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# fMRI Adaptation Reveals Separate Mechanisms for First-Order and Second-Order Motion

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**Ashida H, Lingnau A, Wall MB, Smith AT.** fMRI adaptation reveals separate mechanisms for first-order and second-order motion. *J Neurophysiol* 97: 1319–1325, 2007. First published November 29, 2006; doi:10.1152/jn.00723.2006. A key unresolved debate in human vision concerns whether we have two different low-level mechanisms for encoding image motion. Separate neural mechanisms have been suggested for first-order (luminance modulation) and second-order (e.g., contrast modulation) motion in the retinal image but a single mechanism could handle both. Human functional magnetic resonance imaging (fMRI) has not so far convincingly revealed separate anatomical substrates. To examine whether two separate but co-localized mechanisms might exist, we used the technique of fast fMRI adaptation. We found direction-selective adaptation independently for each type of motion in the motion area V5/MT+ of the human brain. However, there was a total absence of cross-adaptation between first-order and second-order motion stimuli. This was true in both of the two subcomponents of MT+ (MT and MST) and similar results were found in V3A. This pattern of adaptation was consistent with psychophysical measurements of detection thresholds in similar stimulus sequences. The results provide strong evidence for separate neural populations that are responsible for detecting first- and second-order motion.

## INTRODUCTION

Detection of motion is an essential and highly developed function of the human visual system. We can perceive motion of second-order image characteristics (Cavanagh and Mather 1989), such as boundaries defined by contrast differences or local speed differences, as well as motion of first-order signals (boundaries defined by luminance gradients; for a review, see Smith 1994b). Pure second-order motion is a laboratory phenomenon, requiring careful removal of first-order signals to yield an unnatural stimulus, yet we can perceive such motion very readily. In real-life situations, where both types of cue are typically present and are correlated, second-order signals can help to characterize a moving target in a noisy environment with higher accuracy than if first-order signals alone were used (Smith and Scott-Samuel 2001).

Computational studies have depicted three different views of how second-order motion is detected. First, a separate motion pathway was proposed that has nonlinear preprocessing before standard motion computation (Chubb and Sperling 1988). Second, a single pathway of nonlinear detectors was previously shown to be capable of processing both types of motion (Benton and Johnston 2001; Johnston et al. 1992). Such a

model can extract velocity information directly from the space–time images (Marr and Ullman 1981). A third possibility is that a feature-tracking mechanism handles second-order motion (as well as first-order motion in some circumstances), whereas first-order motion is normally detected by dedicated low-level motion sensors (Del Viva and Morrone 1998; Derrington et al. 2004). All models can explain most of the data and, despite nearly two decades of debate, the controversy is unresolved. A parallel debate has more recently developed concerning first- and second-order spatial vision. The two debates are separate: even if the existence of a mechanism for static second-order pattern discrimination is established (e.g., Landy and Oruc 2002), mechanisms for second-order motion detection must still be sought.

Human psychophysics (e.g., Derrington and Badcock 1985; Ledgeway and Smith 1994; Nishida et al. 1997) has tended to indicate separate mechanisms for first-order and second-order motion, but this is not always the case (Hock and Gilroy 2005; Taub et al. 1997). Neuropsychological studies on brain damaged patients have favored separate-pathway models by showing selective deficits for second-order motion (Vaina and Cowey 1996) or first-order motion (Vaina et al. 2000), or differential degradation of detection threshold and speed perception for the two types of stimuli (Greenlee and Smith 1997). Earlier electrophysiology studies showed that the same cells respond to both types of motion in monkey V1/MT (O’Keefe and Movshon 1998) and cat area 17/18 (Mareschal and Baker 1998), which apparently is consistent with single-path models, although their responses are somewhat different, lending some support to dual-path models (see DISCUSSION).

Human functional magnetic resonance imaging (fMRI) studies are expected to provide more information on this issue not only because of their ability to see multiple cortical areas at the same time but also because they allow more direct comparison to results from human psychophysics; however, the results published so far are not conclusive. The first such fMRI study (Smith et al. 1998) suggested separate mechanisms and tentatively identified V3/VP as the earliest cortical site at which second-order motion is encoded. More recently, whereas one fMRI study implicated separate cortical networks (Dumoulin et al. 2003), others showed that both first-order and second-order motion are represented as early as V1 (Nishida et al. 2003; Seiffert et al. 2003), suggesting either a common mechanism or separate mechanisms that both originate in V1.

