Human neural responses involved in spatial pooling of locally ambiguous motion signals

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Amano K, Takeda T, Haji T, Terao M, Maruya K, Matsumoto K, Murakami I, Nishida S. Human neural responses involved in spatial pooling of locally ambiguous motion signals. J Neurophysiol 107: 3493–3508, 2012. First published March 21, 2012; doi:10.1152/jn.00821.2011.—Early visual motion signals are local and one-dimensional (1-D). For specification of global two-dimensional (2-D) motion vectors, the visual system should appropriately integrate these signals across orientation and space. Previous neurophysiological studies have suggested that this integration process consists of two computational steps (estimation of local 2-D motion vectors, followed by their spatial pooling), both being identified in the area MT. Psychophysical findings, however, suggest that under certain stimulus conditions, the visual system can also compute mathematically correct global motion vectors from direct pooling of spatially distributed 1-D motion signals. To study the neural mechanisms responsible for this novel 1-D motion pooling, we conducted human magnetoencephalography (MEG) and functional MRI experiments using a global motion stimulus comprising multiple moving Gabors (global-Gabor motion). In the first experiment, we measured MEG and blood oxygen level-dependent responses while changing motion coherence of global-Gabor motion. In the second experiment, we investigated cortical responses correlated with direction-selective adaptation to the global 2-D motion, not to local 1-D motions. We found that human MT complex (hMT+) responses show both coherence dependency and direction selectivity to global motion based on 1-D pooling. The results provide the first evidence that hMT+ is the locus of 1-D motion pooling, as well as that of conventional 2-D motion pooling.

functional magnetic resonance imaging; integration; magnetoencephalography; middle temporal area

PERCEPTION OF VISUAL MOTION is vital for mobile animals when interacting with their ever-changing environment. It is challenging for the visual system to correctly estimate the global two-dimensional (2-D) movement of an object. This is because visual motion sensors at the initial stages of the visual system have small receptive fields. Local measurements by small receptive fields could render a 2-D movement of an object into one-dimensional (1-D) movements of edge segments, each of which is consistent with, but ambiguous about, the 2-D object motion [i.e., the speed component parallel to the contour is indeterminate, which is known as the aperture problem (Adelson and Movshon 1982)]. In addition, because the receptive field of the initial motion sensors is 1-D (oriented), the extracted signal is always ambiguous 1-D motion, even when the pattern within the receptive field is 2-D. To solve the aperture problem and compute the true global 2-D motion vector, the subsequent stage of visual motion processing must appropriately integrate local 1-D motion signals across orientation and space.

How does the visual system estimate global 2-D motion from 1-D local motion signals? The current prevailing view is “2-D motion pooling,” in which the aperture problem is first solved locally, and then the resulting local 2-D motion signals are pooled over space. In the first stage, a local 2-D motion vector is estimated by integration of local 1-D motion signals across orientation, based on the intersection of constraint (IOC) rule (Adelson and Movshon 1982; Simoncelli and Heeger 2002; Movshon et al. 1985; Newsome and Pare 1988; Rees et al. 2000).

Recent psychophysical studies, however, have indicated that, in addition to 2-D motion pooling, the visual system may use “1-D motion pooling” (Amano et al. 2009a; Lorenceau 1998). This is a one-shot process in which local 1-D motion signals are integrated across orientation and space at the same time. Human psychophysical performance indicates that the visual system uses 1-D motion pooling following an IOC-like rule when local elements are ambiguous 1-D motions (e.g., drifting Gabors), whereas it uses 2-D motion pooling when local elements are unambiguous 2-D motions (e.g., moving dots, drifting plaid Gabors) (Amano et al. 2009a). IOC-based 1-D motion pooling is one of the most elegant mathematical solutions of the aperture problem.

In contrast to 2-D motion pooling, the neural mechanism responsible for 1-D motion pooling remains poorly understood. Simoncelli and Heeger (1998) proposed a computational model of MT that is able to find IOC solutions from selective integration of V1 outputs sensitive to the same 2-D velocity.
More recently, Rust et al. (2006) showed that an elaborated version of this model could well account for MT responses to a wide range of plaid stimuli. However, because Rust et al. (2006) examined only 1-D directional tuning, it remains unknown whether the integration rule is IOC or VA. In addition, although this model has the potential to explain 1-D motion pooling by assuming integration of V1 outputs across different retinal locations, Rust et al. only examined the case in which local motion signals were superimposed as plaids. More recently, Majaj et al. (2007) reported that MT neurons of anesthetized monkeys, which responded to the 2-D pattern motion of plaids, responded only to the component motions rather than to the pattern motion when they were presented in separate locations within the neurons’ receptive fields. Their findings suggest that MT may not be the locus for 1-D pooling. However, the nonoverlapping stimulus used by Majaj et al. (2007) did not perceptually cohere into a global motion.

Using a stimulus optimally designed for coherent 1-D motion pooling, termed global-Gabor motion (Amano et al. 2009a), we attempted in this study to specify a neural substrate of 1-D pooling by using magnetoencephalography (MEG), which allowed us to noninvasively examine the direct neural response evoked by our motion stimuli. To confirm the spatial activity map obtained with MEG, we also used functional magnetic resonance imaging (fMRI). We expected that the cortical areas representing global motion produced by 1-D pooling should show an increase in activity as a function of motion coherence (proportion of signal elements) of global-Gabor motion. We questioned which cortical areas showed this pattern, and whether those areas overlapped with the cortical areas representing global motion produced by 2-D motion pooling, including hMT+. Psychophysical findings by Amano et al. (2009a) could be interpreted as suggesting that 1-D motion pooling takes place in earlier cortical areas than hMT+ in the hierarchy of visual motion processing, because, computationally speaking, 1-D motion pooling (1-stage integration across orientation and space) could precede 2-D motion pooling (2-stage integration consisting of local orientation integration followed by spatial integration). However, one cannot assume a simple one-to-one correspondence between a functional model developed from psychophysics and the anatomic structure of the responsible neural processing; this is why it is important to understand the neural correlate of 1-D motion pooling to complement its functional understanding. In light of a physiological result reported by Majaj et al. (2007), it is also possible that 1-D motion pooling is cortically processed not at or before hMT+, unlike 2-D motion pooling. Alternatively, the same neural mechanisms might be responsible for both 1-D pooling and 2-D pooling, flexibly changing their computation depending on the stimulus (Huang et al. 2007). The neural activity correlated with the coherence of global-Gabor motion, measured in the first experiment, is a necessary but not sufficient condition of the representation of 1-D motion pooling. The second experiment therefore investigated the areas that showed a direction-selective adaptation to the global motion component of global-Gabor motion.

The beamformer analysis (Gross et al. 2001; Van Veen et al. 1997) of MEG responses to global-Gabor motion suggests that neural activity increases with motion coherence in hMT+ as well as in V1, V3A, and intraparietal sulcus (IPS). The cortical activation map for 1-D motion pooling was indistinguishable from that for 2-D motion pooling, not only in MEG responses but also in fMRI responses. The second experiment showed an adaptation effect selective to the 2-D direction of global-Gabor motion only in hMT+. These results represent the first evidence that hMT+ is the locus of 1-D pooling, in addition to that of 2-D pooling.

