Distribution of colour-selective activity in the monkey inferior temporal cortex revealed by functional magnetic resonance imaging

Takuya Harada

DOCTOR OF PHILOSOPHY

Department of Physiological Sciences

School of Life Science

The Graduate University for Advanced Studies

2010

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Abstract

In monkey visual cortex, colour information is primarily processed in the ventral pathway through areas V1, V2, and V4 into the inferior temporal (IT) cortex. Recent studies have shown that the IT cortex, which is situated at the final processing stage of the ventral visual pathway, plays an important role in colour processing. Single cell recording studies have shown that there are numerous colour-selective neurons in the IT cortex, some of which are narrowly tuned to hues and/or saturations and exhibit task-related responses during colour discrimination. In addition, lesion studies have shown that bilateral ablation of the IT cortex disrupts colour discrimination, though ablation of V4 does not. Although many colour-selective neurons have been found in the IT cortex, their distribution in this cortical region remains not fully clear, especially in the anterior part of the IT cortex. In the present study, we explored the distribution of colour-selective activity in the IT cortex using functional magnetic resonance imaging (fMRI) in alert macaque monkeys.

As exploratory examinations, we have measured retinotopic organization, motion-selective activity and shape-selective activity of the visual cortex. The retinotopic organization was obtained by comparing responses to the horizontal meridian and vertical meridian stimuli and was helpful in determining the boundaries of visual areas. The motion-selective activity was obtained by contrasting response to moving random-dot stimuli with that to static random-dot stimuli and used to determine the physiological isoluminance point

of colour grating. The shape-selective activity was obtained by contrasting responses to object image stimuli and scrambled image stimuli. The distribution of the shape-selective activity was later compared with that of the colour-selective activity. These exploratory experiments were required for analyzing the results in the main experiment.

In the main experiments, we examined colour-selective activity in the IT cortex with two types of stimuli: an isoluminant colour grating and a multicoloured ('Mondrian') pattern that have been commonly employed in human fMRI and have identified colour-selective areas/regions in the fusiform gyrus, which is suggested to correspond to the monkey IT cortex. The paradigm using gratings is to compare responses to an isoluminant, colour-varying grating (e.g. a red-blue grating) with responses to a luminance-varying grating. This paradigm identified colour-selective regions in the posterior part of the human fusiform gyrus that is called V8/VO. The paradigm using Mondrian is to compare responses to a multicoloured ('Mondrian') pattern with responses to its achromatic counterpart. This paradigm identified colour-selective regions in the more anterior part of the fusiform gyrus, in addition to the posterior part. Earlier imaging studies of the monkey IT cortex used only the first paradigm, but the second paradigm may elicit more effectively the colour-selective activity in the anterior IT according to the findings in human fMRI. Moreover, Mondrian stimuli may be more suitable for activating higher areas, since the stimuli containing various hues could elicit responses from many neurons, each tuned to a specific hue. For that reason, we have used both grating and Mondrian stimuli to examine colour-selective activity in the

IT cortex. As a result, we found that colour-selectivity is not uniformly distributed in the IT cortex, but is clustered in discrete subregions that are located in the posterior and the anterior part of the IT cortex. The colour-selective activity in the posterior IT was obtained both with the grating and Mondrian stimuli, but the positions of the activity were different dependent on the stimuli. On the other hand, the colour-selective activity in the anterior IT was obtained only with the Mondrian stimuli.

We have examined whether these topographical differences of colour-selective activity depending on the stimuli were attributable to the difference in the luminance contrast between the chromatic Mondrian stimuli and colour grating stimuli: although the luminance contrast in the chromatic Mondrian stimulus matched that in the achromatic Mondrian, the colour grating stimulus contained much smaller amount of luminance contrast than the luminance grating. To examine the possible influence of the luminance contrast in the chromatic Mondrian stimuli, we employed isoluminant Mondrian stimuli that contained much less luminance contrast than the achromatic ones, and compared the distributions of colour-selective activity obtained with this isolumiant Mondrian, the Mondrian containing matched luminance contrast and the isoluminant grating. The results have shown that the topography of the colour-selective activity obtained with the isoluminant Mondrian was very similar to that obtained with the Mondrian containing matched luminance contrast whereas it was very different from that obtained with the isoluminant grating. This indicates that the difference in the distribution of the responses to the Mondrian and grating stimuli in the IT

cortex cannot be attributed solely to the difference in luminance contrast.

We finally compared the distribution of colour-selective activity with that of shape-selective activity in the IT cortex. We found that the colour- and shape-selective activity tends to overlap little in the anterior IT whereas the colour-selective activity in the posterior IT and early visual areas overlapped with the shape-selective activity. This finding was consistent with the results of previous electrophysiological recording experiments comparing the responses of neurons to colour and shape stimuli and suggests that colour and shape information is clustered in different modules specifically tuned to each attribute.

The present study shows that colour-selective activity is clustered in discrete regions of the monkey IT cortex and that these colour-selective regions are distributed in both the anterior and posterior IT. The difference in the response properties and the retinotopy suggests that these regions may correspond to different spots of colour-selective activity reported in the human fusiform gyrus: the colour-selective activity in the posterior IT may correspond to V8/VO which is in the posterior part of the fusiform gyrus, and colour-selective activity in the anterior IT may correspond to V4α and regions in the more anterior part of the fusiform gyrus.

1. Introduction

Colour is an important attribute for object representation. We use colour information to discriminate objects or to detect objects from the background especially if they are ambiguous in luminance levels. Moreover, colour information helps us to recognize objects faster and to remember them better (Gegenfurtner & Rieger, 2000). How is colour information processed in the brain? In humans, the cortical regions that are responsible for colour perception has been identified in the studies of the cortical damage and functional magnetic resonance imaging (fMRI) but there exists limitation in studies using human subjects or patients because invasive methods cannot be applied to humans. In that respect, macaque monkey is the most valuable animal models for human colour perception, since it has very similar colour vision as humans. A lot of neurophysiological recording studies have examined the property and the distribution of colour-selective neurons in monkey visual cortex, and these findings have allowed us to infer mechanisms of colour information processing. However, relatively little has been clarified about how the colour information is processed in higher-order cortical areas. Recently, the demand for linking the findings of monkey neurophysiology and human fMRI has developed the technique of monkey fMRI, which has an advantage for examining the distribution of the activity in the cortex. In the present study, we have examined the distribution of colour-selective activity in higher-order cortical areas using fMRI in monkeys. In the followings, I summarize the findings about

colour information processing in humans and monkeys, and described the experiments that we have conducted in the present study.

Colour-selective regions in the human fusiform gyrus

Previously, in humans, it has been known that lesions in the ventral occipital cortex can produce severe deficits in colour vision, a syndrome known as cerebral achromatopsia (for review, see Zeki, 1990). The finding suggested that the ventral occipital cortex plays an important role for colour perception, but it remained unclear precisely which loci in this cortical region is responsible for colour perception. The development of fMRI technique that uses blood oxygen level-dependent (BOLD) signals as an indirect measure of neuronal activity enabled to examine which region of the human brain is responsible for a specific visual function (Ogawa *et al.*, 1990). Some human fMRI studies have shown that areas in the fusiform gyrus showed colour-selective activity, in addition to the activity in early visual areas such as LGN, V1, V2 and V4. In these fMRI studies, the areas showing colour-selective activity are located in the posterior part of the fusiform gyrus (Hadjikhani *et al.*, 1998, Brewer *et al.*, 2005) as well as in the more anterior part of the fusiform gyrus (Beauchamp *et al.*, 1999, Bartels & Zeki, 2000, Morita *et al.*, 2004). A recent study using electrophysiological recording and microstimulation have also suggested that this more

anterior colour-selective region is involved in colour perception (Murphey *et al.*, 2008).

Colour-selective neurons in the monkey inferior temporal cortex

In monkeys, it has been suggested that the inferior temporal (IT) cortex is situated at the final processing stage of colour information processing. Previous studies have shown that colour information is processed and elaborated through the pathway including the retina, the lateral geniculate nucleus (LGN) and visual cortical areas where colour-selective neurons exist. In the retina and the LGN, colour information is encoded by the colour-opponent neurons, which combine the signals from different classes of cones in specific manners (Derrington *et al.*, 1984; De Valois *et al.*, 2000; Hanazawa *et al.*, 2000). In the cortex, colour information is further processed along the ventral visual pathway, through the primary visual cortex (V1) (Lennie *et al.*, 1990; Hanazawa *et al.*, 2000; Johnson *et al.*, 2001; Conway *et al.*, 2002; Solomon *et al.*, 2004), area V2 (Gegenfurtner *et al.*, 1996) and area V4 (Schein & Desimone, 1990; Kusunoki *et al.*, 2006) and finally reached to the IT cortex. Lesion studies have shown that bilateral ablation of the IT cortex disrupts colour discrimination (Horel, 1994; Heywood *et al.*, 1995; Buckley *et al.*, 1997; Huxlin *et al.*, 2000) although ablation of V4 does not (Heywood *et al.*, 1992; Heywood *et al.*, 1995), and this suggests that the IT cortex plays a key role in colour vision. Moreover, single cell recording studies have shown that there are

many colour-selective neurons in the IT cortex, and that some of them have selectivities for various hues and degrees of saturation (Komatsu *et al.*, 1992; Koida & Komatsu, 2007; Matsumora *et al.*, 2008; Yasuda *et al.*, 2009).

The monkey IT cortex has been suggested to correspond to the human fusiform gyrus according to their location relative to area V4 and analogy of the findings from the lesion studies in monkeys and humans. Whereas the region in the posterior part of the monkey IT cortex, referred to as area TEO, was suggested to correspond to that in the posterior part of the fusiform gyrus (Hadjikhani *et al.*, 1998; Brewer *et al.*, 2005), it has not been clarified which region in the monkey brain correspond to the colour-selective region in the more anterior part of the human fusiform gyrus.

Specificity of neural pathway involved in colour processing

Findings about the distribution of colour-selective neurons provide insight how colour information is processed. Previous studies in early visual areas have suggested that colour information is processed at specific modules there. Some studies have shown that colour-selective neurons in area V1 are concentrated in cytochrome-oxidase (CO) blobs. Neurons in the blobs send projections specifically to CO thin-stripes in V2 where colour-selective neurons are clustered (Livingstone & Hubel, 1984; Lu & Roe, 2008). Such functional

structures, however, become ambiguous as it goes in higher-order areas, such as the IT cortex. Single-unit recording studies in the IT cortex have suggested that there are regions with many colour-selective neurons and regions with little colour-selective neurons in the posterior part of the IT cortex (Komatsu *et al.*, 1992) and the anterior part of the IT cortex (Yasuda *et al.*, 2009). They have suggested that there exist functional modules where colour-selective neurons are clustered that are larger in scale than those in early visual areas. However, relatively little has been reported about their numbers, locations and the extents. To examine the distribution of such colour-selective regions, imaging techniques such as fMRI are suitable because they can examine the activities in larger portion of the brain region simultaneously.

The purpose of the present study

In the present study, we have examined the distribution of colour-selective activity in the monkey IT cortex using fMRI. Before the main experiment, we have also conducted exploratory experiments to measure the map of retinotopic organization, motion-selective activity and shape-selective activity in the visual cortex. These maps were used to analyze and interpret the results in the main experiment. In the main experiment, we have examined the distribution of colour-selective activity in the entire IT cortex. We have found that there

are colour-selective regions distributed in the posterior and anterior part of the IT cortex, which may correspond to human colour-selective region in the posterior and the more anterior part of the fusiform gyrus. Such distributed clustering pattern may provide important insight into the functional organization of the IT cortex with regard to the processing of colour information.

2. Exploratory examination of retinotopic and motion-selective and shape-selective maps

2-1. Introduction

In the present study, we have attempted to examine the distribution of colour-selective activity in the monkey IT cortex using fMRI. Before conducting the main experiment, some basic information such as retinotopic organization of visual areas was required to analyze and interpret the distribution of colour-selective activity. Previous electrophysiological and anatomical studies have shown that early visual areas have retinotopic organization and that the borders of visual areas correspond to the horizontal meridian (HM) or vertical meridian (VM) representations (Gattas *et al.*, 1988). Using the stimuli similar to those used in a previous study by Fize *et al.* (2003), we have measured responses to HM/VM and determined the borders of early visual areas. We have also explored responses selective to motion stimuli to identify area MT/V5. In previous monkey fMRI studies, it has been shown that some regions in the superior temporal sulcus (STS) including area MT/V5 are elicited using various kinds of random-dot motion stimuli (Vanduffel *et al.*, 2001; Nelissen *et al.*, 2006). We have explored motion-selective response in the STS using one kind of random-dot stimuli used in the study by Nelissen *et al.* (2006), and defined this area as region of interest (ROI) to define the physiological isoluminance of the grating stimuli in the subsequent main

experiment. Finally, we have examined shape-selective response in the IT cortex using visual object stimuli. Although previous neurophysiological studies have shown that there exist a large number of shape-selective neurons in the IT cortex, it has not been completely clarified how they distribute there. Some recent monkey fMRI studies have shown that neurons that have shape-selectivity or face-selectivity show patchy distribution in the IT cortex (Tsao *et al.*, 2003; Denys *et al.*, 2004; Pinsk *et al.*, 2005; Bell *et al.*, 2009), and it is important to know the relationship between the distribution of shape-selective activity and colour-selective activity.

2-2. Materials and Methods

Subjects

Two male macaque monkeys (*Macaca fuscata*, 4–7 kg) were used in the present study. Before the experiments, each monkey was implanted with a magnetic resonance-compatible polysulphone headpost, which was anchored to the skull using dental acrylic and small ceramic screws (Uwe Thomas Recording, Giessen, Germany). All surgical procedures were performed while the animal was under general anaesthesia with intravenous injection of Nembutal (a total amount of 39 mg/kg for monkey M1 and 24 mg/kg for monkey M2) following sedation with intramuscular injection of ketamine hydrochloride. After surgery, the monkey was allowed to recover for at least one week before the training began. During this period, antibiotic (Cafazolin, 60 mg) was given every 12 hours. All experimental procedures were conducted in accordance with NIH guidelines and were approved by the Institutional Animal Care and Use Committee of National Institutes of Natural Sciences.