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One reason for the inconsistency among fMRI studies is the relatively coarse spatial resolution of fMRI measurement. Previously, two processes occurring in the same voxel could not be distinguished and so similar activations from two different stimuli would not necessarily indicate a single underlying mechanism. However, fMRI adaptation now allows dissociation of different functional properties of neural populations within voxels (Grill-Spector and Malach 2001). Repeated presentation of similar stimuli causes a reduction of the blood oxygen level-dependent (BOLD) response in cortical regions consisting of neurons that are insensitive to the changes between them, whereas little or no reduction occurs if the two stimuli activate different sets of neurons. We can therefore infer the stimulus selectivity of neurons with a resolution beyond that of the fMRI voxels. Nishida et al. (2003) used adaptation between stimulus blocks and found direction-selective adaptation to both first-order and second-order motion, although they did not test cross-adaptation between the two types and so did not address the question of separate, parallel mechanisms.

fMRI adaptation can be observed both in rapid event-related sequences and in longer blocks (Grill-Spector et al. 2006). A short stimulus of a few seconds can yield selective reduction of responses for basic visual features such as orientation (Boynton and Finney 2003; Fang et al. 2005) or motion direction (Huetel et al. 2004). This approach allows more flexible testing of stimulus specificity within a limited scan time. Larsson et al. (2006) used this technique to assess the mechanisms underlying first-order and second-order orientation discrimination and suggested two separate mechanisms by showing different distributions of adaptation across visual areas and a lack of clear cross adaptation. Note that this result does not necessarily imply separate mechanisms underlying motion detection, as discussed above and in their introduction.

Here we report the results of a rapid fMRI adaptation experiment on first-order and second-order motion. Each type of model predicts a different pattern of results. Separate adaptation, up to a point where the signals are integrated, would be found if there are dual pathways. Similar intra- and cross-adaptation would be evidence for a single mechanism. Partial cross-adaptation is expected if second-order motion detection relies on feature tracking because the feature-tracking mechanism can also be adapted by first-order motion, whereas low-level motion sensors would be adapted only by first-order motion. Our results showed direction-selective adaptation effects in MT+—the “motion area”—for both first-order and second-order stimuli but no cross-adaptation between them, consistent with the dual-processing model.

## METHODS

### Participants

Two of the authors (HA, MW) and three naïve volunteers (JM, PM, WE) participated (aged 20–37, two males and three females). All had normal vision. The experiments were conducted in accordance with the Declaration of Helsinki and were approved by the ethical committee of Royal Holloway, University of London (RHUL). All the participants were screened using a standard procedure before going into the MR scanner. Written informed consent was obtained before each scanning session. One of the authors (HA) and another naïve volunteer (aged 27–38, both males) participated in the psychophysical

experiment. Naïve participants were paid for their time according to standard rates and procedures.

### Data acquisition

Magnetic resonance images were acquired by using a Siemens Trio scanner (3T) in RHUL, with an eight-channel phased-array head coil. T1-weighted anatomical images were acquired at the beginning of each session (MP-RAGE, Siemens,  $1 \times 1 \times 1$ -mm voxels). Functional images were acquired with T2\*-weighted gradient-recalled echo-planar imaging sequences. The voxel size was  $3.0 \times 3.0 \times 3.0$  mm. Fourteen oblique slices were acquired from the occipital lobe with TR = 1 s (TE = 31 ms, flip angle =  $90^\circ$ , field of view =  $192 \times 192$  mm).

### Visual stimulation

Visual stimuli were back-projected onto a screen by a liquid-crystal projector. These were viewed binocularly through a mirror above the head coil. The screen was visible as a circular aperture of  $30^\circ$  diameter. The luminance profile was linearized, with a mean luminance of about  $2,000 \text{ cd/m}^2$ .

The stimulus formed an annulus that subtended from  $1^\circ$  (inner diameter) to  $6^\circ$  (outer diameter) visual angle, which was filled with random dots of 50% contrast (Fig. 1). Each dot consisted of a single screen pixel to minimize first-order artifacts (Smith and Ledgeway 1997). The outer area was filled with mean gray. A small disk (diameter  $\cong 0.4^\circ$ ) was presented in the center for fixation.

The stimulus was a radial sinusoidal pattern of six cycles/round (Fig. 1, see also Ledgeway and Smith 1994). For the first-order stimuli, this was created by adding luminance modulation (LM) to the static noise. For the second-order stimuli, the contrast of the noise was modulated by the sinusoid [contrast modulation (CM)]. In addition to standard gamma correction, the modulation depth of pixels that were darker than the average was adjusted to remove first-order artifacts in the contrast-modulated stimuli (Ashida et al. 2001). The effective modulation contrast was roughly matched between the two motion types (LM: 20% for adaptation and 10% for test, CM: 100% for adaptation and 50% for test). The noise was present throughout the run, with only the modulation appearing and disappearing during events. The speed of motion was always 3.33 Hz (33.3 rpm).