**MATERIALS AND METHODS**

**Subjects.** In experiment 1, eight male subjects participated in the MEG measurement, and five subjects, including four of those eight, participated in the fMRI measurement. For the MEG measurement in experiment 2, we included seven male subjects, five of whom participated in a psychophysical experiment measuring the amplitude of the motion aftereffect. All subjects were healthy and had normal or corrected-to-normal vision. The experimental protocols were approved by the human subjects review board of the University of Tokyo, and the subjects gave their informed written consent.

**Apparatus.** Stimuli were generated using a ViSaGe graphics system (Cambridge Research Systems). Stimuli for MEG experiments were projected by a Digital Light Processing (DLP) projector (V-1100Z, PLUS, Tokyo, Japan) onto a translucent screen (40° × 30°) located 140 cm from the subjects, whereas those for fMRI experiments were projected by a liquid crystal projector (CP-SX13501, Hitachi, Tokyo, Japan) onto a translucent screen (27° × 20°). The refresh rate was 60 Hz, and the pixel resolution was 800 × 600.

**Stimuli.** Global-Gabor or global-plaid stimuli, consisting of numerous Gabor or plaid elements, were used (Amano et al. 2009a). Global-Gabor motion is a stimulus designed for tapping 1-D motion pooling. It consists of numerous spatially distributed, stationary Gabor elements with a drifting-carrier grating. The orientation of the sine-wave carrier in each Gabor is randomly determined (Fig. 1A). The carrier drifts in its orthogonal directions at a rate consistent with a global 2-D velocity. If the global motion direction is rightward/ leftward, carrier drift rate is highest for vertical Gabors and lowest for horizontal Gabors. When all carriers are made consistent with one global 2-D velocity (100% signal), the global-Gabor motion is perceived to move coherently and rigidly in the global motion direction at a speed close to that of the target 2-D vector. Note that if the global motion perception were produced by VA-based 2-D motion pooling of local orthogonal motion vectors of Gabors patches, the perceived motion would be nonrigid and much slower. See Discussion for detailed discussion, as well as for further evidence of the operation of 1-D motion pooling in global-Gabor motion perception.

Global-plaid motion is a stimulus designed for tapping 2-D motion pooling. It is similar to global-Gabor motion except that each element is a plaid element (superposition of 2 sine-wave gratings windowed by a stationary Gaussian) (Fig. 1A). Although the relative orientation of the two sine-wave carriers in each Gabor is always 90° (orthogonal plaid pattern), the base orientation of each element is randomly determined. The 2-D motion direction can be computed within each patch, and the perceived global motion can be explained by the VA of those 2-D motions (Amano et al. 2009a).

For both stimuli, the size of the stationary Gaussian envelope was SD = 0.32° for MEG and 0.20° for fMRI. A total of 192 (full density) or 96 (half density) Gabors or plaids (Fig. 1A) were presented in an annular viewing aperture that had inner and outer diameters of 5° and 27° (MEG) or 3.3° and 18° (fMRI), respectively.

**Experiment 1: MEG.** The first experiment examined coherence dependency of MEG responses for full-density global-Gabor and global-plaid stimuli. In a trial, incoherent motion (0% signal, 100% noise) lasting for 1.0–1.4 s was followed by coherent motion (35, 50, 71, or 100% signal) lasting for 0.5 s (Fig. 1B). The signal Gabors/plaids had carrier motions consistent with a common global 2-D vector (leftward or rightward), whereas the noise Gabors/plaids had carrier motions consistent with 2-D vectors in random directions. The orientation of each Gabor, or the base orientation of each plaid, was
randomly updated every 200 ms from a range covering the full 180° in 10° steps for the purpose of separating responses evoked by local changes at the transition from incoherent to coherent motion. The timing of orientation update was asynchronous among Gabor elements so as to reduce the effects of local orientation changes to global cortical responses. Spatial frequencies were 1.3 cycles/°, and the contrast was set to 20%. The 2-D speed for both the signal and noise Gabors/plaids was 12.8°/s. Four hundred trials were repeated for each subject, in which motion coherence (35, 50, 71, or 100%) and signal direction (leftward or rightward) were randomly selected (100 trials for all motion coherences). Subjects were instructed to fixate on the circle presented at the center of the screen.

Experiment 1: fMRI. To supplement source localization of MEG (see Source analysis of MEG), we used fMRI to estimate the cortical locations activated by global Gabor/plaid stimuli. In each 36-s block, coherently (100% signal) and incoherently (0% signal) moving global Gabors/plaids were each presented for 18 s. During the coherent period, leftward and rightward motions were alternated every 2 s. Within a session, eight blocks were repeated, and at least two sessions (16 blocks in total) were repeated for each subject. Spatial frequencies were 1.9 cycles/°, and the contrast was set to 10%. The 2-D speed for both the signal and noise Gabors/plaids was 8.5°/s. The orientation of each Gabor was randomly updated every 500 ms, and the temporal phase of the alternation was randomized across Gabors. For the purpose of controlling attention (Huk et al., 2001), subjects were instructed to detect the color change of a fixation point (mean interval of 6 s) during the experiments. Although we first tested an event-related design for the fMRI experiment, as was used in the MEG experiments, we could not observe stable responses to the transition from incoherent to coherent motion. Because the main purpose of this fMRI experiment was to localize the neural responses involved in 1-D/2-D pooling with better spatial resolution, we decided to employ a blocked design, which has higher signal-to-noise ratio.

Experiment 1: psychophysics. The psychophysical experiment was conducted in the magnetically shielded room for the MEG measurement. The stimuli were the same as those used in the MEG experiment (35, 50, 71, or 100% coherence) except that global motion direction was randomly chosen from four candidates (leftward, rightward, upward, and downward). Saccade targets were presented at the eccentricity of 4° within the central circular region where Gabor or plaid stimuli were not presented. Subjects were instructed to make a saccade toward the target in the direction of global motion as fast as possible, and the eye movements were recorded using EyeLink 1000 (SR Research, Ontario, Canada). Reaction time (RT) was defined by the median latency of correct saccades.

Experiment 2: MEG. In the second experiment, we employed an adaptation paradigm to test whether neural responses evoked by global-Gabor stimuli are sensitive to the 2-D motion direction. After initial adaptation (60 s), we repeatedly presented a 5-s sequence consisting of a “top-up” adaptation (a short adaptation before each test for maintaining adaptation states, 4 s), a pretest stimulus (incoherent motion, 0.5 s), and a test stimulus (0.5 s) (Fig. 2). Motion coherence was 100% for both test and adaptation stimuli. The 2-D direction of the adaptation stimulus was always rightward, whereas that of the test stimulus was randomly selected between the adapted (rightward) and the opposite (leftward) directions. In the adaptation stimulus, as well as in the test stimulus, Gabor patches were presented at 96 of a possible total of 192 evenly spaced patch locations (half density).
Gabor orientations were random but were kept constant throughout an experimental session so that the 1-D motion (orientation and speed) of each patch was kept constant during the adaptation period. This experiment did not use the 5-Hz orientation update used in the first experiment to obtain maximum local adaptation. Therefore, the response included a transient response component associated with the onset of coherent motion, but this component was canceled out when we compared the response between the test stimuli moving in the adapted and nonadapted directions.

