increments were determined by a pair of interleaved 3-down, 1-up adaptive staircases (one for opposite direction and one for adapted direction trials) that continuously adjusted the test speeds so that each subject would be approximately 80% correct. The resulting psychophysical data (collapsed across scans and scanning sessions) were fit with a Weibull function using a maximum likelihood fitting procedure (Watson, 1979), and the speed increment thresholds were defined as those which yielded 80% correct in the fitted psychometric function. Statistics on the psychophysical data were calculated using a bootstrapping procedure (Efron and Tibishirani, 1993): (1) the original psychophysical data were resampled with replacement 10,000 times; (2) each set of resampled data was fit with a Weibull function and thresholds were estimated (as described above); and (3) statistics (e.g., 95% confidence intervals) were computed on this resampled threshold distribution.

fMRI Data Analysis. fMRI data were preprocessed as described above and response amplitudes were calculated using techniques described in detail elsewhere (Heeger et al., 1999; Huk and Heeger, 2000). Briefly, the mean time series in each visual area during each scan was fit with a sinusoid with the same period as the block-alternation period (36 s), and we extracted the amplitude component of this best-fitting sinusoid while compensating for the hemodynamic delay. The resulting amplitudes were positive when the responses to opposite direction blocks were larger than the responses to adapted direction blocks. Statistics on the amplitudes were computed for each subject, for each visual area, across repeated scans and scanning sessions.

Adapted versus Mixed Direction Experiment

Stimulus and Protocol. Subjects viewed a pair of 10° diameter circular patches centered 7.5° to the left and right of a central fixation point. Patches were filled with white square dots on a black background (dot size = 0.25° wide, density ~1.25 dots/deg²). Left and right patches always moved in opposite directions.

Each scan consisted of a 39 s adaptation period followed by 7 (36 s) cycles; each cycle consisted of alternating adapted direction and mixed direction blocks (Figure 5A).

Psychophysical Task during fMRI Scans. Subjects performed a speed discrimination on the dot motion, indicating which patch (left or right) had moved slightly faster.

fMRI Data Analysis. The fMRI data were analyzed using the same techniques described for the adapted versus opposite direction experiment (above).

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