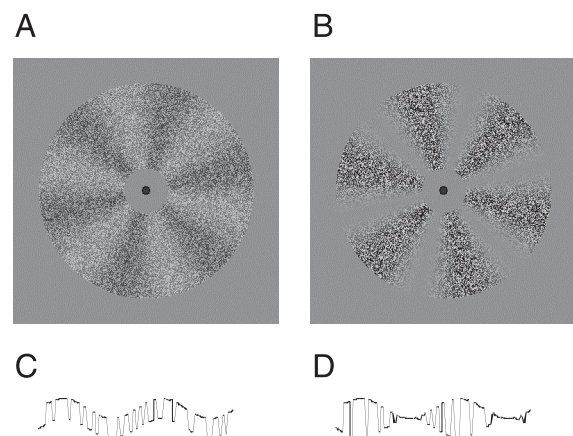


FIG. 1. Schematic views of the visual stimuli. Radial gratings were made by (A) luminance modulation (LM, first-order) or (B) contrast modulation (CM, second-order) of a fine random dot field. Rotation of the spokes was accomplished by moving the modulating waveform while keeping the random dots static. Luminance profiles of modulation are shown for LM (C) and CM (D) stimuli. In the LM case, noise of constant amplitude is superimposed on a low-frequency sinusoidal luminance modulation. In the CM case, noise amplitude varies sinusoidally about a constant luminance level. The central disk served as a fixation mark, the color of which changed randomly at a rate of 1 Hz.

## Procedure

A trial began with a moving grating as an adaptation stimulus, S1 (2 s), followed by an interstimulus interval with no modulation (2 s) and then the test stimulus, S2 (1 s). There was then a 3-s interval with no modulation before the next trial.

There were five test conditions: LM-same, LM-opposite, CM-same, CM-opposite, and control. Same/different refers to direction of motion and the control contained S1 only. These five conditions were repeated five times in a single run with the order balanced using m-sequences (Buras and Boynton 2002). This ensured that any contamination of the averaged time courses by the response to the preceding trial equally affected all event types. Events occurred every 8 s. A run consisted of 26 events, with the first one excluded from the analyses. There were blank periods of 6 s in the beginning and 11 s at the end of each run.

As a precaution in case adaptation effects carried over from one event to the next, the motion type (LM/CM) and direction [clockwise/counterclockwise (CW/CCW)] of S1 were fixed within a given scan run. Eight runs were conducted for each type of S1 across two sessions, four in CW and four in CCW directions, in four alternating blocks of two runs of the same direction (S1 directions were collapsed in the data analyses). There were thus 40 events of each condition per participant. A short rest was given between runs.

A central disk served as a fixation mark, the color of which changed randomly at a rate of 1 Hz. To promote fixation and maintain a constant attentional state, participants were asked to count the number of blue disks and report it after each run.

## Regions of interest

Moving LM stimuli of the same type (Fig. 1A) were used to identify the MT+ region of interest (ROI) in separate block-design runs (motion vs. blank, 15-s blocks). During the motion blocks, the modulation contrast was 20% and the rate of motion was 3.33 Hz (33.3 rpm). The motion direction was reversed every 2.5 s. During the blank blocks, the fixation disk was presented with the unmodulated noise ring. General linear model (GLM) contrast was computed between motion and blank blocks for each participant. The ROI corresponding to MT+ was identified on the basis of both functional activity and its known approximate anatomical location (Dumoulin et al. 2000).

For four of the five participants, areas MT, MST, and V3A were identified for auxiliary analyses. MST was identified on the basis of ipsilateral activation to a circular patch of expanding random dots, presented in one hemifield only (Dukelow et al. 2001; Huk et al. 2002). This method is described elsewhere (Smith et al. 2006). MT was defined by eliminating overlapping MST voxels from MT+. A rotating wedge stimulus (24° angle), used to identify retinotopic areas (Serenio et al. 1995), consisted of a flickering (8 Hz) red-green checkerboard pattern that was scaled with eccentricity  $\leq 12^\circ$ . It rotated clockwise at the rate of 64 s/cycle, and eight cycles were presented. V3A was identified manually on the cortical flatmaps based on the field sign of the polar-phase maps and the characteristic presence of an upper quadrant representation. Whereas MT+, MT, and MST were defined on individual anatomical spaces, V3A was defined in Talairach space that was required for cortical flattening.