Each monkey was trained to perform a fixation task and dimming detection task. The dimming task was used before installing high quality eye tracking system (see Apparatus) or sometimes also used to improve the monkey task performance. In the fixation task, each monkey was required to fixate on a central fixation spot (a square fixation window 2–3 degs on a side) for several seconds (typically for 3 s). In the dimming task, the monkey was

required to respond with an optical switch to the dimming of the fixation spot occurring at a random time after stimulus offset. The monkey had to maintain fixation and its body posture to get a liquid reward; if the monkey made a saccade or the magnitude of the body movement exceeded certain threshold, the trial was aborted without a reward and the inter-trial interval (ITI) was extended. The ITI was also extended if the monkey moved its body during the ITI.

Apparatus

During the experiments, each monkey was seated in the so-called 'sphinx' position in a horizontally oriented, custom-made monkey chair. Using the headpost, the monkey's head was rigidly fixed to a head holder on the chair. Visual stimuli were generated using a VSG 2/5 graphics board with 15-bit resolution (Cambridge Research Systems, Rochester, England) and projected from a LCD projector (800 × 600 pixels, 60 Hz refresh rate; Victor, Yokohama, Japan) onto a screen that was positioned in front of the monkey's eyes at a distance of 47 cm. The display system was calibrated by measuring the spectral power distributions of the red, green and blue primaries using a spectrophotometer (PhotoResearch PR-650 SpectraScan, Chatsworth, CA, USA). Eye movements were recorded using an infrared (IR) eye tracking system (Matsuda *et al.*, 2000), which computed horizontal and vertical eye positions based on the centre of the pupil in an image of the eye captured using an IR-sensitive CCD video

camera (60 Hz interlace; Sony, Tokyo, Japan). IR light was directed at an eye using a fibre optic cable. Body movements were automatically detected in images of the monkey's body captured by a second CCD camera (Akizuki Denshi Tsusho, Tokyo, Japan). The eye-tracking and motion-detection systems sent signals to a computer, which ran custom-made software controlling the behavioural task and stimulus display.

Visual Stimuli and Behavioural Task

In the first experiment (Experiment 1.1), we used wedge stimuli, one of which was centred on the horizontal meridian and symmetric with respect to the fixation point (referred to as the HM stimulus) and the other centred on the vertical meridian (referred to as the VM stimulus). These stimuli were composed of contrast-reversing checkerboard pattern for M1 (contrast reversal at 1 Hz, 1 cycle/deg, 67% contrast, 20° polar angle, 6° radius) and uniform pattern for M2 (contrast reversal at 1 Hz, 100% contrast, 10° polar angle, 9° radius). The wedges did not appear within 0.5° around the fixation point. In the second experiment (Experiment 1.2), we used random dot patterns that appeared within a circular aperture of 4.5° radius (dot size 0.1°, dot luminance 10 cd/m^2). The dots did not appear within 0.7° around the fixation point. The pattern was either moving (expanding / contracting, reversal at 0.5Hz, dot speed 10°/s) or stationary. In the third experiment (Experiment 1.3), we used the object stimuli that are the

same as those used in the study by Tsao *et al.* (2003). We used the sets of stimuli, which they named "fruits" and "technological objects" categories and their Fourier-phase scrambled counterparts, each composed of 16 images (image size 7° × 7°, 60% contrast). Each image was presented for 1 s and two images were sequentially presented in one trial, so that each image appeared twice in a run. The data obtained with different categories were merged in the analysis. These stimuli were presented on a grey background (20 cd/m^2).

The monkey performed a fixation task. Each trial began with the onset of a small central fixation spot, on which monkey had to fixate. After they had maintained fixation within 2° × 2° square fixation window for 400–600 ms, a stimulus was presented for 2000 ms. The fixation spot then disappeared 500 ms after the stimulus offset. Each trial was continued even when a saccade or body movement was detected so that stimulus duration was kept constant across trials. In Experiment 1.1, one monkey (M1) performed a dimming detection task using an optical switch, since the eye-tracking system had not been installed. Each trial began with the onset of a small central fixation spot. The task continued only when the monkey started to hold the switch with its right hand within 1000 ms. After the monkey had held the switch for 500 ms, a stimulus was presented for 500–3000 ms. After 500–1500 ms from the stimulus offset, the fixation spot was dimmed to 50 cd/m^2 and the monkey had to release the switch within 600 ms to get liquid reward. In all experiments, there was an ITI of more than 700 ms, during which no fixation spot appeared.

We used a block design in which each stimulus block consisted of 4 trials with the

same stimulus condition (Fig. 1.1C). In Experiment 1.1, blocks of HM and VM stimuli were arranged in an alternating design, interleaved with a four-trial blank block in which only the fixation spot appeared. The same designs were used for moving and stationary random-dot stimuli in Experiment 1.2, and object and scrambled image stimuli in Experiment 1.3. Each stimulus block was repeated four times within each run, and the order of the blocks was alternated every run. The fixation performance and head movements were analysed offline, and data from runs in which the performance was poor or there was an excessive amount of head movement were discarded (see Data Analysis).

Data Acquisition

Images were acquired using a Siemens 3T Allegra scanner (Siemens, Erlangen, Germany). Functional images were collected using a gradient-echo echo-planar pulse sequence sensitive to BOLD contrast (TR 2 s, TE 20 ms, flip angle 80 deg, 1.25 mm in-plane resolution, slice thickness 1.6 mm, slice gap 0.32 mm, superior-inferior phase-encoding direction). A surface coil (9 cm × 11 cm inner diametre one for Experiment 1.3 in M1 and Experiment 1.1 in M2, 7.5 cm × 8 cm inner diametre one for the other experiments) was positioned immediately over the head. Each volume consisted of 31 oblique slices (M1 in Experiment 1.1) or coronal slices (M1 in Experiment 1.2 and 1.3 and M2 in Experiment 1.1–1.3), covering the occipital

and temporal cortices. Each monkey underwent 12–19 runs in each experiment (116–136 volumes/run for Experiment 1.1; 120–148 volumes/run for Experiment 1.2; 118–120 volumes/run for Experiment 1.3). T2-weighted anatomical images (inversion recovery turbo spin-echo, 0.75 mm in-plane resolution) scanned at the same locations as those used for the functional images, as well as whole brain 3D magnetization-prepared rapid-acquisition gradient-echo (MPRAGE) anatomical images (0.8 mm isotropic voxel), were acquired during each session to register the functional images. High-resolution anatomical images (MPRAGE; 0.5 mm isotropic voxel) were also collected in a separate session, during which the monkey was anaesthetized with Nembutal. The high-resolution anatomical image was aligned with stereotaxic space (the origin was placed at the middle of the interaural line; Saleem & Logothetis, 2007) and used to reconstruct the cortical surface of each hemisphere using CARET software (Van Essen *et al.*, 2001).

Data Analysis

Functional data were analysed using SPM2 (Wellcome Department of Imaging Neuroscience, London, UK) as well as custom Matlab codes. The first and last several volumes (in blank block) in each run were eliminated to allow for stabilization of the magnetization and to equate the number of volumes per run for each monkey and experiment (M1: 136 for

Experiment 1.1, 148 for Experiment 1.2 and 120 for Experiment 1.3; M2: 116 for Experiment 1.1, 120 for Experiment 1.2 and 120 for Experiment 1.3). All functional images were motion-corrected and aligned with a reference functional image from a particular session, and registered to the same-slice position anatomical image. The functional-anatomical registration was improved by adjusting the offset in the phase-encoding direction. The images were then registered to the high-resolution anatomical image in the stereotaxic space and resampled in 1.0-mm isotropic voxels. The data were temporally filtered with a three-point temporal median filter to remove movement-related outliers (Mazaika *et al.*, 2007), and were spatially filtered using a Gaussian filter (2 mm full width at half maximum) to improve signal-to-noise ratios.

The functional data from each run were used for analysis only if the monkey's head did not move too much (the percentage of volumes with head movement over 0.5 mm total translation or over 0.4 deg rotation was < 10%) and the fixation performance was good throughout the run (the overall percentage fixation from the start of fixation to the offset of the fixation spot was more than 95%). With these criteria, we retained more than 10 runs for each monkey in each experiment (M1: 14 for Experiment 1.1, 15 for Experiment 1.2 and 12 for Experiment 1.3; M2: 16 for Experiment 1.1, 15 for Experiment 1.2 and 11 for Experiment 1.3).

We conducted voxel-wise statistical analysis for each monkey based on a general linear model (Friston *et al.*, 1995). To detrend the data, they were globally scaled and high-

pass filtered (2 cycles/total scan time in each run). The signal time course was modelled using a boxcar function convolved with a human canonical haemodynamic response function and run effect. The regressors were set at the onset of the stimulus presentation for each stimulus condition. Head-movement parameters were also included as regressors of no interest. To test hypotheses about regionally specific condition effects, the estimates for each model parameter were compared with the linear contrasts. The resulting set of voxel values constituted a statistical parametric map of the t statistic, SPM{*t*}. The statistical threshold was set at $P < 0.0005$ for Experiment 1.1 and $P < 0.001$ for Experiment 1.2 and 1.3, uncorrected for multiple comparisons. The statistical parametric map was projected onto the surface of each hemisphere using the CARET 'average voxel' method with a 1.5-mm averaging radius. Only clusters with a surface area equal to or greater than 3 mm^2 were retained.

2-3. Results and discussions

Retinotopic organization of visual areas

At the early levels of the visual cortex, transitions between areas are known to be characterized by representations of horizontal/vertical meridians of the visual field (Gattas *et al.*, 1988; Fize *et al.*, 2003). Therefore, we mapped the representation of the HM and VM to identify the borders of these early areas. Figure 1.2 shows the comparison of activity elicited by the HM and VM stimuli, superimposed onto the flattened cortical surface. The yellow and blue colour coded regions that responded significantly more to HM than VM stimuli and to VM than HM stimuli, respectively ($P < 0.0005$, uncorrected for multiple comparisons). The overlying solid black (HM) and white (VM) lines were derived by tracing the local maxima of SPM$\{t\}$.

In early visual areas, according to the finding of the previous electrophysiological studies, we could define the border between V1 and V2 by HM representation, the border between V2 and V3 by VM representation and the border between V3 and V4 by HM in both hemispheres. These segmentations of the areas well corresponded to their location presumed by the anatomical landmarks of these areas. This result was largely consistent with that in the previous study by Fize *et al.* (2003). It should be noted, however, that the activity in the ventral occipital area was relatively weak so that the anterior border of V1 was vague or

disappeared. This tendency was also observed in the previous study, while these differ in varying degrees, and is suggested to be due to signal drop-out caused by susceptibility artefact. In higher-order areas, the most anterior HM representation divided area V4 and the IT cortex. This HM representation extended discontinuously as reported in the previous study (Fize *et al*., 2003). Based on the identification of these visual areas, we could attribute the colour-selective activities to these early visual areas with confidence as shown in chapter 3.

Motion-selective activity obtained with random-dot stimuli

We next identified motion-selective cortical area using random dot stimuli. Figure 1.3 shows the motion-selective activity obtained by contrasting response to moving random-dot stimulus and stationary random-dot stimulus ($P < 0.001$, uncorrected). The most significant activity was found in the STS, which was anterior to the V4 anterior border, in all hemispheres (Fig. 1.3 a). This strong activity was positioned in the lower bank of the STS, suggesting that it corresponds to area MT/V5 though the activity maybe extended to fundus of the superior temporal (FST) or ventral medial superior temporal (MSTv) area, which is suggested to be positioned in the lower bank and fundus adjacent and anterior to STS and in the fundus adjacent and medial to STS, respectively. Fize *et al.* (2003) reported that area MT

and FST can be devided by VM representation, but we could find the VM representation in the motion-selective activity only in one hemisphere (M1 left). The motion-sensitive area in the STS was used as ROI to define the physiological isoluminance of the grating stimuli in the subsequent main experiment.

Strong activity to the motion stimuli was also found in V1, V2d/V3d and V2v/V3v in three or four hemispheres (V2v/V3v: M1 left and right and M2 right). In V4, the activity was observed in the lower bank of the inferior occipital sulcus (IOS) in three hemispheres (M1 left and right and M2 right) but not observed in the gyrus dorsal to the anterior end of the IOS except for one hemisphere (M1 left). These findings are largely consistent with a previous study (Vanduffel *et al.*, 2001).

In the more anterior part of the STS, two patches of activity were observed in addition to the activity in area MT/V5 in one monkey (M1 left and right). The position of the posterior patch was nearly consistent with that of lower superior temporal (LST) area (Fig. 1.3 b) reported in the study by Nelissen *et al.* (2005). The anterior patch was also observed in the previous study but was not further analyzed (Fig. 1.3 c).

Shape-selective activity obtained with object stimuli

We finally examined shape-related activity using object stimuli. Figure 1.4 shows the shape-

selective activity obtained by contrasting response to object stimuli with that to their Fourier-phase scrambled images ($P < 0.001$, uncorrected). In the occipital cortex, the significant activity was observed in V2d/V3d, V2v/V3v and V4. It should be noted that the activity in V1 was weak or not significant except for one hemisphere (M2 left). In the IT cortex, shape-selective activities were located in some discrete regions distributed in the IT gyrus and in the STS. The distribution of the activity was largely consistent over four hemispheres, although the exact locations of them were different among hemispheres. The locations of the activity were around the anterior end of the posterior middle temporal sulcus (PMTS) (Fig. 1.4 a), in the lower bank of the STS at the middle of the IT cortex (Fig. 1.4 b) and around the anterior middle temporal sulcus (AMTS) (Fig. 1.4 c). The findings that the activity was distributed in the IT cortex were consistent with the previous studies (Tsao *et al.*, 2003; Denys *et al.*, 2004).

It should also be noted that there is lack of BOLD signal in some portion of the IT cortex. Figure 1.5 shows the comparison between the anatomical image and the functional image in the same sagittal position. At the position of a crosshair, the signal was acquired in the anatomical image but dropped in the functional image (Fig. 1.5B). It has been suggested that signal in brain regions adjacent to bone and air sinuses is attenuated due to susceptibility-induced field inhomogeneities (Ojemann *et al*., 1997). This region that has no signal was plotted on the cortical surface as the area of signal drop-out in the subsequent main experiment.