Test Gabors were presented at the same patch locations as adaptation Gabors (Fig. 2, A and B), with the orientations of test Gabors the same as (same-orientation condition) or orthogonal to (orthogonal condition) those of adaptation Gabors. Orientation of the Gabor patches for the incoherent motion presented between adaptation and test stimuli was the same as that of the test stimulus in both conditions.

We ran 100 trials for each combination of Gabor type (same-orientation and orthogonal) and test stimulus direction (adapted and nonadapted). Subjects were instructed to fixate on the circle presented at the center of the screen.

**Experiment 2: psychophysics.** To quantitatively evaluate the effect of 2-D adaptation on perceived motion, we conducted a psychophysical experiment to measure the motion aftereffect separately from
MEG measurements. This experiment was conducted in the magnetically shielded room, and the time course of the stimulus was exactly the same as in the MEG experiments. Motion coherence (8.8, 12.5, 17.7, 25, 35.4, or 50%) and global motion direction (leftward or rightward) were randomly changed across trials, with repetition of 20 trials for each combination of coherence and direction. Subjects were instructed to judge the 2-D motion direction by pressing one of two keys on a keyboard. A cumulative Gaussian function was fitted to the psychometric function, and the magnitude of the motion aftereffect was evaluated in terms of the shift of the point of subjective equality (the signed magnitude of motion coherence where the percentage of left/right response was 50%) between conditions with and without adaptation.

**MEG and fMRI data acquisition and preprocessing.** MEG responses were recorded using a whole head MEG system (PQ244OR; Yokogawa, Tokyo, Japan) in a magnetically shielded room. Data were sampled at 500 Hz with a 200-Hz low-pass filter and a 0.3-Hz high-pass filter. Our custom-made MEG system has 230 axial gradiometers and 70 vector sensors, each consisting of 1 axial gradiometer ($\partial B/\partial z$) and 2 planar gradiometers ($\partial B/\partial x$, $\partial B/\partial y$) (Amano et al. 2006a, 2006b, 2009b, 2009c). In the current study, 300 axial gradiometers were used for the analysis, which makes the comparison with previous studies easier. Before we moved on to the main analysis, trials containing eye blinks, eye movements, muscle artifacts, or signal jumps were rejected off-line from further analysis (<10% trials were removed). Noise cancellation methods such as tSSS (Taulu and Hari 2009) were not applied as preprocessing. We used FieldTrip (Oostenveld et al. 2011) for the following analyses.

T1-weighted structural MRI were recorded for all subjects with the 3T Trio, A Tim System (Siemens, Erlangen, Germany). For source reconstruction, individual single-shell models (Nolte 2003) were derived from the segmentation of these structural MRIs.

Functional MR images were acquired with the 3T Trio, A Tim System. The effective voxel size was 3 mm isotropic (field of view = 192 $\times$ 192 mm$^2$). Functional MR images (TR/TE = 1,500/40 ms, flip angle = 90°) were acquired with 20 axial slices covering lateral-occipital and temporo-occipital cortex with no gap.

**Source analysis of MEG.** To estimate the amplitude of responses at the cortical source level, we used the linearly constrained minimum variance (LCMV) beamformer (Van Veen et al. 1997), which has been proven to provide reliable source localization in many studies (Donner et al. 2007; Siegel et al. 2006, 2008). For each source location, we computed a linear spatial filter that passes activity from the source location with unit gain while maximally suppressing activity from other sources. Raw MEG data were low-pass filtered at 40 Hz and baseline-corrected before the LCMV beamformer was applied. In experiment 1, the ratio of activities between periods before ($-150$–$0$ ms) and after ($150$–$300$ ms) the onset of coherent motion was calculated. For each subject and stimulus (global-Gabor and global-plaid), the response with the 100% coherence stimulus was used to create activation maps. We also calculated the response time course within each region of interest (ROI; see ROI analyses), and the peak amplitude/latency was compared across stimulus conditions. In experiment 2, the ratio of activities after the motion onset ($150$–$300$ ms) between the test stimuli moving in the adapted and those moving in the nonadapted directions were analyzed for the same-orientation and orthogonal conditions.

In each experiment, we built a common filter using all the trials for each subject so that the differences in source estimation between stimulus conditions is not artificially produced by the differences of the spatial filter and reflects the true differences in the signals. The data were first averaged across trials to obtain the evoked response after the baseline correction and bandpass filtering, and then the common spatial filter was applied to the averaged data.

For each recording session, forward models were computed using individual single-shell volume conductor models and the measured head positions. Source reconstructions were performed on a grid for each subject that was aligned in a regular 3-D grid of 1-cm resolution. The results were averaged across subjects and then interpolated onto a 1-mm grid.

The series of FieldTrip routines used in the beamformer analysis is “ft_preprocessing” (low-pass filter and baseline correction), “ft_timelockanalysis” (calculation of covariance across all trials in all conditions), “ft_sourceanalysis” (calculation of a common spatial filter), “ft_timelockanalysis” (calculation of covariance for each condition), “ft_sourceanalysis” (application of the common spatial filter to the data for each condition), and “ft_sourcedeB boyc adverage” (average of source distribution across subjects).

**Time-frequency analyses of MEG.** Spectral analyses of the MEG data were performed using “multitaper” spectral estimates based on discrete prolate spheroidal sequences. Transformations to the frequency domain were performed on the single-trial level before data were averaged across trials. We calculated the oscillatory responses relative to the baseline period before coherent motion onsets. Time-frequency transformation was performed using a sliding-window multitaper analysis (250-ms length, 25-ms step size, ±12-Hz spectral smoothing, 5 Slepian tapers).

**Functional ROI analyses.** Data were analyzed using the mrVista analysis package (http://white.stanford.edu/software/) for MATLAB. After the slice-timing correction and motion correction, event-related analyses, including application of general linear models and hypothesis tests to generate contrast maps, were performed. The contrast map between coherent and incoherent motion was calculated for both global-Gabor and global-plaid stimuli. Z value was averaged across subjects after normalization to a template brain (Montreal Neurological Institute, MNI).

**ROI analyses.** We defined the following ROI based on anatomic criteria on the template brain (MNI) and nonlinearly aligned their positions to the individual subjects’ structural MRIs.