## Data analysis

The images were analyzed using Brain Voyager software (Brain Innovation, Maastricht, The Netherlands). The functional images were corrected for slice timing and head movement and temporally high-pass filtered at 0.014 Hz. They were then coregistered to the standard anatomical image for each participant.

Event-related averages of time courses were computed within each ROI for each hemisphere. Responses during the period 0–4 s from the onset of S1 were averaged for each run and were used as baselines to compute percentage signal change. The time courses were averaged

across runs within each participant and then across participants, for each type of S1–S2 pair, with the absolute motion directions of S1 collapsed.

An adaptation index for each adapt-test condition was computed on the basis of the averages, across participants, of percentage signal changes collapsed between  $t = 6$  s and  $t = 12$  s, corresponding to the period when most of the response relates to S2. The average of the baseline condition was subtracted from that of each condition to give  $A_{opp}$  and  $A_{same}$  for each stimulus pair (LM–LM, LM–CM, CM–LM, CM–CM). Then the adaptation index  $AI$  was given as  $(A_{opp} - A_{same}) / (A_{opp} + A_{same})$  for each pair. The 95% confidence intervals were computed by using a nonparametric bootstrap procedure (Efron and Tibshirani 1993). Adaptation indices were computed 10,000 times from random sampling of hemispheres with replacement, with the size of the data set being the same as the original data. The 2.5 and 97.5% quantiles were taken as the lower and upper bounds of the confidence intervals.

## Psychophysics

In fMRI, as in psychophysics, adaptation may also result in improved performance. An example is facilitation in the form of priming (Maccotta and Buckner 2004). We thus conducted an auxiliary psychophysical experiment to consider the possible perceptual manifestation of the effect we found, by measuring the changes of detection threshold in each S1–S2 condition.

The stimulus configuration was the same as in the fMRI experiment, but to create low-contrast modulation (especially for LM stimuli), we used a VSG 2/5 framebuffer (Cambridge Research Systems) that has 14-bit grayscale resolution and a 17-in. CRT monitor (NANA0 F57T,  $1,024 \times 768$  pixels, 60-Hz refresh, mean luminance of  $40 \text{ cd/m}^2$ ), which was viewed from a distance of 44 cm with the aid of a head-and-chin rest. After the S1 stimulus of 2 s and a blank (with background noise) of 2 s, a test stimulus (S2) was presented for 1 s. The participants judged whether they saw the second moving grating and responded by using a keypad.

The type and direction of S1 were fixed in a single run, as in the main experiment, and one type of S2 was tested in a single run. Modulation contrast was adjusted by a 1-up–1-down double-random staircase procedure, in which two staircases for both motion directions were intermixed within a single run. Two runs were conducted for each S1–S2 pair. By collapsing the motion direction of S1, four measures of thresholds were obtained for each condition.

Adaptation indices were computed in the same way as described above for the fMRI data, on the basis of averaged sensitivities (i.e., reciprocals of thresholds) across participants as  $A_{same}$  and  $A_{opp}$ . The 95% confidence intervals were computed by using a nonparametric bootstrap procedure, as described earlier for the fMRI data, in which the runs were randomly sampled with replacement.

## RESULTS

### fMRI adaptation

Figure 2 shows averaged time courses of the BOLD signals in MT+, with separate panels for adaptation to LM and CM. Averaged responses between  $t = 6$  s and  $t = 12$  s (after the offset of the S2 stimuli) are shown to the right. As is evident from these plots, direction-selective adaptation occurred in MT+ when the stimulus type (LM/CM) was the same for S1 and S2. That is, responses were reduced, reflecting common neural processing, when S2 moved in the same direction as S1. This is consistent with neural adaptation of direction-sensitive neurons within each of two separate detection mechanisms. When S1 was LM and S2 was CM (Fig. 2, left, red and orange lines) and when S1 was CM and S2 was LM (Fig. 2, right, green and turquoise lines), there was no direction-selective adaptation. The adaptation indices in