3. Distribution of colour-selective activity in the anterior IT cortex

3-1. Introduction

In monkeys, colour information is primarily processed in the ventral pathway through V1, V2, and V4 into the inferior temporal (IT) cortex. Although many studies suggest that V4 and its surrounding areas play an important role in colour perception (for review, see Gegenfurtner 2003; Conway, 2009), recent studies have shown that the anterior part of the IT cortex, or area TE, is also involved in colour perception. This region contains numerous colour-selective neurons, some of which are narrowly tuned to hues and/or saturations (Komatsu *et al.,* 1992) and exhibit task-related responses during colour discrimination (Koida & Komatsu, 2007; Matsumora *et al.,* 2008). In addition, lesion studies have shown that bilateral ablation of the anterior IT disrupts colour discrimination (Horel, 1994; Heywood *et al.*, 1995; Buckley *et al.,* 1997; Huxlin *et al.,* 2000), though ablation of V4 does not (Heywood *et al.,* 1992; 1995).

The aforementioned studies highlight the role of the anterior IT in colour perception, but it is not clear about how colour-selectivity is distributed in this region, as compared with the distribution in earlier areas such as V4. Recent fMRI studies revealed that colour-selectivity is clustered in discrete millimetre-scale patches in the posterior IT (Conway & Tsao, 2006; Conway *et al.,* 2007), but these studies did not cover the anterior IT. Some

studies have suggested that colour-selective neurons are clustered in subregion(s) within the anterior IT (Komatsu *et al.,* 1992; Tootell *et al.,* 2004), but there is variation in the numbers, locations, and extents of these subregions among the studies. Moreover, colour-selective neurons also existed at various sites within the anterior IT (Desimone *et al.,* 1984; Komatsu *et al.,* 1992; Kobatake & Tanaka, 1994), suggesting a possibility that colour-selective neurons are widely distributed in this region.

In the present study, we used fMRI in alert monkeys to clarify the functional organization of colour-selectivity in higher-order areas, including the anterior IT. In human fMRI, two different paradigms have been commonly employed and have identified colour-selective areas/regions in the human fusiform gyrus, which is suggested to be corresponding to the monkey IT cortex. One is to compare responses to an isoluminant, colour-varying pattern (e.g. a red-blue grating) with responses to a luminance-varying pattern. This paradigm using gratings could identify colour-selective regions in the posterior part of the human fusiform gyrus, what they called V8/VO (Hadjikhani *et al.,* 1998; Mullen *et al.,* 2007). The other is to compare responses to a multicoloured ('Mondrian') pattern with responses to its achromatic counterpart. This paradigm using Mondrian could identify colour-selective regions in the more anterior part of the fusiform gyrus, in addition to the posterior part (Beauchamp *et al.,* 1999; Bartels & Zeki, 2000; Wade *et al.,* 2002; 2008). Earlier imaging studies of the monkey IT cortex used only the first paradigm (Tootell *et al.,* 2004; Conway & Tsao, 2006; Conway *et al.,* 2007), but the second paradigm may elicit more effectively the

colour-selective activity in the anterior IT according to the findings in human fMRI. Moreover, Mondrian stimuli may be more suitable for activating higher areas, since the stimuli containing various hues could elicit responses from many neurons, each tuned to a specific hue. For that reason, we used both the first and the second paradigms. We found that colour-selectivity is not uniformly distributed in the IT cortex, but is clustered in multiple discrete subregions that are differentially responsive to the Mondrian and grating stimuli. This distributed clustering pattern may provide important clues to the functional organization related to colour processing in the IT cortex.

3-2. Materials and Methods

Visual stimuli and behavioural task

In the first experiment (Experiment 2.1), we used chromatic and achromatic Mondrian stimuli that were comprised of a 6 × 6 array of rectangular patches (6° × 6°). For each presentation, the colour of each patch in the chromatic Mondrian stimulus (Fig. 2.1A top-left) was chosen randomly from the 12 chromaticities shown in Figure 2.1B. These chromaticities correspond to points that equally divide the sides of a triangle whose vertices correspond to the chromaticities of the RGB primaries of the LCD projector. The luminance of each patch was chosen randomly from a contrast range of ±80% around the mean luminance of 20 cd/m^2. The achromatic Mondrian stimulus (Fig. 2.1A top-right) had the same luminance contrast as the chromatic one, but the chromaticities of the patches were the same as that of the grey background (CIE x = 0.31, y = 0.33). These stimuli were presented for 2000 ms in a cosine temporal envelope (0.25 Hz) on a grey background (CIE x = 0.31, y = 0.33, 20 cd/m^2). The chromatic and achromatic Mondrian stimuli were hence identical in spatiotemporal structure.

In the second experiment (Experiment 2.2), we used colour-varying and luminance-varying radial sine wave gratings (5° radius), both of which were of low spatial frequency (0.33 cycles/deg) and moved slowly inward or outward (1 Hz). The colour-varying grating (Fig. 2.1A bottom-left) was modulated along an axis between the chromaticities of the red

and blue primaries. This red-blue grating was made by superimposing a red-black grating and a blue-black grating in antiphase with a luminance ratio of 2.3 (red-black range, 0–28 cd/m^2; blue-black range, 0–12 cd/m^2). This resulted in 40% luminance contrast. The luminance ratio was chosen to replicate the stimuli used in an earlier monkey fMRI study, in which they determined the luminance ratio of colour-varying grating that elicited the least activity in area MT (Conway & Tsao, 2006). The luminance-varying grating (Fig. 2.1A bottom-right) was made by superimposing the same two gratings in an isophase relationship (100% contrast). The luminance ratio between the red and blue gratings was nearly constant (2.3) at all points, so that the chromaticity of the whole grating remained constant. These grating stimuli were presented for 2400 ms (in a raised-cosine temporal envelope for the first and last 400 ms) on a purple background whose chromaticity and luminance were the same as the mean chromaticity and luminance of the gratings (CIE x = 0.35, y = 0.19, 20 cd/m^2). The direction of movement was randomly switched for each presentation.

In the third experiment (Experiment 2.3), we used five kinds of stimuli: three Mondrian stimuli and two grating stimuli. These stimuli were presented for 2000 ms on a grey background (CIE x = 0.31, y = 0.33, 20 cd/m^2) within the same run. Of the three Mondrian stimuli, two were the same as the chromatic and achromatic stimuli in Experiment 2.1. In addition, we employed a photometrically isoluminant chromatic Mondrian stimulus, which was identical to the chromatic Mondrian except that all patches had the same luminance as the background (20 cd/m^2). The remaining two grating stimuli were colour-

varying and luminance-varying gratings with the same spatial configuration as the stimuli used in Experiment 2.2. The colour-varying grating was a red-blue grating made as in Experiment 2.2, except that the luminance ratio between the red and blue grating was set at 1.0 for M1 and 2.3 for M2. These luminance ratios were determined in a separate experiment, where five colour-varying gratings having different luminance ratios (0.67, 1.00, 1.50, 2.33 and 3.00) were presented to determine which one elicited the least activity in area MT of each monkey. The ROI of area MT was defined as spherical, 2-mm regions centred on the local maxima of SPM{*t*}measured in the exploratory experiment that explored motion-selective response. The luminance-varying grating was an achromatic white-black grating that varied only in luminance around a grey background (100% contrast).

The monkeys performed a fixation task (Fig. 2.1C bottom). Each trial began with the onset of a small central fixation spot, on which the monkeys had to fixate. After they had maintained fixation within 2° × 2° square fixation window for 400–600 ms, a stimulus was presented for 2000–2400 ms. The fixation spot then disappeared 100 ms after the stimulus offset. Each trial was continued even when a saccade or body movement was detected so that stimulus duration was kept constant across trials. In those cases, a reward was not given in about half of the runs, but was given in the remaining half of the runs. In Experiment 2.3, to improve fixation performance, one money (M1) was also required to respond with an optical switch to the dimming of the fixation spot occurring at a random time after stimulus offset to get a reward (the reaction time had to be < 900 ms). In all experiments, there was an ITI of

more than 700 ms, during which no fixation spot appeared.

We used a block design in which each stimulus block consisted of 4 trials with the same stimulus condition (Fig. 2.1C top). In Experiments 2.1 and 2.2, blocks of colour and luminance stimuli were arranged in an alternating design, interleaved with a 4-trial blank block in which only the fixation spot appeared. Each stimulus block was repeated six times in Experiment 2.1 and four times in Experiment 2.2 within each run, and the order of the blocks was alternated every run. In Experiment 2.3, the five stimulus blocks were arranged in a pseudorandom order and interleaved with blank blocks. Each stimulus block was repeated two times within each run. The fixation performance and head movements were analysed offline, and data from runs in which the performance was poor or there was an excessive amount of head movement were discarded (see Data Analysis).

Data acquisition

Same MRI machine and parameters as described in chapter 2 were used to obtain functional and anatomical imaging data. A different surface coil (9 cm × 11 cm inner diametre; Takashima Seisakusho, Tokyo, Japan) was used. Each volume consisted of 31 coronal slices, covering the occipital and temporal cortices. Each monkey underwent 17–52 runs in each experiment (175–185 volumes/run for Experiment 2.1; 125–135 volumes/run for Experiment

2.2; 156 volumes/run for Experiment 2.3).

Data analysis

Experimental details are similar to those in the exploratory experiments, with the specific modifications described below. We equated the number of volumes per run for each monkey and experiment (M1: 175 for Experiment 2.1, 125 for Experiment 2.2 and 156 for Experiment 2.3; M2: 171 for Experiment 2.1, 128 for Experiment 2.2 and 156 for Experiment 2.3). The functional data from each run were used for analysis only if the monkey's head did not move too much (the percentage of volumes with head movement over 0.5 mm total translation or over 0.5 deg rotation was < 5%) and the fixation performance was good throughout the run (the overall percentage fixation from the start of fixation to the offset of the fixation spot was more than 95%). We also discarded a run if the percentage of rewarded trials in the run was < 70%. With these criteria, we retained more than 16 runs for each monkey in each experiment (M1: 20 for Experiment 2.1, 17 for Experiment 2.2 and 52 for Experiment 2.3; M2: 26 for Experiment 2.1, 25 for Experiment 2.2 and 48 for Experiment 2.3). The high-pass filter was applied at 2 cycles/total scan time in each run for Experiments 2.1 and 2.2, 1 cycle/total scan time in each run for Experiment 2.3.

Visual area definition

To define areal boundaries, the cortical surfaces were registered to the macaque F99UA1 atlas using surface-based registration of spherical maps as constrained by sulcal landmarks on the individual and atlas hemispheres (Van Essen, 2002). The anterior border of area V4 was determined based on the areal partitioning scheme of Lewis & Van Essen (2000) , which was located slightly anteriorly compared with that determined by the retinotopic organization in the exploratory experiment. We adopted this partitioning scheme to strictly dissociate the activity in V4 and in the IT cortex. The IT cortex was then defined as the temporal lobe region extending from the anterior V4 border to the temporal pole, including the lateral surface and lower bank of the superior temporal sulcus (STS). The IT cortex was further divided into the anterior IT and posterior IT based on the anterior-posterior stereotaxic coordinates. The coordinates for the anterior-posterior border were defined as the midpoint between the anterior end of the anterior middle temporal sulcus (AMTS) and the posterior end of the posterior middle temporal sulcus (PMTS), the latter of which corresponded to the anterior border of V4. The borders of the early cortical areas (V1, V2/V3, V4) were also determined by the same partitioning scheme, which well corresponded to those determined by the retinotopic organization. The lateral geniculate nucleus (LGN) was defined based on an anatomical atlas (Saleem & Logothetis, 2007).

Colour-selectivity index (CSI)

To quantitatively examine response magnitudes and degrees of colour-selectivity, we selected a voxel that showed the most statistically significant difference between its responses to colour and luminance (i.e. local maxima of SPM{t} obtained by contrasting colour vs. luminance) within the LGN, V1, ventral V2/V3 and V4 in each hemisphere in each experiment. We also selected from the lateral surface of the IT cortex a voxel in the anterior IT and one in the posterior IT using the same criteria. When there was not significant activation at the threshold of $P < 0.001$, we lowered the threshold to $P < 0.01$ to select the voxel; this lower threshold was used only for the posterior IT in M1 left in Experiment 2.2.

The raw time series for these voxels were extracted, high-pass filtered and converted to units of percent signal change relative to the baseline computed by averaging signals obtained from the periods for 4 s prior to the stimulus blocks. To exclude movement-related artefacts, we removed signals occurring at the time of large head movements (see Data Analysis). The time series was aligned with block onset (the onset of the first stimulus in each stimulus block) and averaged across the stimulus blocks for each condition (colour or luminance). The mean response amplitude for each stimulus condition was computed by averaging signals between 6 and 20 s after the block onset and then averaging across

hemispheres. We then assessed the colour-selectivity by computing a CSI from the mean response amplitude. The CSI was defined as follows:

$$CSI = (R_{COL} - R_{LUM}) / (R_{COL} + R_{LUM})$$

,where R_{COL} is the response amplitude to the colour stimuli (chromatic Mondrian stimulus or colour-varying grating stimulus) and R_{LUM} is the response amplitude to the luminance stimuli (achromatic Mondrian stimulus or luminance-varying grating stimulus). An index with a larger value indicates a higher selectivity for colour.

Correlation analysis

To assess the topographical similarity of the colour-selective activities elicited by different types of stimuli or in different experiments, we examined the spatial correlations among the activities. For this analysis, we defined ROIs on the lateral surface of the IT cortex (surrounded by the lips of the STS and the occipitotemporal sulcus; OTS) in the posterior IT (PostIT ROI) and anterior IT (AntIT ROI), which were divided in the same way described in the 'Visual area definition' section. These were restricted to visually responsive voxels that were defined by contrasting summed responses during all stimulus conditions with responses during the fixation baseline ($P < 0.001$, uncorrected for multiple comparison). For comparison across experiments, voxels that were visually responsive in any one of the

experiments were included in the ROIs. For each of these ROIs, we computed a Pearson correlation coefficient between a pair of unthresholded SPM{*t*}, each obtained by contrasting the colour condition with the corresponding luminance condition. The statistical significance was assessed for each pair using a permutation test in the following way. The stimulus conditions were randomly shuffled in each run in order to produce 'null' data for SPM{*t*} (e.g. shuffled colour vs. luminance). We obtained 1000 null data for each stimulus type and for each experiment, and the correlation coefficients were computed using 1000 pairs of the null data. If the correlation coefficient (or the average of the correlation coefficients across all hemispheres) obtained using real data was greater than the 95th percentile of that obtained using the null data, then it was deemed to be significant at the $P < 0.05$ level.