In both experiments 1 and 2, the hMT+/+ ROI for each subject was defined by the voxels within a sphere with a 1-cm radius centered at $x = \pm 45, y = -75, z = 0$ (MNI coordinate) (Dumoulin et al. 2000). For the four subjects who went through a hMT+/+ localizer scan with fMRI, the anatomically defined ROI matched well with the functionally defined ROI. The V1 ROI was defined by the voxels within a sphere with a 1-cm radius centered at $x = \pm 10, y = -80, z = 0$ (Dougherty et al. 2003). We also defined a putative V3A ROI, an area known to be sensitive to various kinds of visual motion, by the voxels within a sphere with a 1-cm radius centered at $x = \pm 25, y = -85, z = 30$. In addition to hMT+ and V3A, activities in IPS were also studied, since Fanini and Assad (2009) reported that the majority (61%) of lateral intraparietal (LIP) neurons are direction selective. The putative IPS1/2 ROI, reported to be a human homolog of LIP (Silver and Kastner 2009), was defined by the voxels within a sphere with a 1-cm radius centered at $x = \pm 20, y = -75, z = 45$ (Silver 2005; Swisher et al. 2007). The results for left and right ROI were pooled for each location.

**RESULTS**

**Experiment 1: MEG responses to global-Gabor and global-plaid motions.** We used global-Gabor motion to drive the neural mechanism for 1-D motion pooling (simultaneous integration of local 1-D motion signals across orientation and space) (Amano et al. 2009a). The first experiment was designed to identify the cortical areas that showed, as an index of the brain activity correlated with 1-D motion pooling, an increase in activity as a function of the level of motion coherence (proportion of signal elements embedded in noise elements). In addition to global-Gabor motion, we also used global-plaid motion to drive the neural mechanism for 2-D motion pooling (spatial integration of local 2-D motion signals, each derived from local integration of 1-D motion across
orientation) (Amano et al. 2009a). The question addressed was how similar, or different, the cortical activity for 1-D pooling and that for 2-D pooling were. As described in the Introduction, past studies have indicated that 1-D pooling and 2-D pooling are functionally different computations driven by different stimuli (Amano et al. 2009a) and may be carried out in separate cortical areas (Majaj et al. 2007). This section describes the results of the main MEG experiment, and the next section describes the supporting data obtained with fMRI.

We recorded MEG responses evoked by the onset of these motion stimuli at four coherence levels (Fig. 1; see MATERIALS AND METHODS, Experiment 1: MEG, for details). Figure 3, A and B, shows an example of overlaid waveforms and isocontour maps of MEG responses to 100% global-Gabor and global-plaid motion, low-pass filtered at 40 Hz and averaged across trials. For both stimuli, the response peaked at around 200–250 ms from the motion onset. Isocontour maps (Fig. 3B), computed from the averaged data of a single subject within a 20-ms window around the peak latency (indicated by a gray band in Fig. 3A), were similar between the two stimuli and were also similar to those obtained for the onset of grating motion (Amano et al. 2005, 2006b) or for the onset of coherent random-dot motion (Amano et al. 2005). An extra peak around 180 ms was found for the global-plaid stimulus, and comparison of the isocontour map between global-Gabor and global-plaid stimuli suggests that the activity in the right hemisphere is less prominent for global-Gabor, at least for this subject, but this initial peak was not clearly observed for the other subjects.

To estimate the source location of the responses evoked by coherent global-Gabor or global-plaid motion stimuli, we applied the LCMV beamformer on the response low-pass filtered at 40 Hz (see MATERIALS AND METHODS, Source analysis of MEG). Figure 3C shows the time course of MEG responses averaged over the voxels within the left hMT+ ROI (see MATERIALS AND METHODS; ROI analyses) for different magnitudes of motion coherence of global-Gabor and global-plaid motion. The time course is from the subject whose overlaid waveform and topographical maps are shown in Fig. 3, A and B. The left hMT+ response peaked around 200–250 ms from stimulus onsets, and the peak amplitude increased with motion coherence for both stimuli.

Figure 4 shows the activation pattern of 100% coherent global-Gabor or global-plaid stimuli, averaged across all subjects. The beamformer analysis indicated neural activities in a temporo-occipital area of both hemispheres, close to hMT+ (Ahlfors et al. 1999; Bundo et al. 2000; Hasnain et al. 1998; Kawakami et al. 2002; Matsumoto et al. 2004). The source distribution was similar between global-Gabor and global-plaid stimuli, and the averaged coordinate of the voxel within the temporo-occipital area that showed the maximum response during the stimulus period (0.15–0.3 s) was similar between global-Gabor (means ± SE; $x = -48.8 \pm 4.0, y = -66.3 \pm 2.6, z = -1.3 \pm 3.5$ for the left hemisphere and $x = 55.0 \pm 2.7, y = -76.3 \pm 3.8, z = 0 \pm 3.8$ for the right hemisphere) and global-plaid stimuli ($x = -53.8 \pm 2.6, y = -70.0 \pm 4.2, z = 0 \pm 3.3$ for the left hemisphere and $x = 48.8 \pm 3.5, y = -72.5 \pm 3.7, z = 2.5 \pm 3.1$ for the right hemisphere). These

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**Fig. 3.** MEG responses evoked by global-Gabor and global-plaid stimuli at 100% coherence. A: overlaid waveform for a single subject. A vertical black line indicates the timing of stimulus onset, a change from incoherent to coherent motion. B: isocontour maps of the global-Gabor and global-plaid responses for 100% coherence, averaged within a 20-ms window around the peak latency, indicated by the shaded region in A. Both isocontour maps indicate the stimulus onset evoked activity in temporo-occipital areas. C: time course of left human MT complex (hMT+) response evoked by global-Gabor and global-plaid stimuli at each coherence level, calculated by linearly constrained minimum variance (LCMV) beamformer. The time course is from the subject whose overlaid waveform and topographical maps are shown in A and B.
coordinates are in good agreement with the location of hMT+ indicated in the fMRI literature (Dumoulin et al. 2000). This suggests that the brain areas involved in 1-D pooling and 2-D pooling are indistinguishable, at least at the limited spatial resolution of MEG. Readers might notice in Fig. 4 that the activity in the right hemispheres appears to be larger for the global-plaid stimulus than for the global-Gabor stimulus. However, the asymmetry was not systematic across subjects and was not statistically significant.

Figure 5 shows the effect of motion coherence on the peak amplitude and peak latency of V1, hMT+, and putative V3A and IPS responses, averaged across all subjects (see MATERIALS AND METHODS, ROI analyses). The data were pooled across hemispheres, because the asymmetry was not significant. Two-way repeated-measures ANOVA (coherence/stimulus type) was conducted for both the peak amplitude and latency. The peak amplitude of hMT+ significantly increased with motion coherence \[ F(1.8, 27.6) = 43.5, P < 0.001 \], and the slope of the linear regression was significantly greater than 0 \( P < 0.05 \) except for the global-Gabor response in IPS. The stimulus type (global-Gabor vs. global-plaid) did not have a significant effect on the peak amplitudes. The peak latency was affected by neither motion coherence nor stimulus type in all 4 ROI.
the linear regression was significantly larger than zero for both global-Gabor and global-plaid stimuli \( (P < 0.05) \). There was no significant difference between global-Gabor and global-plaid stimuli. The peak latency was systematically affected by neither motion coherence nor stimulus type. The interaction was not significant for both amplitude and latency. Mauchly’s sphericity test showed that the assumption of sphericity is violated for the effect of coherence and interaction on the amplitude, so the degree of freedom was corrected with Huynh-Feldt correction.