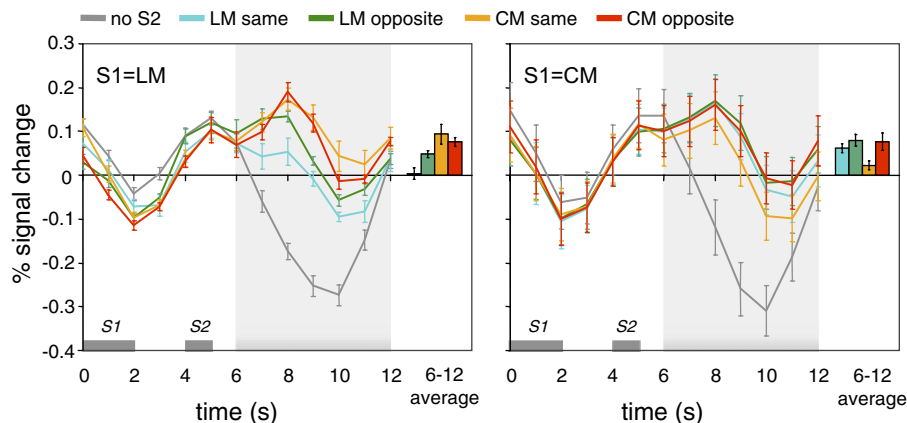


FIG. 2. Results in MT+, averaged across 5 participants (10 hemispheres). *Left*: results for first-order adaptation ( $S1 = LM$ ). *Right*: results for second-order adaptation ( $S1 = CM$ ), with the motion direction of  $S1$  collapsed and the direction of  $S2$  expressed in relative terms (same or different). Curves show the event-related time courses of BOLD signal changes. Gray bars at the *bottom* indicate the period of stimulation for  $S1$  and  $S2$ . At *time 0*, the response is still falling from the previous event. Between 0 and about 6 s, all time courses are broadly in register, reflecting a common  $S1$  stimulus, but then they diverge, reflecting differential responses to  $S2$ . Bar graphs (*right*) show averaged signals for each condition between  $t = 6$  s and  $t = 12$  s (shown by the pale gray background in the time course plots). Error bars show SEs. Direction-specific adaptation is evident as a reduction of the response to the same direction relative to the opposite direction, and occurred when  $S1$  and  $S2$  were of the same stimulus type, both LM or both CM, but not when they were different.

Fig. 3 confirm that reliable adaptation occurred only when the stimulus type was the same for  $S1$  and  $S2$ . Cross-adaptation between LM and CM motion was not found after adapting to either LM or CM motion.

It might be argued that insufficient control of attention could have caused a significant artifact because BOLD responses in MT+ are significantly increased by attention (Huk et al. 2001). However, we believe that such an effect, if any, was not crucial for the following reasons. First, the demanding task at fixation should have minimized attention to the stimuli. Second, the modulation contrast of  $S2$  was halved from that of  $S1$  and the two stimuli never looked the same. It is unlikely that the participant's attention was captured only when the stimulus type changed. Third, attention alone cannot explain the whole pattern of results. Attention to direction change could lead to larger responses for opposite motion regardless of the stimulus type, but this was not the case. Attention to a change in stimulus type could lead to larger responses for cross-adaptation conditions regardless of direction, but neither was this consistently the case. Simultaneous attention to both variables predicts that the largest response would occur for the condition with stimulus change and direction change, but these

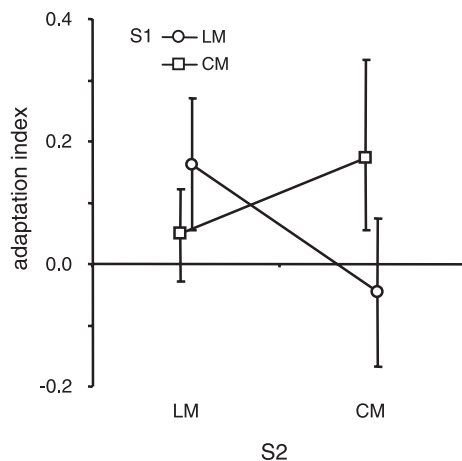


FIG. 3. Adaptation index in MT+, computed from the averaged signal changes across participants. Error bars indicate 95% confidence intervals that were estimated by using a bootstrap procedure. See text for details.

responses were no larger than two of the remaining three conditions. It is possible that attention to stimulus change could obscure the effect of direction change if there were saturation of the response, but the use of a low  $S2$  contrast makes saturation unlikely.

There was a slight hint of adaptation in the LM probe stimuli after adapting to CM stimuli. Although partial cross-adaptation from CM to LM is one possible interpretation, it must be remembered that complete elimination of first-order artifacts is not easy even after careful calibration. It is therefore safer (and parsimonious) not to take this small effect as genuine unless confirmed by more thorough investigation. Minor contamination could be crucial at the threshold level but is not necessarily so in our suprathreshold experiment. Note that a first-order artifact would also be expected to result in apparent cross-adaptation in the opposite direction (from LM to CM); this was not the case.

In four of the five participants, two subcomponents of MT+, MST and MT, and area V3A were separately analyzed (Figs. 4, 5, and 6, respectively). The results showed very similar trends in all these areas.