3-3. Results and Discussion

Colour-selective activity: Mondrian stimulus

We first measured colour-selective activity by presenting chromatic and achromatic Mondrian stimuli to alert monkeys while they performed a fixation task. Because the chromatic and achromatic stimuli differed only in colour/luminance conditions, the difference between the activities to these stimuli should reflect the relative sensitivity to colour and luminance. We defined the differential activity between the chromatic and corresponding achromatic stimuli as 'colour-selective activity' in the present study. Figure 2.2 shows the distribution of the colour-selective activity obtained by contrasting the chromatic Mondrian with the achromatic Mondrian in one monkey (M2). The colour-selective activity was mapped onto the reconstructed cortical surface of the right hemisphere (Fig. 2.2A and B) and superimposed on the sagittal and coronal sections (Fig. 2.2C and D). In the occipital cortex, colour-selective activities were found in V1 (on the opeculum), V2d/V3d (in the posterior bank of the lunate sulcus), V2v/V3v (in the inferior occipital sulcus; IOS), V4d (in the anterior bank of the lunate sulcus and on the prelunate gyrus) and V4v (in the anterior bank and the anterior lip of the IOS). In addition, activation was also found in the LGN (data not shown). Overall, the locations of the activated regions in these areas were consistent with those reported in an earlier fMRI study of colour-selective activity in monkey visual cortex (Conway *et al.*, 2007).

We also found colour-selective activity in the IT cortex. This activity was not uniformly distributed, but was clustered in two discrete regions, each covering ~35 mm^2. One of the regions was located in the lateral bank of the AMTS and the other was located on the gyrus anterior to the PMTS in the right hemisphere (Fig. 2.2A–C). These regions of colour-selective activity were observed bilaterally, though the position of the activity varied slightly across hemispheres (Fig. 2.2C and D). Although signal drop-out due to susceptibility-induced field inhomogeneities (Ojemann *et al.*, 1997) occurred in some areas of the IT cortex (black regions in Fig. 2.2A and B), a signal was obtained from most of the IT, so that signal drop-out cannot account for the presence of discrete colour-selective regions.

Colour-selective regions were consistently found in the anterior IT in all four hemispheres examined and in the posterior IT in three of the four hemispheres. Figure 2.3 shows the spatial distributions of the activity in the IT cortex in all four hemispheres. With respect to the sulcal landmarks (AMTS and PMTS), the locations of the activated regions in the anterior and posterior IT were largely consistent across hemispheres. The activated regions in the anterior IT were located in the fundus of the AMTS in both hemispheres of M1, on the gyrus lateral to the posterior end of the AMTS in the left hemisphere of M2, and in the lateral bank of the AMTS in the right hemisphere of M2. The activated regions in the posterior IT were located near the anterior end of the PMTS in the right hemisphere of M1 and on the gyrus 2–3 mm anterior to the anterior end of the PMTS in both hemispheres of M2. In addition, there were bilateral activations in the lower bank of the anterior STS in M2 but

not M1.

Figure 2.5B shows the *t*-values taken from the voxels showing the most significant colour-selective activity within the LGN, V1, V2/V3, V4, the posterior IT and the anterior IT averaged across hemispheres. This indicates that the most statistically significant colour-selective responses were observed in V1 and V4, and less though still highly significant responses were seen in the IT cortex. Taking into consideration that the *t*-statistics reflect not only response magnitude but also the amount of noise that could be affected by susceptibility-induced field inhomogeneity, we also looked at the response magnitude of those voxels (Fig. 2.5A and C) and assessed the colour-selectivity by calculating the CSI from the response magnitude (Fig. 2.5D left). The CSI varied among colour-selective areas/regions in a manner that differed from statistical significance. The CSIs were higher in early areas such as the LGN and V1 than in extrastriate areas such as V2/V3 and V4. Notably, the CSIs were higher in the IT cortex than extrastriate areas; in particular, the CSI was higher in the anterior IT than in the early areas. This suggests that the degree of colour selectivity in the IT cortex is comparable to or even higher than that in earlier areas such as V1 and V4.

Colour selective activity: grating stimulus

We next examined colour-selective activity using a red-blue colour-varying grating and a

luminance-varying grating. We designed the stimuli so as to replicate those in earlier imaging studies in monkeys (Tootell *et al.*, 2004; Conway & Tsao, 2006; Conway *et al.*, 2007). The colour grating was modulated between highly saturated red and blue, with 40% luminance contrast. In the luminance grating, luminance was modulated with 100% contrast, which was much larger than that of the colour grating. The gratings were of low spatial frequency (0.33 cycles/deg) and moved slowly (1 Hz).

Colour-selective activities obtained by contrasting the colour grating with the luminance grating were found in the LGN, V1, V2/V3 and V4. The observed activities in these early visual areas were largely consistent with those obtained with the Mondrian stimuli, but the activations tended to be stronger and broader. Colour-selective activities were also found in the posterior IT (Fig. 2.4). These activities were located in the lower bank of the PMTS or on the gyrus ventral to the PMTS in all hemispheres and in the lower bank of the posterior STS in two hemispheres (M1 left and M2 left). The colour-selective regions observed near the PMTS were close to, but slightly more posterior than, those observed with the Mondrian stimuli in the posterior IT (Fig. 2.3). In one monkey (M2), we also observed bilateral activation in the medial bank of the OTS. These results were largely consistent with the earlier studies (Conway & Tsao, 2006; Conway *et al.*, 2007). No significant activity was seen in the anterior IT of either monkey.

The regional distribution of CSIs obtained with the grating stimuli (Fig. 2.5D right) was similar to that obtained with the Mondrian stimuli (Fig. 2.5D left), in that the CSIs were

higher in the early areas than the extrastriate areas. There was, however, a general tendency for CSIs obtained with the grating, especially for the early areas, to be higher than those obtained with the Mondrian. This tendency, together with the absence of significant grating-evoked activation in the anterior IT, suggests that the colour grating is effective for eliciting colour-selective activity in the early and extrastriate areas, whereas the colour Mondrian is especially effective for activating the anterior IT.

Stimulus dependencies of colour-selective activities in the IT cortex

Both Mondrian and grating stimuli elicited colour-selective activities along the ventral pathway, including the IT cortex. However, the relative strengths of the activities elicited by the two stimulus types differed in the anterior IT. Moreover, the locations at which they elicited colour-selective activities tended to differ, especially in the posterior IT. There are differences in several aspects between the two stimulus types, some of which are likely responsible for the observed differential activation in the IT cortex. Colour Mondrian stimuli contain a richer variety of colours than grating stimuli, which may account for the difference in elicited activities. In addition, the luminance contrast in the chromatic Mondrian stimulus matched that in the achromatic Mondrian, whereas the colour grating stimulus contained much less luminance contrast than the luminance grating. Consequently, contrasting

responses to the colour grating with responses to the luminance grating will subtract away regions that are sensitive to both colour and luminance contrast. This also could account for the differences obtained with the two types of stimuli. To examine the effect of luminance contrast on the activity, we conducted a separate experiment (Experiment 2.3) in the same two monkeys with the aim of measuring response to a new Mondrian stimulus that was photometrically isoluminant, along with responses to the Mondrian stimuli used in Experiment 2.1. This isoluminant Mondrian contained much less luminance contrast than the achromatic one (±80%), even if there existed residual luminance contrast due to the individual difference in the psychophysical/physiological isoluminance points. In addition, to directly compare the colour-selective activities obtained with different types of stimuli, we also measured responses to a red-blue chromatic grating as well as responses to an achromatic grating in which only luminance was modulated around a grey background, within the same run. The red-blue grating, in which residual luminance contrast may possibly become large, was adjusted to be physiologically isoluminant for each monkey (see Material and Methods). We then performed a detailed analysis on the topography of the colour-selective activities in the IT cortex.

Figure 2.6A–C shows detailed maps of colour-selectivity on the IT gyrus in one hemisphere obtained with different types of colour stimuli. In each map, SPM$\{t\}$ obtained by contrasting the chromatic stimuli and corresponding achromatic stimuli are shown using a pseudo colour scale without statistical thresholding in the visually-responsive regions of the

IT gyrus (Fig. 2.6D). These maps allow for visual inspection of the topography of both strong and weak activation across the IT cortex. The isoluminant Mondrian stimulus produced weak but significant colour-selective activity in the anterior and posterior IT (isoMon, Fig. 2.6A) at locations that mostly overlapped those activated by the Mondrian stimulus containing matched luminance contrast (Mon, Fig. 2.6B). Note also that the spatial distributions of activities within the anterior and posterior IT were similar, irrespective of the presence of luminance contrast. To quantitatively assess the relationship between the spatial distributions of the colour-selective activities, the correlation coefficient (r) was computed between a pair of unthresholded colour-selective activity maps (unthresholded SPM{t}) across all visually responsive voxels in the anterior IT (AntIT ROI) and the posterior IT (PostIT ROI). This analysis revealed that there is a significant positive correlation ($P < 0.05$, permutation test) between the colour-selectivity maps of isoMon and Mon in both the posterior and anterior IT (Fig. 2.6A and B; AntIT: $r = 0.590$, PostIT: $r = 0.627$), and this significant positive correlation was observed in all four hemispheres examined (AntIT: $r = 0.584$, PostIT: $r = 0.604$ on average; Fig. 2.6E). Thus, reducing the luminance contrast in the colour stimulus to nearly zero did not affect the topography of the colour-selective activity across the IT cortex, although it reduced the magnitude of the colour-selective activity. This reduction in the activation seen with the isoluminant stimulus suggests that this region is sensitive to luminance contrast as well as to colour contrast.

By contrast, the pattern of the activity obtained with isoluminant Mondrian (isoMon,

Fig. 2.6A) was different from that obtained with the colour grating (Gra, Fig. 2.6C). Figure 2.6E shows that there was no significantly positive correlation between the maps obtained with these two different stimulus types (AntIT: $r = 0.179$, PostIT: $r = 0.091$ on average). Thus, the difference in the topography of the colour-selectivity obtained with the Mondrian and grating stimuli cannot be simply attributed to the contribution of the luminance contrast to the activity; it should instead reflect differences in other stimulus parameters. The correlation analysis also showed that the maps obtained with the same types of stimuli in different experiments were significantly correlated; that is, the responses were reproducible across experiments even though there were long time intervals between the experiments.

Comparison of distributions between colour- and shape-selective activities

We have shown that the colour-selective activity in the IT cortex is distributed in the discrete regions. In the exploratory experiments, we also measured the shape-selective activity using the same monkeys as those in the main experiment (see chapter 2). These enabled us to compare the distribution of colour-selective activity with that of shape-selective activity, although there is possibly a slight change in alignment of anatomical and functional images caused by the interval between the experiments. Figure 2.7 shows the boundaries of colour-selective activity obtained with the Mondrian stimuli and shape-selective activity obtained

with the object stimuli superimposed on the flattened surfaces ($P < 0.001$, uncorrected for multiple comparisons). In the most anterior part of the IT cortex, the colour- and shape-selective activities located around the AMTS overlapped very little. On the other hand, the activities in the STS, in the posterior IT and in V4, tended to overlap, although the activity in the posterior IT did not overlap in one hemisphere (M2 right).

4. Discussion

In this study, we observed robust colour-selective activity along the ventral pathway in monkeys. Both spatially large and statistically significant colour-selective responses were found in areas V1, V2/V3 and V4, which is consistent with earlier imaging studies in monkeys (Tootell *et al.*, 2004; Conway & Tsao, 2006; Conway *et al.*, 2007; Wade *et al.*, 2008). In addition to these activities, we found that colour-selective activity is clustered in discrete regions of the monkey IT cortex, and that these colour-selective regions are distributed in both the anterior and posterior IT. Colour-selective regions in the anterior IT are located in or around the AMTS, and possibly in the anterior part of the STS. In the posterior IT, they are located near the PMTS and in the posterior part of the STS. Moreover, we found that different regions of the IT cortex are activated by Mondrian and grating stimuli. This difference in the response patterns was preserved, even when different types of stimuli were presented in the same run, indicating the difference cannot be explained by fluctuations in the signal intensity across runs. Taken together, these findings suggest that there are multiple colour-selective subregions with differing stimulus selectivities distributed in the anterior and posterior IT cortex. This distributed clustering pattern may be analogous to those for some visual categories (Logothetis *et al.*, 1999; Tsao *et al.*, 2003; 2006; Pinsk *et al.*, 2005) and provide important insight into the functional organization of the IT cortex with regard to the processing of colour information.

Colour-selective subregions in the anterior IT

Using Mondrian stimuli, we found a colour-selective region in or around the AMTS in the anterior IT. This suggests that, although colour-selective neurons may be scattered across the anterior IT cortex, this activated region contains larger numbers of colour-selective neurons and/or neurons that are more strongly colour-selective. Previous electrophysiological and imaging studies showed that there are numerous colour-selective neurons in the anterior IT (Komatsu *et al.*, 1992; Komatsu & Ideura, 1993; Tamura & Tanaka, 2001; Edwards *et al.*, 2003; Koida & Komatsu, 2007), and some studies have suggested that there are subregions with a relatively high proportion of colour-selective neurons in or around the AMTS (Komatsu *et al.*, 1992; Tamura & Tanaka, 2001; Tootell *et al.*, 2004; Yasuda *et al.*, 2004). Our present results are consistent with the findings of those earlier studies.

It should be noted, however, that different stimuli were used in those earlier studies, and the reported colour-selective subregions were in slightly different locations. For instance, using simple geometric shapes that were painted uniformly with single colours, Komatsu *et al.* (1992) and Yasuda *et al.* (2004) found that many colour-selective neurons are clustered in regions on the lateral bank of the AMTS and the gyrus lateral and slightly posterior to the AMTS. On the other hand, Tamura & Tanaka (2001) found that neurons preferring colourful

natural image stimuli were more frequently located in the region medial/ventral to the AMTS than in the region lateral/dorsal to the AMTS. Using 2-deoxy glucose (2DG) imaging with grating stimuli, Tootell *et al.* (2004) identified colour-selective regions on the gyrus posterior to the AMTS. Thus, colour-selective responses are commonly observed around the AMTS, but the precise locations are not entirely consistent.