V3A activity was much weaker but showed similar tendencies, and the effect of motion coherence on the peak amplitude was significant \( [F(3,45) = 16.4, P < 0.001] \). Neither the effect of stimulus type nor the interaction was significant. The effect of coherence, the effect of stimulus type on the peak latency, and their interaction were not significant. Mauchly’s sphericity test showed that the sphericity assumption was not violated.

In addition to hMT+ and V3A, the involvement of parietal areas in motion perception has been suggested in several studies (Fanini and Assad 2009; Williams et al. 2003). In agreement with this, the peak amplitude of IPS also showed significant dependency on coherence \( [F(2,1,31.6) = 11.6, P < 0.001] \), and the slope of the linear regression was significantly larger than zero for the global-plaid stimulus (Fig. 6). There was no significant difference between global-Gabor and global-plaid stimuli. The peak latency was systematically affected by neither motion coherence nor stimulus type. The interaction was not significant for both the amplitude and latency. Mauchly’s sphericity test showed that the assumption of sphericity was not violated.

Finally, V1 peak amplitude also showed significant dependence on the coherence of global-Gabor or global-plaid motion \( [F(3,45) = 19.4, P < 0.001] \). The effect of stimulus type and the interaction were not significant. Statistical details of each ROI are summarized in Table 1.

In summary, the beamformer analysis showed the cortical activity responding to the motion coherence of global-Gabor motion \( (1-D\text{ motion pooling}) \) in hMT+, V3A, IPS, and V1, but it was not significantly different, in any region, from the cortical activity responding to the motion coherence of global-plaid motion \( (2-D\text{ motion pooling}) \).

Because the inverse problem of MEG is ill posed, and source localization results are dependent on the localization method, we also analyzed the data with minimum norm estimates \( \text{(MNE)} \), which is another typical source localization technique (Hamalainen and Ilmoniemi 1994). The results were similar between beamformer and MNE (data not shown). The peak amplitude was significantly increased by coherence for both hMT+ and IPS \( [F(3,45) = 5.6, P = 0.002, \text{and } F(3,45) = 3.4, P = 0.03, \text{respectively}] \). The effect of stimulus type was not significant in any areas. The peak latency in hMT+, V3A, and IPS ROI was systematically affected by neither motion coherence nor stimulus type. However, unlike the beamformer analysis, the MNE analysis indicated that neither V1 nor V3A was significantly affected by coherence. With regard to this discrepancy, fMRI results showed coherence-dependent responses in V1 and V3A (see below), supporting the results of beamformer analysis. The MNE analysis is not very sensitive to deep cortical activity, and this may be the reason why it was less sensitive to the activity in V1 and V3A.

Consider next the temporal aspects of MEG responses. Although the peak latency and amplitude of stimulus-locked evoked response was similar between global-Gabor and global-plaid stimuli (Fig. 5), the time-frequency analysis in the sensor domain (see MATERIALS AND METHODS, Time-frequency analyses of MEG) indicated that the onset latency of alpha and beta

![Fig. 6. Results of sliding-window multitaper analysis (5-cycle window length, 25-ms step size, spectral smoothing of 0.4 × center frequency), averaged across trials, each block of sensors (40 sensors around right/left temporal area and 80 sensors around occipital area), coherence levels, and subjects. Suppression of 10- to 40-Hz activity relative to baseline \( (0.2–0.8 \text{ s}) \) was prominent for both stimuli. Also, the suppression was more pronounced for global-plaid than for global-Gabor stimuli, and its onset latency was faster.](http://jn.physiology.org/DownloadedFrom)
activities tends to be earlier for global-plaid than for global-Gabor motion (Fig. 6). In this analysis, the estimated power reflects not only evoked responses but also induced responses, given that time-frequency analysis was first applied on single-trial data before data were averaged across trials. The difference in the onset latency might reflect a difference in computation between global-Gabor and global-plaid motion.

To see whether there is a behavioral correlate of the latency difference of the oscillatory activities between global-Gabor and global-plaid motion (Fig. 6), we additionally measured RT to the coherence onset of global-Gabor and global-plaid stimuli for seven subjects (see MATERIALS AND METHODS, Experiment 1: psychophysics). The results indicated a decrease in RT with motion coherence \(F(3,18) = 18.9, P < 0.001\) (Fig. 7), which can be accounted for by the integrator model of time-locked MEG response (Amano et al. 2006a). This is because an increase in the peak amplitude reduces the latency for the integrated response to exceed a certain threshold. The results also showed that RT was shorter for global-plaid than for global-Gabor stimuli by about 50–80 ms, and the difference was significant \(F(1,6) = 8.8, P = 0.02\). This difference in behavioral RT might be related to larger delta and beta activities and their shorter onset latencies for global-plaid stimuli than for global-Gabor motion.

Experiment 1: BOLD responses to global-Gabor and global-plaid motions. The first MEG experiment indicated the similarity of cortical activity for 1-D motion pooling and 2-D motion pooling, including the strong responses in hMT+. For the purpose of obtaining further evidence of this finding, we also measured fMRI responses to 100% and 0% global-Gabor stimuli or global-plaid stimuli (see MATERIALS AND METHODS, Experiment 1: fMRI). Figure 8A shows the regions significantly activated by 100% coherence compared with 0% coherence for global-Gabor stimuli or global-plaid stimuli, averaged across subjects. The results clearly show that coherent global-Gabor/global-plaid motion activated hMT+ in both hemispheres, supporting the source localization of MEG responses. The averaged coordinates of the voxel within the temporo-occipital area that showed the maximum response were again similar between global-Gabor \((x = -51.0 \pm 1.8, y = -71.0 \pm 1.0, z = -3.0 \pm 2.5\) for the left hemisphere and \(x = 42.0 \pm 2.0, y = -66.0 \pm 2.4, z = 1.0 \pm 3.3\) for the right hemisphere) and global-plaid stimuli \((x = -49.0 \pm 2.4, y = -67.0 \pm 1.2, z = 0.0 \pm 2.7\) for the left hemisphere and \(x = 45.0 \pm 3.2, y = -64.0 \pm 1.0, z = 3.0 \pm 2.0\) for the right hemisphere). These coordinates are consistent with the peak location of MEG sources and with fMRI studies that used

Table 1. Effect of stimulus type and motion coherence on peak amplitude or peak latency of V1, hMT+, V3A and IPS responses