We also analyzed the data in the earlier retinotopic areas V1 and V2, but the time courses were noisy and adaptation could not be reliably assessed. Our method was effective in MT+, but it might not have been optimal for earlier areas for several reasons. First, the presence of background visual noise could have increased the noise in the response. Unlike MT+ and V3A, where large population of cells are direction selective and have relatively large receptive fields, there are many cells in V1 that are either not direction selective or are sensitive to local luminance changes caused by the noise pattern. The responses of such irrelevant cells might have obscured those of relevant cells. Second, the interval of 2 s between  $S1$  and  $S2$  was chosen as the minimum for linear summation of responses for  $S1$  and  $S2$  (Boynton and Finney 2003), which we expected to ease saturation, but shorter intervals may be optimal for V1. Finally, our preliminary observations suggested that the short TR of 1 s could have reduced the signal-to-noise ratio. Because Nishida et al. (2003) previously reported that direction selec-

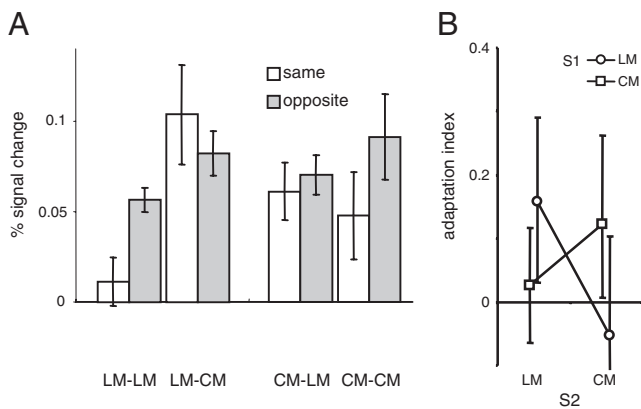


FIG. 4. Results in MT for 4 participants (8 hemispheres). *A*: percentage signal strength averaged across the period between  $t = 6$  s and 12 s, computed in the same way as the bars in Fig. 2. Error bars show SEs. *B*: adaptation indices with the error bars showing 95% confidence intervals.

tivity to second-order motion is found as early as V1, it is likely that individual adaptation to LM and CM motion occurs in V1. There was a hint of such individual adaptation in V1 in some participants, but it was not reliable.

### Psychophysics

Figure 7*A* shows the results for one of the authors (HA) and a paid naïve volunteer (NH). For both observers, an increase of threshold in the “same” direction is seen for LM–LM and CM–CM but not in the LM–CM and CM–LM conditions. Figure 7*B* shows the adaptation indices. This plot resembles the adaptation index plots in Figs. 3–6, showing clear intra-order adaptation but no cross-adaptation. Adaptation in the CM–CM condition is weaker than that in the fMRI data, whereas adaptation in the LM–LM condition is comparable, but this is largely explained by the naïve observer who did not participate in the fMRI experiment. These results are in line with those obtained in the more thorough investigation of Nishida et al. (1997). In sum, psychophysical results are similar to the fMRI results and it is highly likely that the fMRI adaptation we observed is correlated with perceptual adaptation.

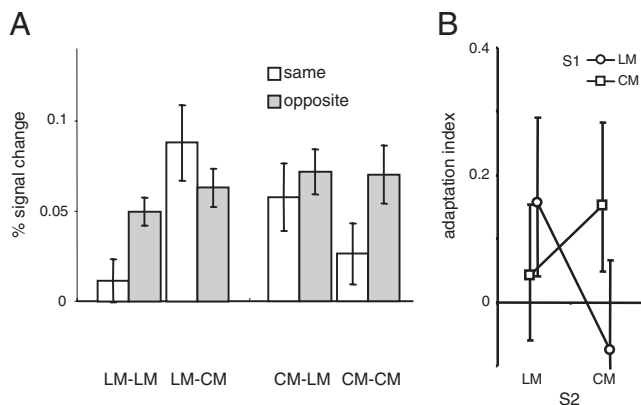


FIG. 5. Results in MST for 4 participants, as in Fig. 4. *A*: percentage signal strength with SEs. *B*: adaptation indices with 95% confidence intervals.