When we used Mondrian stimuli, we found that the activation was located in the fundus/lateral bank of the AMTS, or on the gyrus lateral and slightly posterior to the AMTS. This location is close to where colour-selective neurons were observed by Komatsu *et al.* (1992) and Yasuda *et al.* (2004), but is different from the results by Tamura & Tanaka (2001). This suggests that colour stimuli with simple geometrical patterns are effective for activation of the fundus/lateral bank of the AMTS, whereas more complex object images are necessary for activation of the area medial to the AMTS. Although the grating stimuli used in the present study is similar to those used by Tootel *et al.* (2004), we did not observe clear activation in the anterior IT with this stimulus. However, the grating stimuli did evoke weak localized activation near the posterior end of the AMTS (Fig. 2.6C), which may be strong enough to be detected by 2DG imaging, but not strong enough to be detected by fMRI.

Colour-selective subregions in the posterior IT

Using colour grating stimuli, we found colour-selective activity in a region ventral to the PMTS and in a region in the posterior STS within the posterior IT. Judging from the sulcal landmarks, the region near the PMTS is likely in area TEO. In earlier 2DG imaging and fMRI studies using grating stimuli, colour-selective activity was detected in TEO (Tootell *et al.*, 2004; Conway *et al.*, 2007), and a positron emission tomography study in monkeys also reported strong activation in TEO when monkeys performed a colour discrimination task (Takechi *et al.*, 1997). With respect to the numbers and positions of the colour-selective subregions, our present results obtained using colour grating stimuli are largely consistent with those earlier findings.

Colour-selective regions in the posterior IT activated by Mondrian stimuli were located more anterior than those activated by grating stimuli. Judging from the sulcal landmarks, these regions are located in TEO or extend into the posterior part of area TE. Given that TEO has a coarse retinotopy (Boussaoud *et al.*, 1991; Brewer *et al.*, 2002; Yasuda *et al.*, 2009), the difference between the locations of the activated regions might in part reflect the difference in the extents of the two stimulus types in the visual field. However, the retinotopy cannot, by itself, explain the positional difference of the activations because the visually responsive regions obtained with each stimulus type largely overlapped. It is more likely that these regions have different stimulus selectivities.

Colour-selective activation in the posterior IT in response to the grating and Mondrian stimuli suggest clustering of colour-selective neurons in these regions. Yasuda *et al.* (2009)

recently found that sharply tuned colour-selective neurons are clustered in a region around the PMTS. This region is close to the region in which grating stimuli evoked the colour-selective activation. An earlier electrophysiological study found a column containing neurons selective for multicoloured patterns in the IT gyrus, slightly anterior to the PMTS (Fujita *et al.*, 1992), at a position close to where we found colour-selective activity using Mondrian stimuli. However, this study did not examine whether the presence of those neurons was consistent across individuals, or whether they were clustered in this region. We suggest that columns preferring multicoloured patterns relatively concentrated in regions anterior to the PMTS.

Colour-selective activity in the STS

A recent study in which single-unit recording combined with fMRI revealed that a patch in the posterior STS contains a high proportion of colour-selective neurons (Conway *et al.*, 2007). By contrast, little is known about how colour-selective neurons distribute in the anterior part of the STS. Although earlier electrophysiological studies found colour-selective neurons in the anterior STS, there has been no study that conducted a systematic mapping around this region and no imaging study that addressed this issue. In our study, strong colour-selective activations in the anterior part of the STS were found only in two hemispheres of one monkey using Mondrian stimuli. This implies that there are colour-

selective subregions in the anterior STS, but they were not effectively activated by our Mondrian or grating stimuli.

Potential influence of susceptibility artefact

Although we examined colour-selective activity in the entire IT cortex, we might have underestimated colour-selective activity in some regions, especially around the middle of the IT gyrus, where there was a region affected by susceptibility artefact. The locations of the affected region varied, depending on the hemisphere, some of which were close to or overlapped the colour-selective regions in the anterior and posterior IT. The susceptibility artefact may explain why some colour-selective regions were not reliably identified in some hemispheres, and also why the statistical significance of the colour-selectivity was relatively weak. This also leaves the possibility that some colour-selective activities in this region could have been overlooked. Measurements with methods that are free of the susceptibility artefact will be needed to test this possibility.

Stimulus dependent activation of colour-selective subregions

Our results have shown that Mondrian and grating stimuli produce different patterns of colour-selective activation in the IT cortex. A remarkable difference was seen in the anterior IT; the Mondrian activated a region in the anterior IT, whereas the grating did not. This is in accordance with human fMRI studies; Mondrian stimuli activate multiple colour-selective areas/regions extending from the posterior to the anterior part of the fusiform gyrus (Beauchamp *et al.*, 1999; Bartels & Zeki, 2000; Brewer *et al.*, 2005), whereas isoluminant gratings produce colour-selective activation in a relatively posterior part of the fusiform gyrus, but not in more anterior regions (Hadjikhani *et al.*, 1998). This suggests that Mondrian stimuli are more suitable for identifying higher-order colour-selective areas/regions located more anteriorly within the ventral cortex.

Given that Mondrian and grating stimuli differ in many aspects – e.g., luminance contrast, chromatic structure, spatiotemporal frequency, global shape and motion – which is the critical factor responsible for the differential activation in higher-order areas is an intriguing question. To address that question in part, we used an isoluminant Mondrian stimulus to assess the influence of luminance contrast and found that the magnitudes of responses to nearly isoluminant Mondrian were diminished in the IT cortex. This suggests that the use of isoluminant stimuli is less effective for identification of colour-selective regions in the IT cortex, probably because these regions are sensitive to luminance contrast as well as colour contrast. However, the difference in the responses to the Mondrian and grating stimuli in the IT cortex cannot be attributed solely to the difference in luminance contrast; the

topography of the colour-selectivity within the anterior and posterior IT was largely invariant with respect to luminance contrast (Fig. 2.6).

A salient difference between the Mondrian and grating stimuli is in their chromatic structure. Whereas the colour grating was modulated only along a red-blue axis, the colour Mondrian contained a variety of hues. This difference might have caused the difference in the responses across areas/regions, depending on the colour tuning characteristics. Some areas/regions, typically the LGN, contain colour-selective neurons broadly tuned either to L-M or S-(L+M) cone-opponent signals (Derrington *et al.*, 1984; De Valois *et al.*, 2000; Hanazawa *et al.*, 2000), whereas other areas/regions contain colour-selective neurons narrowly tuned to hues and/or saturations (Lennie *et al.*, 1990; Komatsu *et al.*, 1992; Gegenfurtner *et al.*, 1996; Hanazawa *et al.*, 2000; Kusunoki *et al.*, 2006; Conway *et al.*, 2007; Kotake *et al.*, 2009). A multicoloured Mondrian stimulus may effectively elicit responses in regions containing many such hue-selective neurons, but a red-blue grating stimulus may not, since this grating cannot activate neurons narrowly tuned to specific hues such as green, yellow, orange, etc. This may explain why some colour-selective subregions in the IT were effectively activated by the Mondrian stimulus but not by the grating stimulus.

In addition, the Mondrian and grating stimuli differ with respect to their spatiotemporal structures, such as spatial frequency, temporal frequency, global shape and motion. For example, the grating stimulus contained only low spatial and temporal frequencies (0.33 cycles/deg, 1 Hz), whereas the Mondrian stimulus contained a variety of

spatial frequencies and an even lower temporal frequency (0.25 Hz). The difference in the spatiotemporal frequency could affect overall colour responsivity in V1 and V4, where responses to colour contrast are dependent on these factors (Schluppeck & Engel, 2002; Wade *et al.*, 2008). However, little is known about the extent to which colour responsivity and response topography in the monkey IT are dependent upon the spatiotemporal structure of the stimuli. Consequently, which factor was most critical for the difference in the responses between to Mondrian and grating stimuli remains an open question for future study.

Functional organization in the IT cortex

Our results have shown that the colour-selective activity in the IT cortex is distributed in the discrete regions. This spatial distribution suggested a possible analogy with the organization in the IT cortex recently reported for the shape-selectivity (Tsao *et al.*, 2003; Denys *et al.*, 2004). We have also measured the shape-selective activity in the exploratory experiments using the same monkey, which enabled us to compare the distributions of colour- and shape-selective activities in the IT cortex. The comparison between colour- and shape-selective activities showed the tendency that the colour- and shape-selective activities overlap little in the anterior IT (Fig 2.7). On the other hand, the colour-selective activity in the posterior IT overlapped with the shape-selective activity. These findings are consistent with the result of

previous electrophysiological recording experiments comparing the neuronal response to colour with that to shape stimuli (Yasuda *et al.*, 2004; 2009).

Functional correspondence between cortical areas in humans and monkeys

Do the regions we found in the monkey IT cortex correspond to any human areas/regions? Previous fMRI studies in humans revealed the presence of colour-selective areas/regions along the fusiform gyrus. These include V4 (McKeefry & Zeki, 1997), V8 (Hadjikhani *et al.*, 1998), the VO cluster (Brewer *et al.*, 2005), V4α (Bartels & Zeki, 2000) and regions on the anterior part of the fusiform gyrus (Beauchamp *et al.*, 1999; Bartels & Zeki, 2000; Brewer *et al.*, 2005). Among these, human V8 and the VO cluster are retinotopic areas lying next to V4 (Hadjikhani *et al.*, 1998; Wade *et al.*, 2002; Brewer *et al.*, 2005), whereas V4α and the regions in the anterior fusiform gyrus are presumably non-retinotopic areas located far anterior to V4. Correspondingly, single-cell activity recorded from monkeys suggests that there are retinotopic maps in the posterior part of the IT cortex (Boussaoud *et al.*, 1991; Yasuda *et al.*, 2009), but not in the anterior part of the IT cortex. The presence of retinotopic organizations and the anatomical locations with respect to V4 suggests that colour-selective regions in the macaque posterior IT may correspond to human V8/VO, and those in the macaque anterior IT may correspond to human V4α and the regions in the anterior fusiform

gyrus, although there are some differences in the configuration of the retinotopic map between the monkey posterior IT and human V8/VO. Recent human fMRI studies and single-unit recording experiments in monkeys seem to shed some light on this issue. Recent imaging studies have suggested that in humans the anterior fusiform regions are active during conscious colour perception (Nunn *et al.*, 2002; Morita *et al.*, 2004; Murphey *et al.*, 2008) or when subjects perceive object colour and retrieve knowledge about object colour (Martin *et al.*, 1995; Zeki & Marini, 1998; Chao & Martin, 1999; Simmons *et al.*, 2007). These observations appear to be consistent with the recent findings that the activities of colour-selective neurons in the anterior IT correlate with the monkey's colour judgment (Koida & Komatsu, 2007; Matsumora *et al.*, 2008) and colour-object association (Edwards *et al.*, 2003).

5. Conclusion

We have successfully applied fMRI to awake monkeys and obtained activities in the visual cortical areas to various kinds of stimuli that are largely consistent with previous electrophysiological and fMRI experiments. Specifically, we have extensively examined the distribution of colour-selective activity in the monkey IT cortex using fMRI and obtained new findings about the functional organization of the IT cortex related to colour processing. The colour-selective activity was obtained using Mondrian stimuli and grating stimuli, which has been commonly used in human fMRI. We have found that colour-selective activity is clustered in discrete regions of the monkey IT cortex and that these colour-selective regions are distributed in both the anterior and posterior IT. The colour-selective region in the anterior IT, which has not been reported in previous monkey fMRI, may correspond to the V4α and regions on the anterior part of the fusiform gyrus reported in previous human fMRI.

Acknowledgements

I would like to express sincere gratitude to all people who helped me during my doctoral study. It would not have been possible to accomplish the study without their help and support. My deepest appreciation goes to Dr. N. Goda for his enlightening guidance and inspiring instruction in the development and completion of the study. I am also deeply grateful to Prof. H. Komatsu for his constant supervision and suggestion through the doctoral program.

I would also like to thank Dr. M. Ito for giving me constructive comments and suggestions for the study. Special thanks are also to Dr. H. Toyoda for teaching me about the fMRI technique and protocol. I am indebt to Prof. N. Sadato and Dr. T. Ogawa for reviewing the manuscript and giving me valuable advice.

I would also like to extend my gratitude to all laboratory members. In particular, M. Togawa and T. Ohta greatly helped in establishing the experimental systems and training the monkeys. I also want to thank my colleague, T. Banno for his advice and encouragement. All other members inspired me in research and life during the long hours in the laboratory.

Last, but by no means least, I would like to thank my parents and sister for their understanding, constant encouragement and big help.

Abbreviations

2DG, 2-deoxy glucose; AMTS, anterior middle temporal sulcus; BOLD, blood oxygen level-dependent; CO, cytochrome-oxidase; CSI, colour-selectivity index; fMRI, functional magnetic resonance imaging; HM, horizontal meridian; IOS, inferior occipital sulcus; IR, infrared; IT cortex / IT gyrus, inferior temporal cortex / gyrus; ITI, inter-trial interval; LGN, lateral geniculate nucleus; MPRAGE, magnetization-prepared rapid-acquisition gradient-echo; OTS, occipitotemporal sulcus; PMTS, posterior middle temporal sulcus; ROI, region of interest; STS, superior temporal sulcus; VM, vertical meridian.