<table>
<thead>
<tr>
<th></th>
<th>V1</th>
<th>hMT</th>
<th>V3A</th>
<th>IPS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DOF F value P value</td>
<td>DOF F value P value</td>
<td>DOF F value P value</td>
<td>DOF F value P value</td>
</tr>
<tr>
<td>LCMV</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stimulus</td>
<td>1 1.1 0.31</td>
<td>1 0.10 0.76</td>
<td>1 1.9 0.19</td>
<td>1 0.12 0.73</td>
</tr>
<tr>
<td>Coherence</td>
<td>3 19.4 &lt;0.001</td>
<td>1.8 43.5 &lt;0.001</td>
<td>3 16.4 &lt;0.001</td>
<td>2.1 11.6 &lt;0.001</td>
</tr>
<tr>
<td>Interaction</td>
<td>3 1.5 0.24</td>
<td>3 0.50 0.68</td>
<td>3 0.87 0.47</td>
<td>3 1.9 0.14</td>
</tr>
<tr>
<td>MNE</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stimulus</td>
<td>1 0.011 0.92</td>
<td>1 0.005 0.95</td>
<td>1 0.12 0.74</td>
<td>1 0.12 0.74</td>
</tr>
<tr>
<td>Coherence</td>
<td>3 2.5 0.073</td>
<td>3 5.6 0.002</td>
<td>3 0.67 0.57</td>
<td>3 3.4 0.03</td>
</tr>
<tr>
<td>Interaction</td>
<td>3 1.7 0.18</td>
<td>3 0.12 0.95</td>
<td>3 0.80 0.47</td>
<td>3 0.70 0.56</td>
</tr>
</tbody>
</table>

Data are degrees of freedom (DOF), F value, and P values indicating the effects of stimulus type and coherence, as well as their interaction, on peak amplitude or peak latency of V1, human MT complex (hMT+), V3A, and intraparietal sulcus (IPS) responses. Each activity was estimated with linearly constrained minimum variance (LCMV) beamformer and minimum norm estimates (MNE).

Fig. 7. Reaction time to the onset of coherent global-Gabor and global-plaid motion, as a function of coherence. The stimulus was exactly the same as in the MEG experiment (Fig. 1), and the reaction time was measured by the onset timing of saccade. The error bars show SE across subjects. The reaction time decreased significantly with motion coherence, and the difference between global-Gabor and global-plaid stimuli was significant.
We calculated the BOLD amplitude within V1, hMT+V3A, and IPS ROI for each stimulus. Figure 8B shows the Z value averaged across all voxels within ROI. Two-way ANOVA suggested that the main effect of stimulus was not significant, whereas that of area was significant [F(3,27) = 5.9, P = 0.003]. The post hoc test suggested that the difference between hMT+ and IPS (P = 0.008) and the difference between V3A and IPS (P = 0.019) were significant. The results suggest that the responses evoked by the contrast between 100% and 0% global-Gabor motion is the strongest in hMT+ and that this area is a main processing locus for 1-D motion pooling and 2-D motion pooling, as well as for 2-D motion pooling.

Figure 9 compares the activity pattern across two methodologies (MEG and fMRI) and across two stimuli (global-Gabor and global-plaid) at three axial slices. The activity in hMT+ is evident for both stimuli and for both fMRI and MEG (middle slice of each panel in Fig. 9). The activated location matches the conventional hMT+ localizer (Dumoulin et al. 2000). In addition to hMT+, V3A of both hemispheres was activated by coherent global-Gabor and global-plaid motions. The averaged coordinates of the voxel around V3A that showed the maximum response were again similar between global-Gabor (x = −27.0 ± 3.4, y = −89.0 ± 3.7, z = 23.0 ± 3.0 for the left hemisphere and x = 24.0 ± 4.8, y = −89.0 ± 4.3, z = 17.0 ± 3.7 for the right hemisphere) and global-plaid stimuli (x = −22.0 ± 2.0, y = −93.0 ± 2.5, z = 17.0 ± 3.0 for the left hemisphere and x = 17.0 ± 2.5, y = −92.0 ± 2.5, z = 23.0 ± 4.4 for the right hemisphere). The activated regions (hMT+ and V3A) were very similar between global-Gabor and global-plaid stimuli, suggesting that neural populations involved in 1-D motion pooling and 2-D motion pooling are not distinguishable with the resolution of the cortical structure of V3A is not ideal for MEG measurement, which is not very sensitive to the activities in gyrus.

The data were averaged across hemispheres and subjects, and the error bars show SE across both. The first series of experiments revealed a close similarity in cortical activity between 1-D motion pooling and 2-D motion pooling, including strong responses in hMT+ in both cases. The second experiment focused on the neural correlates of 1-D motion pooling and examined the nature of their representations from the effect of motion adaptation on MEG responses. We controlled the magnitudes of local and global adaptations to see whether the cortical activity shown by a given cortical area actually represented the global-motion component of 1-D motion pooling. Prolonged observation of a moving pattern results in the motion aftereffect in which a physically static pattern appears to move in the opposite direction (Mather et al. 1998). We investigated MEG responses measured while motion af-
tereffects were induced after adaptation to a global-Gabor stimulus globally moving leftward with 100% coherence. The test stimulus was a global-Gabor stimulus globally moving leftward or rightward. The orientation of each Gabor was randomly determined for the adaptation stimulus, whereas that for the test stimulus was the same as (same-orientation condition, Fig. 2A) or orthogonal to (orthogonal condition, Fig. 2B) that for the adaptation stimulus. We estimated a direction-selective response from the difference in test activity between the adapted and nonadapted test directions. We expected that the direction-selective response in the same-orientation condition would reflect adaptation of local detectors as well as adaptation of the 1-D pooling system. On the other hand, because local adaptation was minimized in the orthogonal condition, we expected that the direction selectivity in this condition would mainly reflect adaptation of the 1-D pooling system.

Figure 10A shows an example of psychometric functions obtained in a psychophysical experiment carried out separately from MEG measurements. The horizontal axis is the motion coherence of the test stimulus. The negative and positive coherences correspond to nonadapted (leftward) and adapted (rightward) motion directions, respectively (see MATERIALS AND METHODS, Experiment 2: psychophysics). Adaptation increased the rate at which the test direction was seen as opposite to the adapted direction, thereby shifting the psychometric function compared with the no-adaptation condition (baseline condition). Figure 10B shows the magnitude of the motion aftereffect, evaluated in terms of lateral shift of psychometric function, averaged across subjects. Response bias measured without presenting an adaptation stimulus was subtracted from the data. In both the same-orientation and orthogonal conditions, significant shifts of psychometric function indicated clear induction of motion aftereffect \( t(4) = 3.7, P = 0.02, \) and \( t(4) = 6.2, P < 0.005, \) respectively. The difference between the same-orientation and orthogonal conditions was not significant. As noted above, the motion aftereffect observed in the orthogonal condition can be ascribed mainly to adaptation to 2-D global motion produced by 1-D motion pooling.