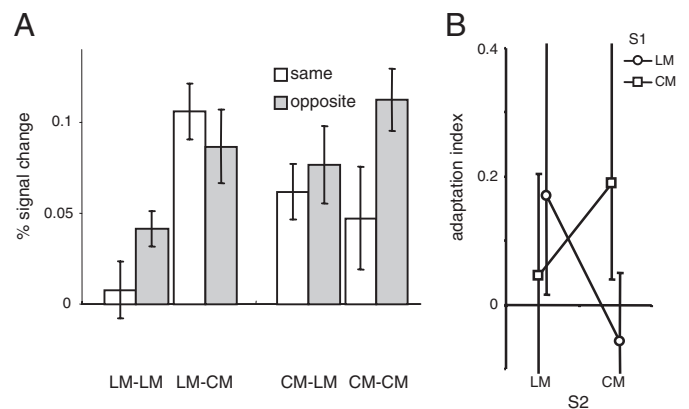


FIG. 6. Results in V3A for 4 participants, as in Figs. 4 and 5. *A*: percentage signal strength with standard errors of the mean. *B*: adaptation indices with 95% confidence intervals.

### DISCUSSION

#### Separate mechanisms for first-order and second-order motion

We found order-specific adaptation of BOLD responses to first-order (LM) and second-order (CM) motion. This pattern of results parallels the psychophysical results of adaptation. It is also consistent with order-specific disorders of motion perception found in some patients (Greenlee and Smith 1997; Vaina and Cowey 1996; Vaina et al. 2000). Taken together, our findings strongly suggest the existence of separate neural mechanisms that are responsible for encoding the two types of motion, even if these mechanisms are intermixed in the same brain areas (Nishida et al. 2003; Seiffert et al. 2003). Our result therefore favors dual-pathway models that assume a separate second-order motion pathway rather than single-mechanism models (Benton et al. 2001; Johnston et al. 1992). Such dual-path models often assume nonlinear preprocessing followed by standard motion detection (Chubb and Sperling 1988; Lu and Sperling 1995; Nishida and Ashida 2000; Wilson et al. 1992), although our result does not directly support any specific scheme of motion sensors. It also remains an open question whether the initial-stage mechanism of the second-order motion pathway is shared by the second-order pattern analysis mechanisms shown by Larsson et al. (2006).

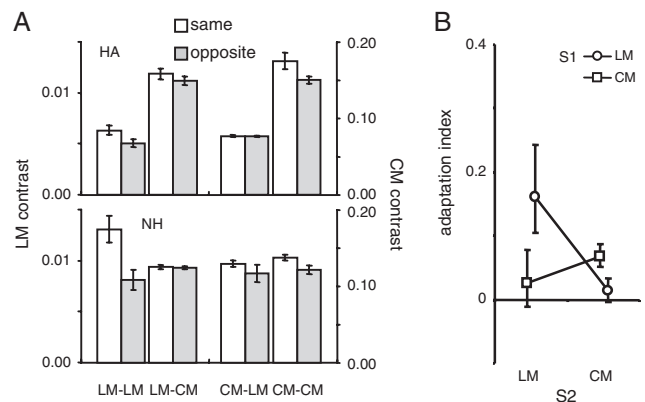


FIG. 7. Results of the psychophysical experiment. *A*: detection thresholds of the S2 stimulus for each S1–S2 condition. Two panels show the results of 2 observers. Threshold contrasts for LM tests are shown by the left-hand ordinate, and those for CM tests are shown by the right-hand ordinate. Error bars show SEs across runs. *B*: adaptation indices with 95% confidence intervals.

Second-order motion can be detected by a higher-order feature-tracking mechanism (Del Viva and Morrone 1998; Derrington et al. 2004; Scott-Samuel and Georgeson 1999; Seiffert and Cavanagh 1998; Smith 1994a). Smith (1994a) presented evidence for two methods of detecting second-order motion: a dedicated mechanism based on second-order motion energy and a feature-tracking method probably shared by first-order stimuli. In contrast, by examining many psychophysical results in the literature, Derrington et al. (2004) concluded that there is no reason to assume dedicated second-order sensors but that a feature-tracking mechanism suffices. Portions of our results may be explained if second-order motion is detected by a higher-order feature-tracking mechanism, whereas first-order motion is detected by lower-level motion sensors. However, a feature-tracking mechanism requires greater attentional resources (Ashida et al. 2001; Derrington et al. 2004) and should have been highly suppressed by the fixation task. Adaptation to CM stimuli therefore should have been much smaller than actually observed. Another point is that feature tracking does not operate exclusively for CM stimuli but for both LM and CM stimuli (Del Viva and Morrone 1998; Smith and Ledgeway 2001). Therefore if CM motion is detected entirely by feature tracking whereas LM motion is mainly detected by lower-level filters, partial cross-adaptation from LM to CM motion is expected even if it does not occur in the opposite direction; however, we did not find cross-adaptation in either direction. Third, if second-order motion is detected by feature tracking, it is necessary to conclude that this process occurs in V1 because direction-specific adaptation for second-order motion occurs in V1 (Nishida et al. 2003). This seems unlikely, given the high-level nature of the process. Our finding indicates that dedicated second-order detectors do exist at least for relatively high modulation contrast. However, we also do not exclude the possibility that a feature-tracking mechanism works cooperatively (Smith and Ledgeway 2001) or exclusively at lower contrasts.