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Figure 1.1

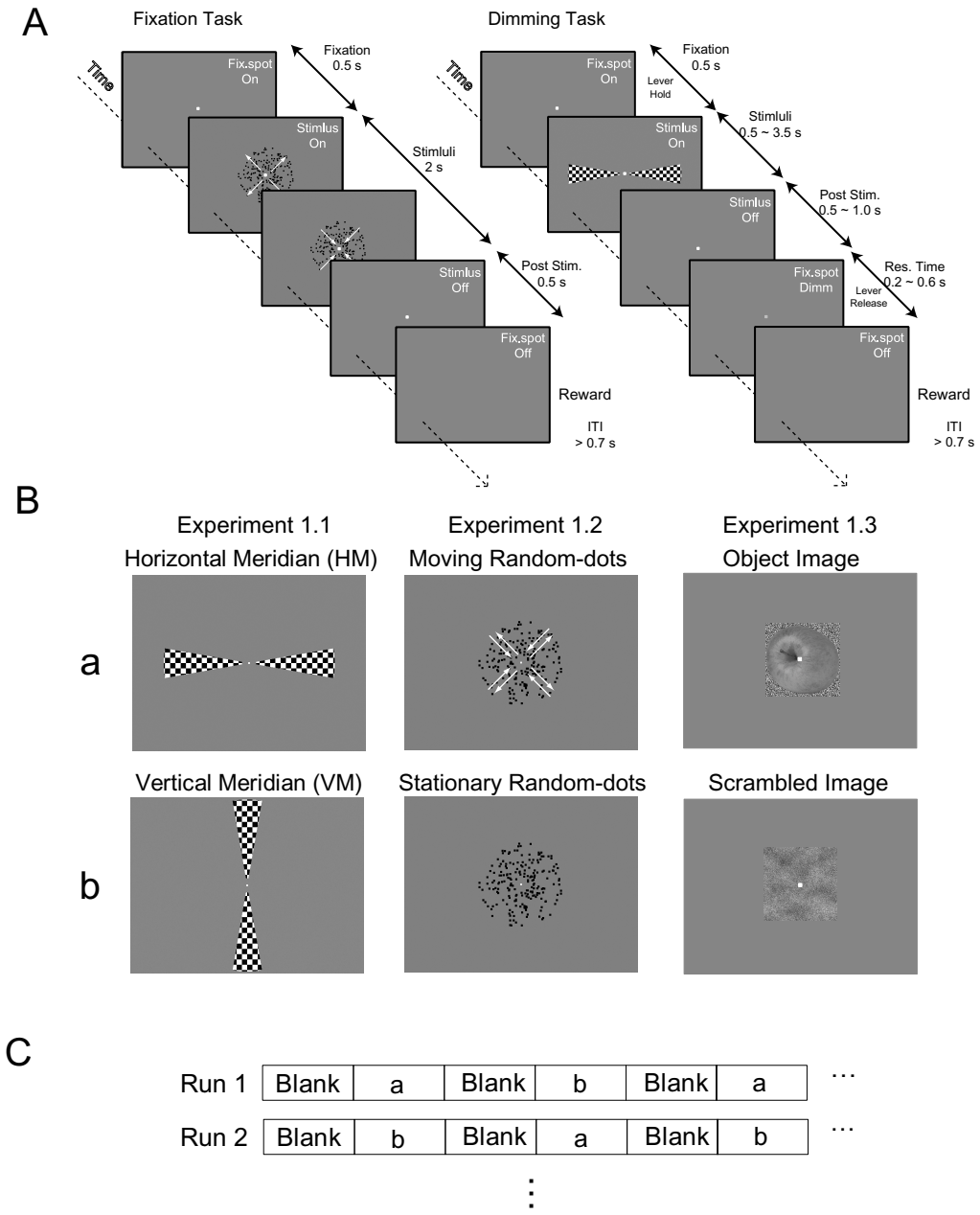

Fig. 1.1. Tasks and stimuli in the exploratory experiments. (A) Time sequence of the fixation task (left) and the dimming detection task (right). (B) Horizontal meridian and Vertical meridian stimuli used in Experiment 1.1 (left) and moving random-dot and stationary random-dot stimuli used in Experiment 1.2 (centre) and object image and scrambled image stimuli used in Experiment 1.3 (right). (C) The experimental paradigm of the measurements. Block of (a) and (b) were composed of the stimuli in the upper and lower row, respectively. ITI, inter-trial interval.

Figure 1.2

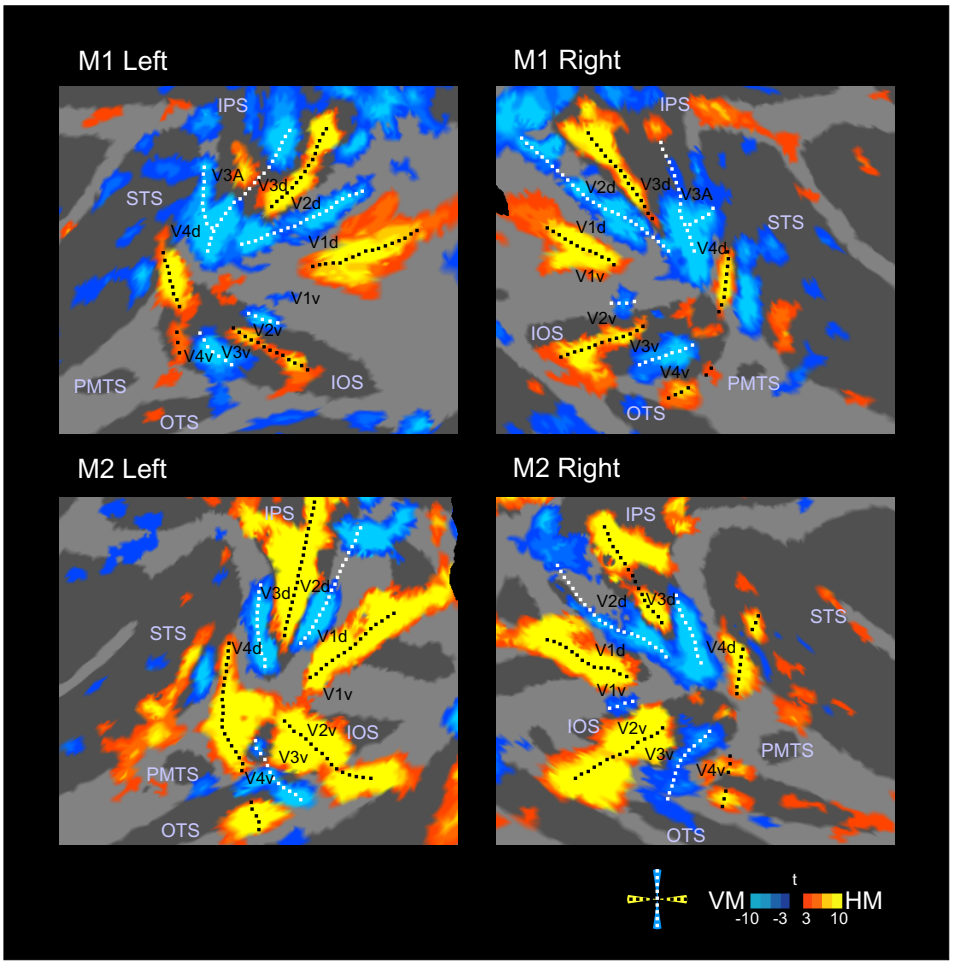

Fig. 1.2. Retinotopic organization of the visual cortex in four hemispheres indetified by comparing the activities to the HM and VM stimuli. Statistical parametric maps (SPM{*t*}) indicating voxels that show significantly different activity between when the subject is viewing horizontal meridian (HM) stimuli and vertical meridian stimuli (VM) are superimposed on the flattened cortical surface. Yellow colour codes HM-VM and blue colour codes VM-HM ($P < 0.0005$, uncorrected for multiple comparisons). Black and white dotted lines represent the horizontal and vertical meridians, respectively. AMTS, anterior middle temporal sulcus; IOS, inferior occipital sulcus; IPS, intraparietal sulcus; OTS, occipital temporal sulcus; PMTS, posterior middle temporal sulcus; STS, superior temporal sulcus.

Figure 1.3

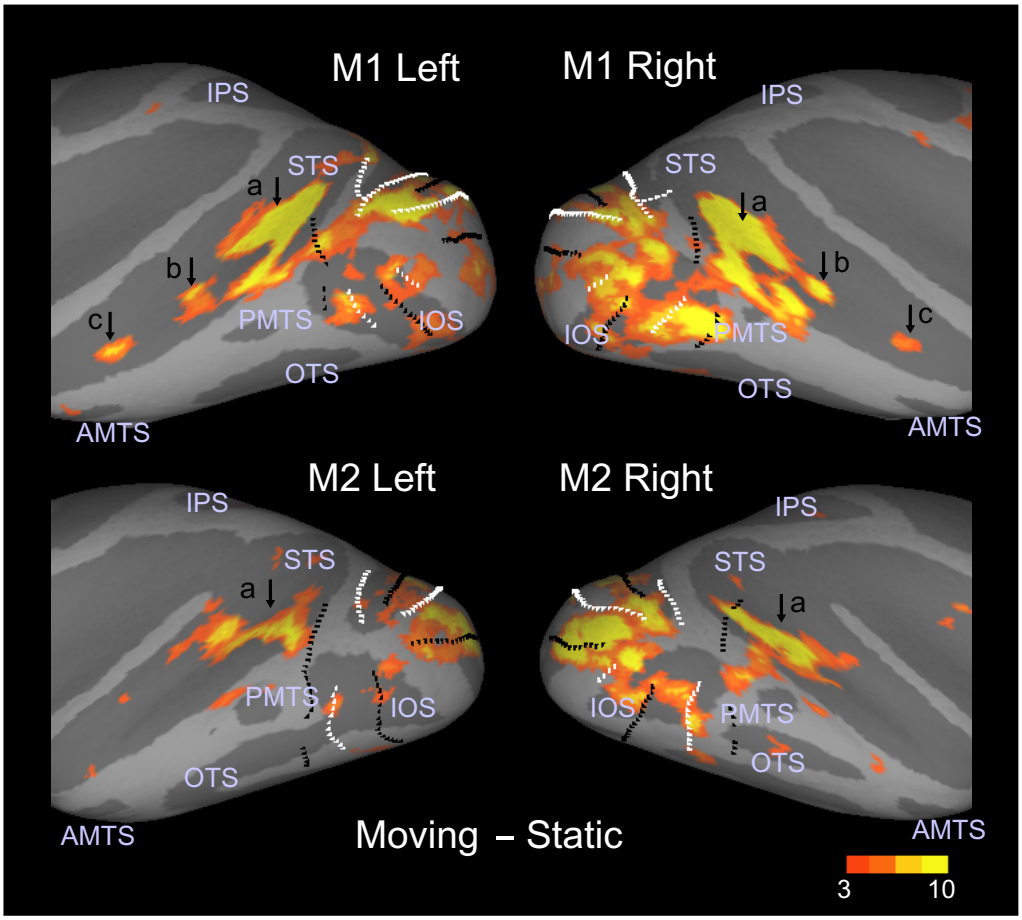

Fig. 1.3. Motion-selective activity in the visual cortex in four hemisheres. Statistical parametric maps (SPM{*t*}) indicating voxels that are significantly more active when the subject is viewing moving random-dot stimuli than stationary ones ($P < 0.001$, uncorrected for multiple comparisons) are superimposed on the inflated cortical surface. Black and white dotted lines represent the horizontal and vertical meridians, respectively.

Figure 1.4

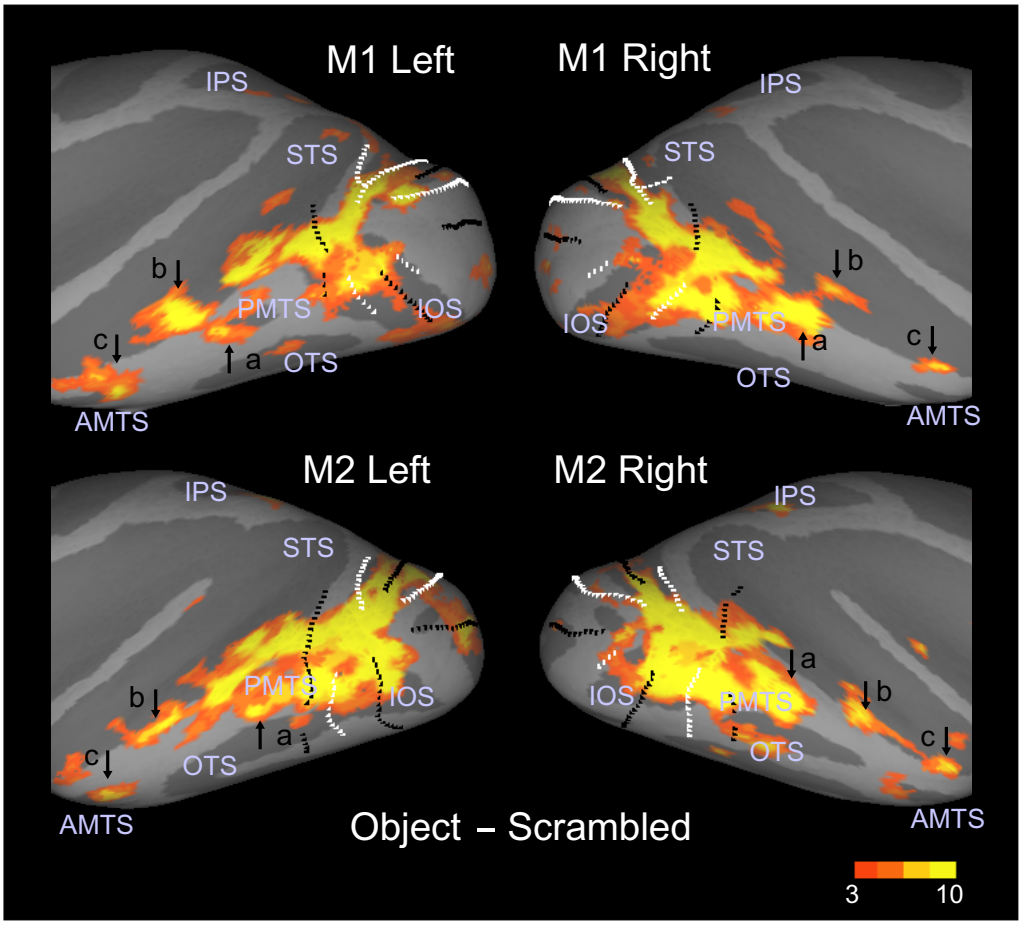

Fig. 1.4. Shape-selective activity in the visual cortex in four hemisheres. Statistical parametric maps (SPM{*t*}) indicating voxels that are significantly more active when the subject is viewing object image stimuli than Fourier-phase scrambled image stimuli ($P < 0.001$, uncorrected for multiple comparisons) are superimposed on the inflated cortical surface. Black and white dotted lines indicate positions that represent the horizontal and vertical meridians, respectively.