We studied 2-D direction selectivity of MEG responses using stimuli exactly the same as those used in the psychophysical experiment except that the test coherence was always 100%. Figure 11A shows the averaged source distributions, estimated by LCMV beamformer, for each condition (see MATERIALS AND METHODS, Source analysis of MEG). A difference in activity between adapted and nonadapted test stimuli was found in the region around hMT+ in both the same-orientation and orthogonal conditions. The averaged coordinates of the voxel within the temporo-occipital area showing the maximum difference between adapted and nonadapted test stimuli were very similar to the coordinates showing the maximum response in experiment 1 (see MATERIALS AND METHODS, ROI analyses). Figure 11B shows the MEG amplitude evoked by the nonadapted 2-D direction divided by that evoked by the adapted 2-D direction. Direction-selective adaptation makes this ratio <1.0. Both V1 and hMT+ showed direction-selective adaptation in the same-orientation condition, whereas only hMT+ showed direction-selective adaptation in the orthogonal
condition. These results suggest that hMT+ responses evoked by coherent global-Gabor motion are sensitive to the 2-D direction, and thus reflect the 1-D pooling computation (i.e., simultaneous integration of 1-D signals across orientation and space). For both V3A and IPS, the activity ratio was not significantly different from 1 in either adaptation condition ($P > 0.05$).

**DISCUSSION**

Human psychophysical performance indicates that the human visual system adaptively switches between 1-D motion pooling and 2-D motion pooling depending on whether the aperture problem can be solved locally or globally (Amano et al. 2009a). Neural activities involved in the two stages of 2-D motion pooling have been extensively studied, with plaid stimuli (in which 2 drifting gratings at different orientations are superimposed) for cross-orientation integration and with global motion stimuli (consisting of moving random dots, some of which are coherently moving in the same direction) for spatial integration (Aspell et al. 2005; Britten et al. 1993; Lam et al. 2000; Movshon et al. 1985; Nakamura et al. 2003; Newsome et al. 1989; Rees et al. 2000; Salzman et al. 1992; Siegel et al. 2006; Smith et al. 2005). Both cross-orientation integration and spatial integration are localized in monkey MT or in hMT+.

On the other hand, the neural substrates of 1-D motion pooling remain unspecified. The current study shows a close similarity between cortical areas contributing to 1-D motion pooling and those contributing 2-D motion pooling. It further presents several lines of evidence supporting hMT+ as being the locus of 1-D motion pooling, as well as that of 2-D pooling.

### 1-D motion pooling vs. 2-D motion pooling

Consider first the relationship between 1-D motion pooling and 2-D motion pooling. It is theoretically possible for the 2-D motion pooling process to detect global 2-D motion from global-Gabor stimuli by means of taking the orthogonal motion vector as a default solution of the aperture problem at each location and then integrating those orthogonal vectors over space. One might therefore suspect that global-Gabor motion is detected by the 2-D motion pooling process and that this is the reason we found no difference in the pattern of cortical activity between global-Gabor and global-plaid stimuli. However, this interpretation is inconsistent with a number of psychophysical findings (Amano et al. 2009a). First, if orthogonal motion vectors are spatially pooled, the perceived global-Gabor motion should be highly nonrigid and have a speed about one-half that of the true 2-D global motion. However, the perceived global motion for a 100% coherent global-Gabor stimulus is rigid and as fast as the true 2-D motion (whereas the perceived motion for a global-plaid stimulus that simulates local orthogonal motions of a coherent global-Gabor stimulus is nonrigid and slow) (Amano et al. 2009a). This indicates that global-Gabor stimuli activate the 1-D pooling process, which approximately follows the IOC rule, rather than the 2-D pooling process, which approximately follows the VA rule. In addition, the perceived direction of global-Gabor motion consisting of two symmetric 1-D components (type I) remains nearly veridical even when the relative orientation density is significantly varied (Amano et al. 2009a). This is also consistent with IOC-based 1-D pooling, but not with VA-based 2-D pooling. Finally, although the perceived direction of type II global-Gabor motion, in which the two component orthogonal vectors were both located on one side of the global 2-D vector, is not perfectly consistent with the IOC prediction (because the perceived motion is nonrigid), it is significantly shifted away from the VA prediction, in the direction of the IOC prediction (Amano et al. 2009a).

Despite these clear psychophysical differences in the rule of motion pooling between global-Gabor stimuli (1-D pooling) and global-plaid stimuli (2-D pooling), in the present study we found very similar cortical activities near hMT+ for both stimuli. One possible reason is that the same neurons can integrate both 1-D signals and 2-D signals and switch the computation depending on the information available (Huang et al. 2007). It is also possible that different subpopulations of neurons are involved in 1-D pooling and 2-D pooling, but the difference is not detectable by measuring overall population activity.

We also found a notable difference between 1-D pooling and 2-D pooling: behavioral RT was shorter for global-plaid onset than for global-Gabor onset by about 50–80 ms. This decrease in RT might be related to a previous study showing that MT neurons initially respond primarily to the component of motion
Fig. 11. Direction selectivity of MEG responses to global-Gabor stimulus. A: ratio of source power between nonadapted and adapted test stimuli for the same-orientation and orthogonal conditions. A difference in activity was found in the region around hMT+ in both conditions. B: the MEG amplitude evoked by the nonadapted 2-D direction divided by that evoked by the adapted 2-D direction, averaged across all subjects. The error bars show SE across subjects. Both V1 and hMT+ showed direction-selective adaptation in the same orientation condition, whereas only hMT+ showed direction-selective adaptation in the orthogonal condition. *P < 0.05; **P < 0.01; ***P < 0.001.

perpendicular to a contour's orientation, but the responses gradually shift to encode the true stimulus direction over a period of ~60 ms (Pack and Born 2001). Longer RTs for the global-Gabor stimuli might reflect the process to calculate global 2-D motion from locally ambiguous motion. This process can be more time-consuming than the local calculation of 2-D motion, which is enough for the detection of global motion direction of global-plaid stimuli, at least for high coherence levels. Increased delta and beta activity and their earlier onset for global-plaid stimuli might correspond to this local 2-D motion calculation. We cannot exclude the possibility that global-plaid motion captures more attention than global-Gabor motion, which would result in shorter RTs and shorter onset latencies of beta for global-plaid stimuli, although there is no direct evidence of such a difference in attentional capture strength. Further study is necessary to elucidate the temporal differences between these two types of stimuli.

1-D motion pooling in hMT+. The current study shows that hMT+ plays a critical role in 1-D motion pooling. The beamformer analysis of MEG responses to global-Gabor stimuli revealed neural activities in the temporo-occipital area of both hemispheres, close to hMT+. The activity in this area showed a proportional increase with the motion coherence of the global-Gabor stimuli. The MEG response to global-plaid stimuli, which expectedly tapped the 2-D pooling process, was also localized at similar cortical locations. Furthermore, fMRI response to coherent global-Gabor motion, along with that to global-plaid motion, was localized at similar cortical locations around hMT+. Finally, the MEG response at hMT+ showed direction-selective adaptation to the global motion component of global-Gabor motion.