#### *Relation to single-unit physiology*

O'Keefe and Movshon (1998) reported that a subset of cells in macaque MT respond to both first-order motion and second-order motion. They also found similar cells in V1, although the sample was much smaller. They did not confirm cue-invariant processing (i.e., invariant responses to first-order and second-order motion) in most MT cells, but suggested that some cells may be cue invariant. They also found that preferred spatial frequency was lower for second-order motion than for first-order motion, whereas direction tuning was similar for both types of stimuli. Their finding is generally consistent with our finding of independent adaptation in human MT+, although the exact site of fMRI adaptation is unknown, as we discuss in the next subsection.

Mareschal and Baker (1998, 1999) examined cells in cat area 18 and argued in support of the dual-pathway model by showing significant differences in the spatiotemporal properties of first-order and second-order stimuli to which the cells respond. Ledgeway et al. (2005) also examined cells in cat area 18 and found different contrast response functions for first-order and second-order motion stimuli. Their conclusions too are generally consistent with ours.

The fact that these single-cell studies report that cells responsive to second-order stimuli also respond to first-order stimuli is a potential problem for the dual-pathway interpreta-

tion. There appear to be no reports of cells that respond to second-order motion exclusively, whereas our results suggest the existence of such exclusively second-order cells. We can explain this apparent discrepancy by three points. First, cells that code second-order motion may be sensitive to the carrier structure in a direction-selective way, because spatiotemporal properties are different for first-order and second-order stimuli (Mareschal and Baker 1998). Second, as discussed by Larsson et al. (2006), second-order-only cells may have been overlooked by the procedure of isolating cells using first-order stimuli (Baker and Mareschal 2001). Finally, Sawamura et al. (2006) suggested, based on single-unit recording of macaque inferior temporal cortex, that adaptation might be more selective to stimulus properties than the response of cells. In other words, adaptation measured either by single-unit recording or by BOLD fMRI might underestimate the range of stimuli to which the neurons are responsive, suggesting that stimulus-specific fMRI adaptation might be observed even when the underlying mechanisms involve neurons that respond to both types of stimuli, albeit with different response profiles. If so, our results may not imply completely separate neural populations but partially intermixed ones. This would explain why some neurons respond to both types of motion stimuli even if there are distinct neural channels. Note, however, that there has been no evidence that the finding of Sawamura et al. is directly applicable to our case of adaptation in MT+ because the repetition suppression in their study, measured in the inferotemporal cortex with fast repetitions of many kinds of pictures, is likely correlated with priming (facilitation) rather than conventional adaptation (Maccotta and Buckner 2004).

#### *Possible site of adaptation*

Our result of separate direction-selective adaptation to first- and second-order motion in MT+ appears to be consistent with the incomplete cue invariance found by O'Keefe and Movshon (1998) as described above. fMRI adaptation found in area MT+, however, does not necessarily imply that adaptation occurs within MT+ because adapted input signals from the previous processing levels could lead to a similar result (Grill-Spector et al. 2006; Larsson et al. 2006). Actually, a single-unit study of macaques suggested that adaptation to visual motion in MT probably reflects gain control in earlier sites because adaptation was specific to the spatial location despite the larger receptive fields of MT cells (Kohn and Movshon 2003). Our result of similar trends in MT+ and V3A is consistent with this idea. Absence of cross-adaptation in MT+ therefore does not necessarily contradict a popular idea that separate detection is followed by integration of the two streams at the level of MT/MST (Nishida and Ashida 2000; Wilson et al. 1992). We could not identify the origin of adaptation because of unstable results in the early retinotopic areas including V1 with our experimental design. Further investigation would require optimized stimulation and scanning parameters for such areas.

In conclusion, initial separate detection of first-order and second-order motion is suggested by our finding of direction-selective BOLD adaptation to visual motion that is specific to first-order and second-order motion. Two questions remain unanswered: Where does direction-selective adaptation originate? and how/where are motion signals integrated across stimulus types? These questions highlight methodological challenges of fMRI

adaptation in terms of asking about the hierarchical structure of the system, given that upstream adaptation affects later areas and adaptability might vary across areas.

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