Figure 1.5

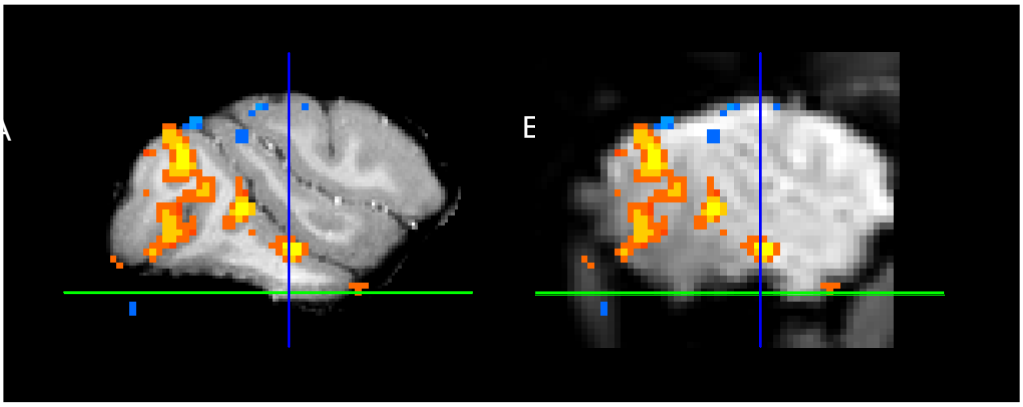

Fig. 1.5. Signal acquired from the IT cortex in the experiment that measured shape-selective activity. The anatomical (left) and functional (right) images sectioned in the same sagittal position. Crosshair with blue and green indicates the position where the signal was dropped in the functional image but not in the anatomical image.

Figure 2.1

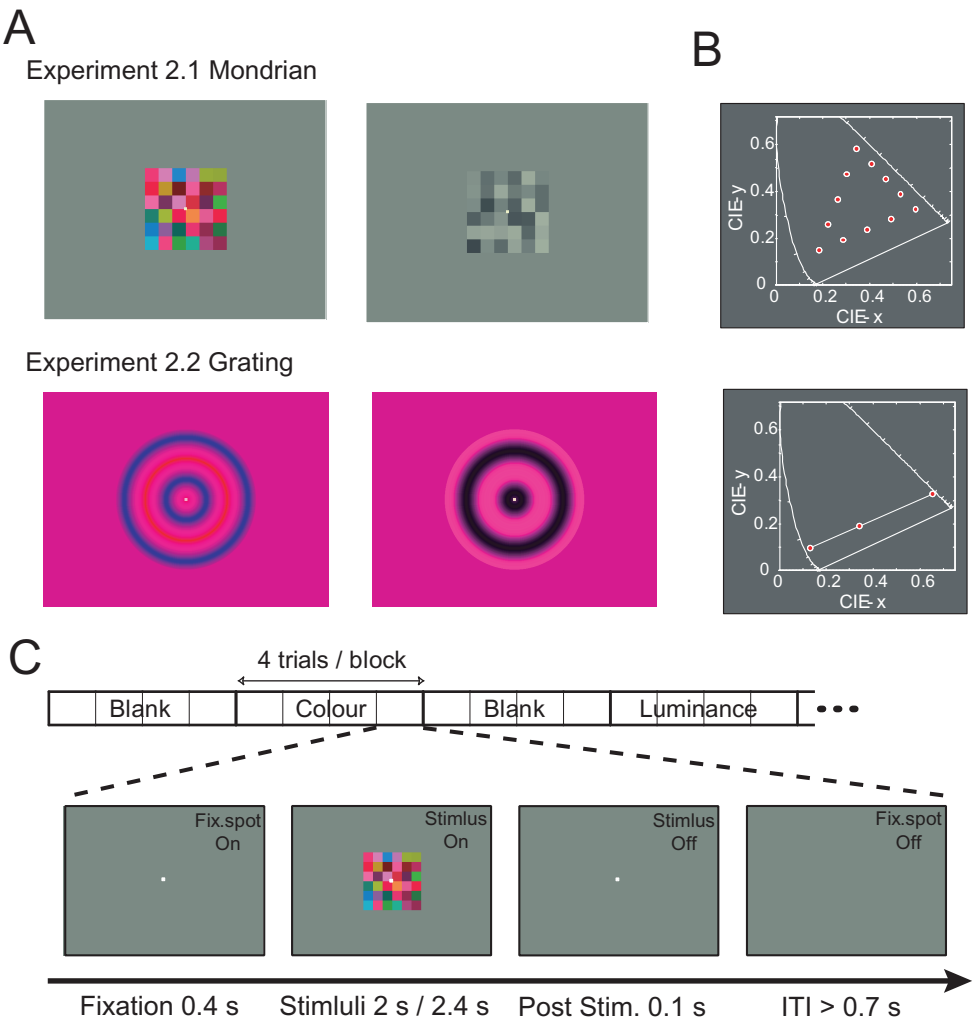

Fig. 2.1. Stimuli and task in the main experiment that measured colour-selective activity. (A) Chromatic (top-left) and achromatic (top-right) Mondrian stimuli used in Experiment 2.1, and colour-varying (bottom-left) and luminance-varying (bottom-right) grating stimuli used in Experiment 2.2. (B) The CIE-xy chromaticity coordinates of each colour stimulus (top: Mondrian; bottom: grating). (C) The experimental paradigm and time sequence of the fixation task that the monkeys performed during the measurements.

Figure 2.2

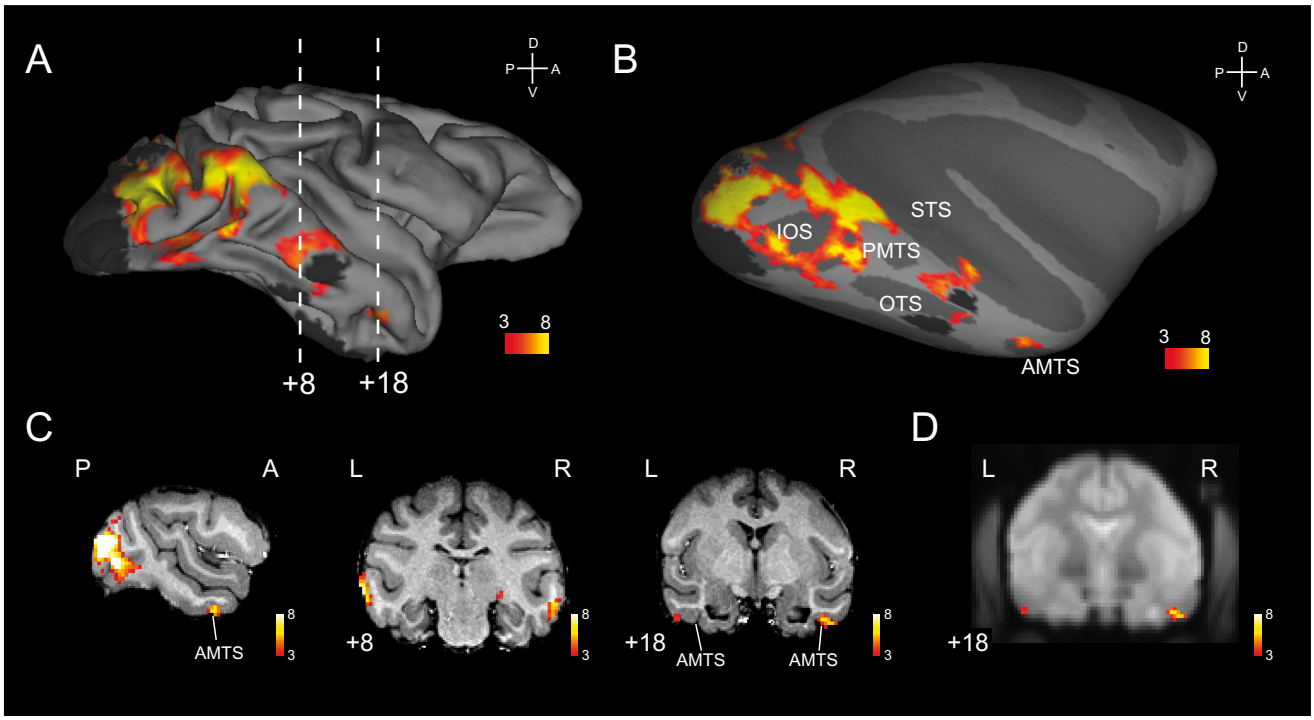

Fig. 2.2. Colour-selective activity elicited by Mondrian stimuli in monkey M2. (A and B) Statistical parametric maps (SPM{*t*}) indicating voxels that are significantly more active when the subject is viewing a chromatic Mondrian stimulus than an achromatic one ($P < 0.001$, uncorrected for multiple comparisons) are superimposed on the folded cortical surface (A) and inflated surface (B) of the right hemisphere of M2. The colour scales indicate the t-scores. The overlaid black regions indicate signal drop-out. (C) Statistical parametric maps are superimposed on sagittal (left hemisphere) and coronal sections of M2. The locations of the coronal sections are indicated in millimetres relative to the interaural line (positive values are anterior) and by the vertical dashed lines on the surface map (A). (D) Statistical parametric maps are superimposed on a mean functional image. The position of the section is the same as the right section in (C). A, anterior; D, dorsal; L, left; P, posterior; R, right; V, ventral.

Figure 2.3

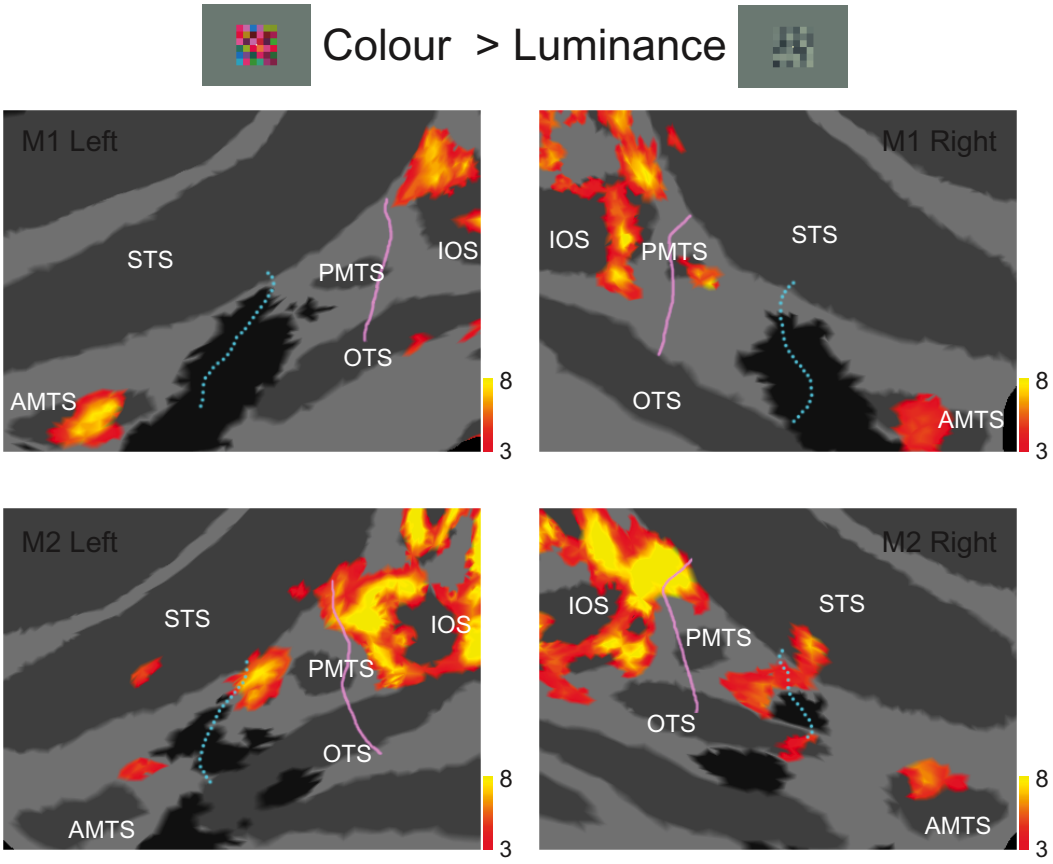

Fig. 2.3. Colour-selective activity elicited by Mondrian stimuli in the IT cortex in four hemispheres. Colour-selective activities are superimposed on the flattened surfaces of the IT cortex in four hemispheres ($P < 0.001$, uncorrected for multiple comparisons). The solid light purple lines indicate the anterior border of V4, and the dotted light blue lines indicate the border between the anterior and posterior IT (see Materials and Methods).

Figure 2.4

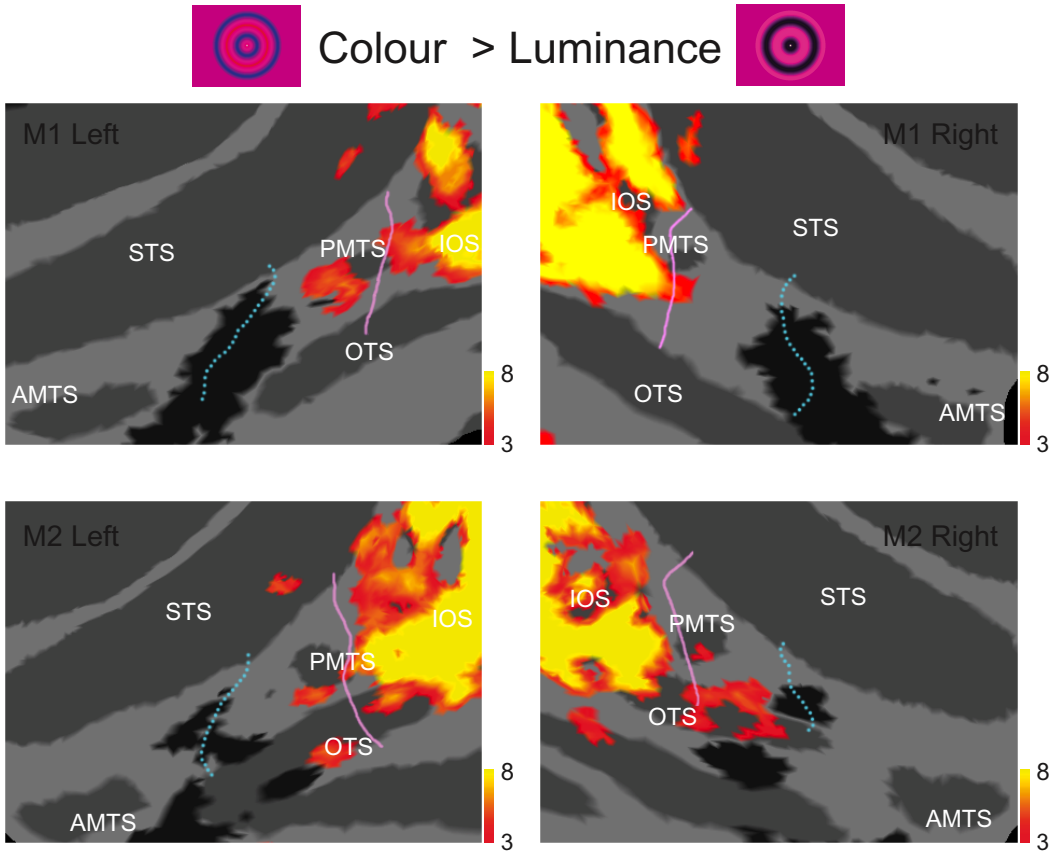

Fig. 2.4. Colour-selective activity elicited by the grating stimuli in the IT cortex in four hemispheres. Statistical parametric maps indicating the voxels that are significantly more active when the subject is viewing the colour grating than the luminance grating are superimposed on the flattened surfaces of the IT cortex in four hemispheres ($P <$ 0.001, uncorrected for multiple comparisons).