In apparent disagreement with the hMT+ activity evoked by global-Gabor motion, Majaj et al. (2007) did not find evidence that monkey MT neurons spatially integrate 1-D motion signals. One possible reason for this discrepancy is that MEG and single-unit recording measure different aspects of neuronal activities. It is generally accepted that MEG mainly measures excitatory postsynaptic potential (EPSP) of a population of neurons, which can be dissociated from spiking activities. Although a recent study suggested that multi-unit activity is correlated with the gamma-band power and delta-band phase of EEG (Whittingstall and Logothetis 2009), the relation between MEG/EEG responses and unit activities remains to be clarified. Another possible reason is that Majaj et al. (2007) simplified the stimulus into a grating pair that did not yield perceptual integration and thus did not activate the 1-D pooling process. It has been shown that the same neurons can change the way motion is integrated depending on the stimulus (Huang et al. 2007). It would be of interest to see how those neurons respond to 1-D motion stimuli that yield good perceptual integration. Indeed, a recent conference presentation that used stimuli similar to global-Gabor concluded that monkey MT neurons integrate spatially distributed 1-D motion signals (Clark and Bradley 2008). Given the limited spatial resolution of MEG, it is also possible that the motion pooling activities we observed were mainly from MST, which we did not analyze separately from MT. In the future, it would be interesting to use high-resolution fMRI to separate the responses of MT and MST (Amano et al. 2009d) to the global-Gabor stimulus. Furthermore, lesion studies to test if 1-D pooling deficit is always accompanied by 2-D pooling deficit would be critical to the argument as to whether 1-D and 2-D pooling share common neural substrates.

Rust et al. (2006) proposed a cascade linear-nonlinear model operating on the afferent responses of a population of nonlinear V1 neurons to account for both component MT cells and pattern MT cells. Their model successfully accounted for the response to several plaid stimuli but cannot deal with the 1-D pooling because it implicitly assumes that orientation integration is local. The current experiment suggests that relaxing this assumption might be necessary under some stimulus conditions.

1-D motion pooling in other cortical areas. The MEG activity showed a proportional increase with the motion coherence not
only in hMT+ but also in V1, V3A, and IPS. However, the fMRI response to coherent global-Gabor/plaid motion was weak in IPS. V1, V3A, and IPS did not show direction-selective adaptation to the global motion component of global-Gabor motion. Therefore, the present findings indicate that hMT+ is the central area involved in 1-D motion pooling, although V1, V3A, and IPS might also be involved in the cortical network for global motion processing.

There is a report that 9% of V1 cells of the awake macaque are sensitive to the 2-D direction of plaid (Guo et al. 2004). Although the stimulus used in this study was significantly different from ours, we cannot exclude a possibility that a small proportion of V1 neurons responded to global 2-D motion in our case as well. However, the response of visual areas might increase with the coherence of global-Gabor motion even when those areas do not explicitly represent global motion. Although our stimulus was designed in such a way that different elements stimulate different local motion sensors, some sensors located at element boundaries might be stimulated by more than one element. This accidental motion integration by local motion sensors could increase the cortical response in proportion to the motion coherence of the stimulus. Because the accidental motion integration will not lead to a proper global motion, psychophysics can exclude this factor by asking the observer to make accurate judgments about global motion (e.g., choice from 8 possible directions) (Amano et al. 2009a). On the other hand, the MEG and fMRI measurements we report in the first experiment cannot exclude this factor because they are sensitive to population activities. This might explain why early visual areas like V1 showed coherence dependency but not direction-selective adaptation to global motion. Another factor that might cause the coherence-dependent V1 response is attention. It has been shown that V1 response is highly susceptible to attention (Watanabe et al. 2011). If higher coherence captures more attention, a stronger V1 response could be induced.

V3 has been found in macaque to have cells sensitive to the pattern direction of plaid (Gegenfurtner et al. 1997), although the proportion is relatively low (3/39). Our fMRI result suggests that V3A, which might partly overlap with V3, is activated by coherent global-Gabor and global-plaid motions.

Using an ambiguous apparent motion display, Williams et al. (2003) found that the responses of many LIP neurons correlated with perceived motion direction, whereas the correlation was weaker for MT and MST neurons. Their results suggest that parietal neurons reflect perceived motion more strongly than MT and MST neurons. Fanini and Assad (2009) found that a majority (61%) of LIP neurons are direction selective and that the tuning bandwidth is much wider than that for MT neurons. We found that IPS shows significant coherence dependency (Fig. 5), although the direction selectivity to 2-D motion was not significant (Fig. 8B). These results might suggest that IPS, as well as hMT+, is involved in 1-D pooling, but the functional difference between these areas is not clear from the current study.

One fMRI study has examined cortical activities related to 1-D motion pooling (Fang et al. 2008), but the interest was not in motion processing per se but in how shape processing in V1 and the lateral occipital complex (LOC) is modulated by motion-based perceptual grouping. This is unlikely a relevant factor in our study, because global motion perception with our global-Gabor and global-plaid stimuli was not accompanied by correlated shape changes.

Effects of motion coherence on MEG and fMRI responses. The cortical map shown in Fig. 8 is the result of an fMRI experiment in which we compared the cortical response between 0% coherence and 100% coherence. In a preliminary experiment, we also measured BOLD responses to global-Gabor and global-plaid stimuli while changing the motion coherence continuously, but unlike in MEG measurements, we could not find a linear increase in the BOLD response. A recent fMRI study (Kayser et al. 2010) suggests a possible account of this result: it shows that hMT+ activity increases with coherence of random-dot motion if the task is motion irrelevant, but rather decreases with coherence if the task is motion relevant. Because we asked the participants to perform a motion-irrelevant fixation task during fMRI measurements, the effect of motion coherence could have been apparently reduced by a top-down modulation. In contrast, the peak amplitude of MEG responses showed very clear coherence dependency irrespective of the concomitant task, which suggests that time-locked MEG responses might reveal bottom-up sensory motion responses more directly than fMRI responses. This is a potential advantage of MEG over fMRI in the study of sensory processing of global coherent motion but certainly requires further clarification.

Siegel et al. (2006) reported gamma-band modulation as a function of motion coherence. Our global-plaid stimuli are similar to their coherent random-dot motion in the sense that subjects perceive global motion by spatially integrating local 2-D signals. In the current study, we did not find such modulation in hMT+, although the gamma activity in IPS tended to increase with coherence (P < 0.1) (data not shown). Several studies have also failed to replicate their result (Handel et al. 2007; Holiday and Meese 2008). This could be because a laboratory environment with very small noise is necessary to obtain their effects, since modulation of gamma-band activity is very small. Further studies are necessary to elucidate the functional role of gamma-band activity in motion processing.

Conclusions. In the current study, we attempted to specify the neural substrate of 1-D motion pooling by using global-Gabor motion, an optimal stimulus for this purpose (Amano et al. 2009a). Although the response to coherent global-Gabor motion was found in several areas, including V1, hMT+, V3A, and IPS, direction selectivity to global-Gabor motion was found only in hMT+. These results provide the first evidence that hMT+ is the locus of 1-D pooling, in addition to that of 2-D pooling.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.
AUTHOR CONTRIBUTIONS

REFERENCES