Figure 2.5

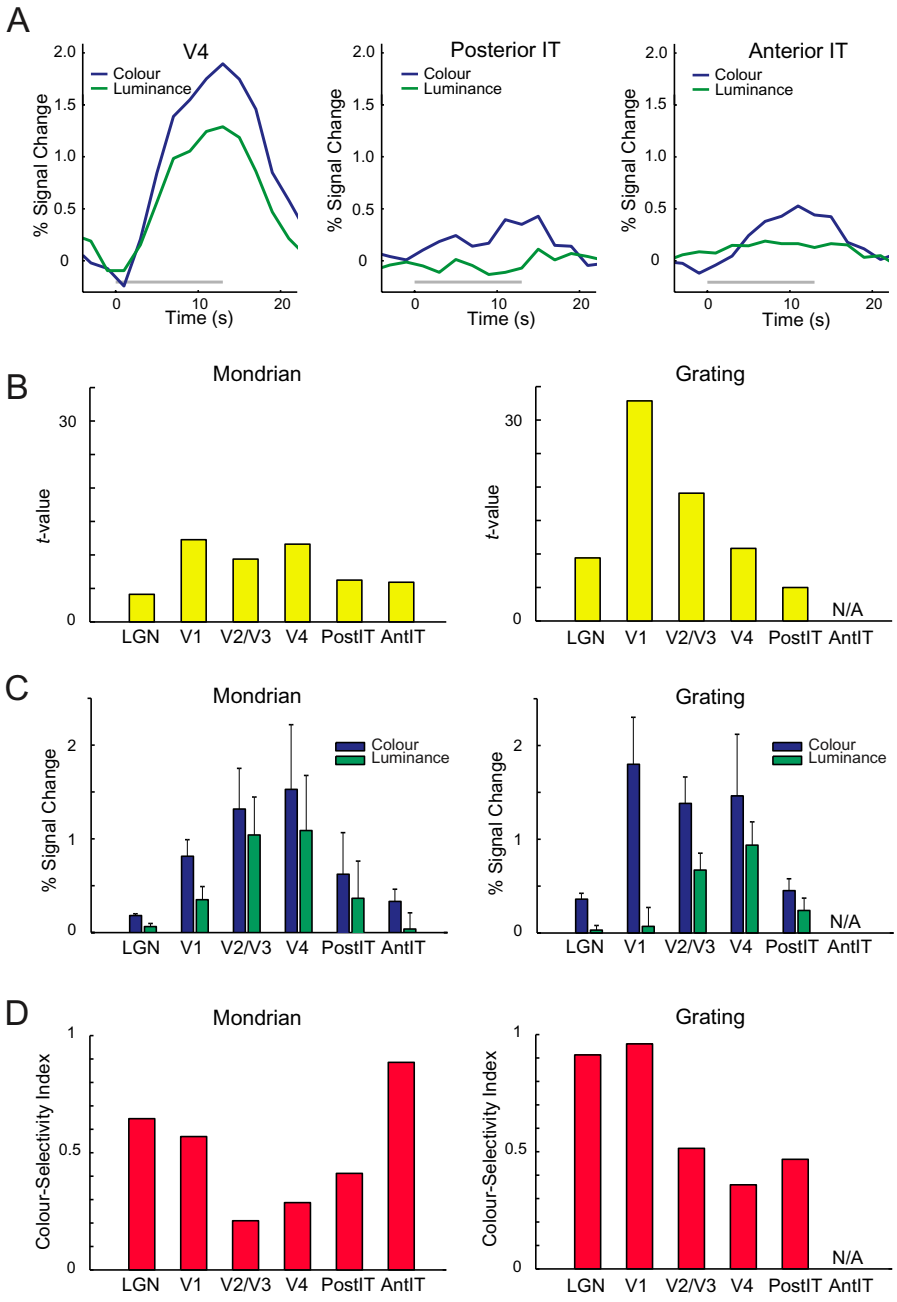

Fig. 2.5. Comparison of colour-selective activity among regions/areas. (A) Time courses of the activation elicited by Mondrian stimuli in the most significant voxel within V4, the posterior IT and the anterior IT in the right hemisphere of M2. The blue and green solid lines indicate the time courses obtained from blocks of the colour and luminance stimuli, respectively. The visual stimulation epoch is indicated by the horizontal grey bars. (B) T-values taken from the most significant voxel within V1, V2/V3, V4, the posterior IT (PostIT) and the anterior IT (AntIT). (C) Mean amplitudes of the responses elicited by the colour and luminance stimuli taken from the most significant voxels and averaged across three or four hemispheres are indicated by solid blue and green bars, respectively. Error bars indicate standard error of the mean. (D) Colour-selectivity indices (CSIs) calculated from the mean response amplitudes across four hemispheres. The response amplitude and CSI for the anterior IT were not plotted for the grating stimulus because it elicited no activation in the anterior IT. LGN, lateral geniculate nucleus.

Figure 2.6

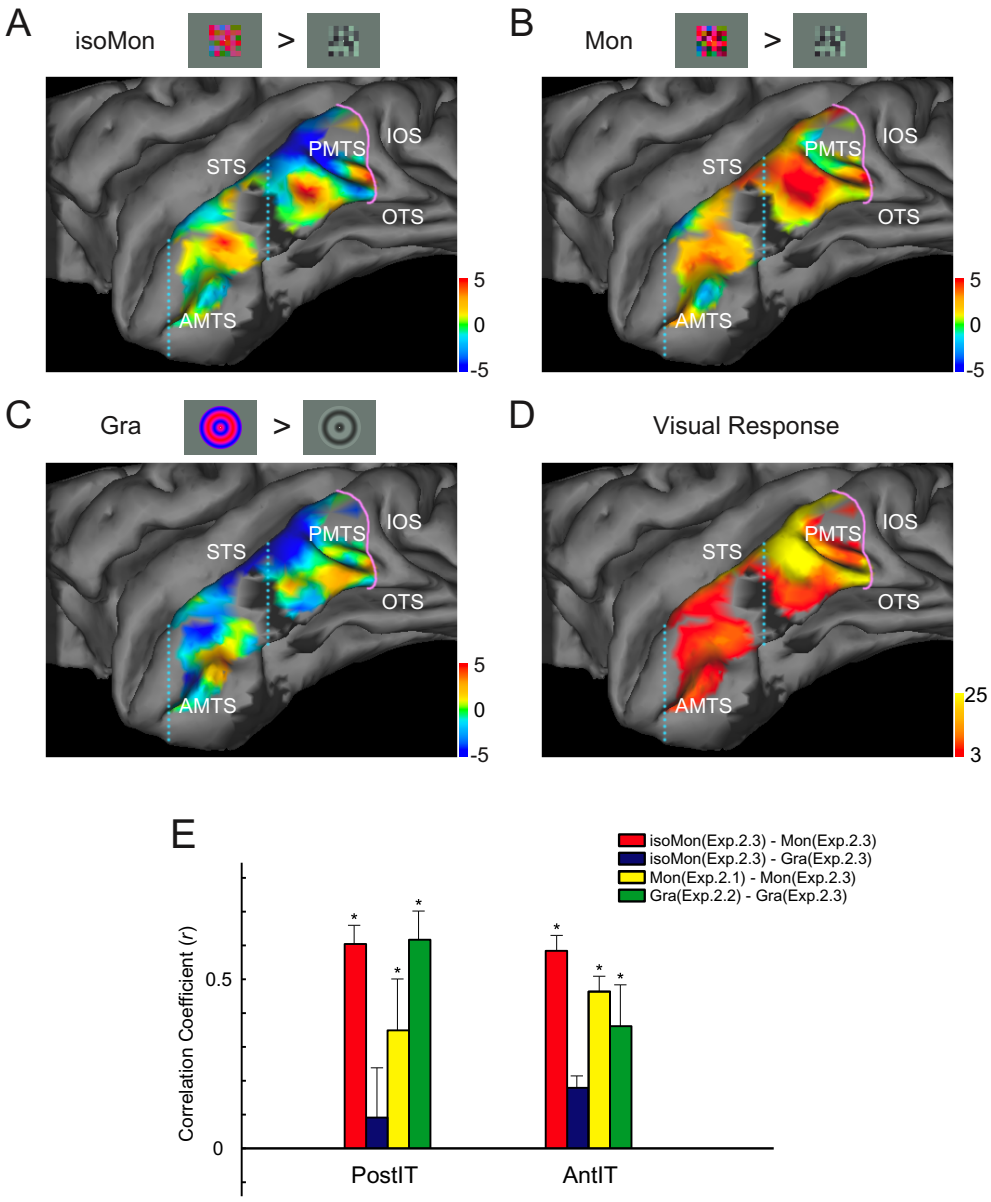

Fig. 2.6. Comparison between the patterns of colour-selective activity obtained with different types of stimuli. (A-C) Colour-selective response maps superimposed on the IT gyrus of the folded cortical surface of M2. These maps were obtained by contrasting isoluminant chromatic Mondrian vs. achromatic Mondrian (A, isoMon), chromatic Mondrian vs. achromatic Mondrian (B, Mon), and chromatic grating vs. achromatic grating (C, Gra) in Experiment 2.3. The maps were not statistically thresholded, but were restricted to the visually responsive region shown in (D). Positive values (green to red) represent the biased responses to chromatic stimuli, and negative values (green to blue) represent the biased responses to achromatic stimuli. (D) The visually responsive region superimposed on the same surface seen in the other three panels. This map was obtained by contrasting summed responses during all stimulus conditions with the responses during the fixation baseline in Experiment 2.3 ($P < 0.001$ uncorrected for multiple comparisons). (E) Correlation coefficient between pairs of colour-selective response maps in the posterior IT (PostIT ROI) and the anterior IT (AntIT ROI) averaged over four hemispheres. The column colour represents the pair of colour-selective response maps. The error bars represent the standard error of the mean over four hemispheres. The asterisks indicate that the average correlation coefficients between the pairs of maps were significantly positive ($P < 0.05$, permutation test).

Figure 2.7

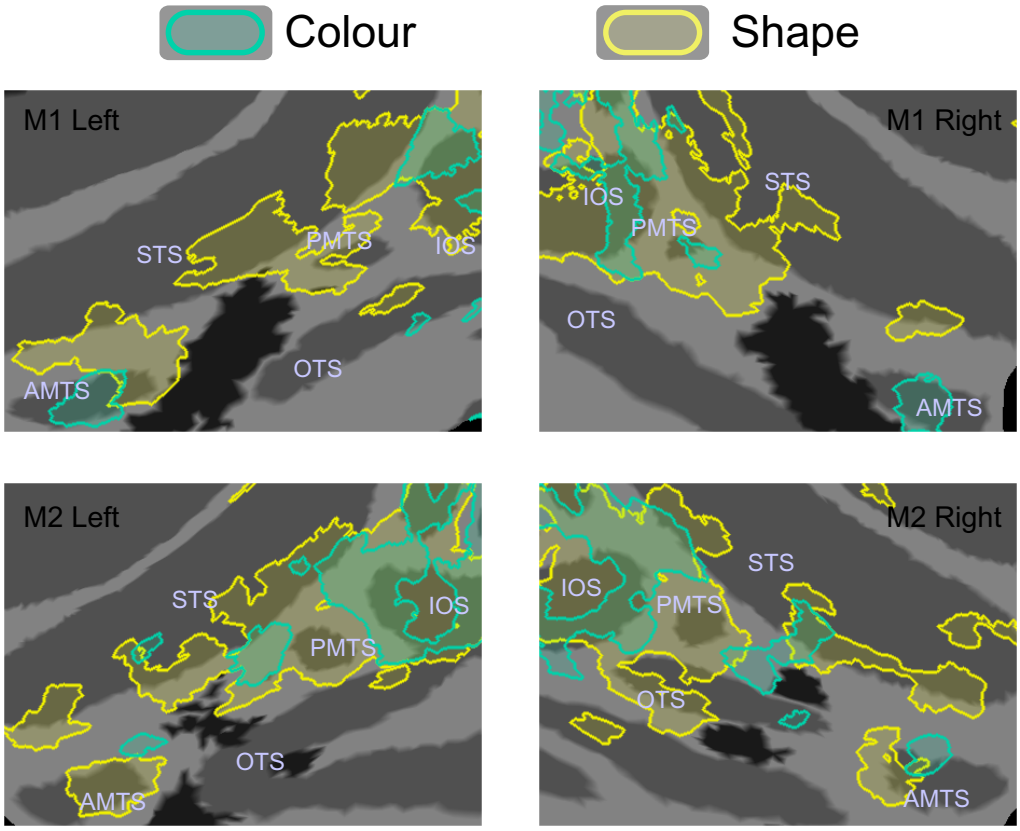

Fig. 2.7 Comparison of the distribution between colour- and shape-selective activities. Boundaries of colour- ($P < 0.001$, uncorrected for multiple comparisons) and shape-selective activity ($P < 0.001$, uncorrected for multiple comparisons) were superimposed on the flattened cortical surfaces in four hemispheres. Green and yellow lines indicate the boundaries of colour- and shape- selective activity, respectively.