We used positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) in human subjects to investigate whether the ventral and dorsal visual stream cooperate when active judgements about color have to be made. Color was used as the attribute, because it is processed primarily in the ventral stream. The centrally positioned stimuli were equiluminant shades of brown. The successive color discrimination task was contrasted to a dimming detection task, in which retinal input was identical but with double the number of motor responses. The stimulus presentation rate was parametrically varied and a constant performance level was obtained for all conditions. The visual activation sites were identified by retinotopic mapping and cortical flattening. In addition, one psychophysical and two fMRI experiments were performed to control for differences in visuospatial attention and motor output. Successive color discrimination involved early visual areas, including V1 and VP and the ventral color-responsive region, as well as anterior and middle dorsal intraparietal sulcus, dorsal premotor cortex and pre-SMA. Cortical regions involved in dimming detection and motor output included area V3A, hMT/V5+, lateral occipital sulcus, posterior dorsal intraparietal sulcus, primary motor cortex and SMA. These experiments demonstrated that even with color as the attribute, successive discrimination, in which a decision process has to link visual signals to motor responses, involves both ventral and dorsal visual stream areas.

Keywords: decision, featural attention, functional imaging, human, parietal cortex, tonic/phasic modulation

Introduction

Considerable evidence has accumulated that the visual system is organized into a ventral occipitotemporal stream (‘what’ system) and a dorsal occipitoparietal stream (‘where’ system) (Ungerleider and Mishkin, 1982). The initial distinction was based on the different visual attributes processed in the two streams (Ungerleider and Mishkin, 1982; Van Essen et al., 1992). Additional distinctions based upon the behavioral goal and nature of the cognitive operations have since been suggested. According to Goodale et al. (1991), the ventral stream plays a major role in perceptual judgements, whereas the dorsal stream processes visual information in order to control and guide motor activities. Recently, Fias et al. (2002) have demonstrated that tasks involving the same attribute and the same behavioral goal (perceptual judgement), but differing in the cognitive operations required, will engage the ventral and dorsal streams differently.

There is also mounting evidence for cooperation between the two pathways. Single cell and functional imaging studies have shown that judgements about visual attributes, such as orientation (Cornette et al., 1999; Faillenot et al., 2001), direction of motion (Ferrera et al., 1994; Cornette et al., 1998) and shape of objects (Kraut et al., 1997; Grill-Spector et al., 2000; Denys et al., 2002; James et al., 2002) involve both ventral and dorsal pathway regions. However, these features are processed, at least partially, in the dorsal pathway (Saito et al., 1986; Newsome and Paré, 1988; Felleman and Van Essen, 1991; Galletti et al., 1991; Colby et al., 1993; Sereno and Maunsell, 1998; Lauwers et al., 2000). Hence, the involvement of dorsal regions in orientation and direction judgements could simply reflect their selectivity for these attributes. Several studies have suggested the involvement of dorsal parietal regions in decision processes, particularly human intraparietal sulcus (Deiber et al., 1991; Leonards et al., 2000; Faillenot et al., 2001; Peusken et al., 2001) and the lateral intraparietal area (LIP) in monkeys (Shadlen and Newsome, 1996, 2001; Platt and Glimcher, 1999). A much stronger case for cooperation between the two streams could be presented if the dorsal parietal regions could be shown to be involved in decisions whose perceptual basis is located primarily in the ventral stream. Therefore, in the current study we used color as the attribute because it is processed in the ventral stream, as has been extensively documented by physiological, anatomical, behavioral and imaging data in monkeys (Zeki, 1973, 1978, 1983; Ungerleider and Mishkin, 1982; Van Essen and Maunsell, 1983; Felleman and Van Essen, 1991; Heywood et al., 1992; Komatsu et al., 1992; Takechi et al., 1997; Vanduffel et al., 1997; Huxlin et al., 2000; Nelissen et al., 2002). Studies of patients with cerebral achromatopsia have also indicated that the ventral occipitotemporal cortex is crucial in the processing of color information (Meadows, 1974; Damasio et al., 1980; Zeki, 1990; Beauchamp et al., 2000).

Human functional imaging studies have suggested that a posterior ventral area in fusiform gyrus or collateral sulcus is specifically involved in color processing (Lueck et al., 1989; Zeki et al., 1991; Sakai et al., 1995; Clark et al., 1997; Hadjikhani et al., 1998; Wandell, 1999; Wade et al., 2002). This area has been variously designated as the human homologue of monkey area V4 (Zeki et al., 1991), the unique human area V8 (Hadjikhani et al., 1998) and area V0 (Wandell, 1999). These studies involved passive viewing conditions, in which chromatic stimuli were contrasted with their achromatic counterpart. In the present study, color is used in an active discrimination task, in which visual stimuli have to be linked to...
a motor response. Corbetta et al. (1991) used an active color discrimination task and the same color-containing stimuli in both the experimental and control task. However, the stimuli contained multiple attributes and were not equiluminant. Beauchamp et al. (1999) used an active color sequencing task, but contrasted chromatic with achromatic stimuli, so that retinal input was not matched in the experimental and control task.

In the current combined PET and fMRI study, we used a successive color discrimination task – temporal same different (TSD; Orban et al., 1997; Cornette et al., 2001) – with equiluminant stimuli which were difficult to verbalize. The TSD task was contrasted to a dimming detection control task (DIM) that was matched for retinal input. Consequently, in our study, subjects could rely only on color for their judgements and the retinal-input confound between tasks was removed. We parameterically varied the stimulus presentation rate to investigate the time course (tonic versus phasic) of attentional modulation (Rees et al., 1997; Cornette et al., 1999). By adjusting the stimulus differences, performance levels were equalized across all conditions. Furthermore, psychophysical and fMRI control experiments were performed in which both visuospatial attention and motor output were carefully matched between the TSD and DIM conditions.

Retinotopic cortical areas were mapped (Sereno et al., 1995; DeYoe et al., 1996; Engel et al., 1997) in each subject to identify the visual cortical areas involved in the successive color discrimination task.

Materials and Methods

Subjects
We studied 12 (mean age 23.3 years, range 20–26) and four (mean age 26.5 years, range 22–31) male volunteers in the PET and fMRI main experiments, respectively. The latter four subjects also participated in the fMRI retinotopic mapping experiment and three of them were included in the control experiments. All subjects were right-handed as judged by the Edinburgh Inventory (Oldfield, 1971). They all had normal or corrected (contact lenses) to normal vision and normal color vision, which was tested with the Ishihara color plates (Kanehara, Tokyo, Japan). There was no history of neuropsychiatric disease or drug abuse. The studies were approved by the ethical committee of the K.U. Leuven Medical School and of the University of Antwerp. Written informed consent was obtained from each subject in accordance with the Declaration of Human Rights (Helsinki, 1964).

Stimulus Characteristics

The stimuli used in the PET and fMRI main experiment were generated on-line with a PC using a TIGA-diamond (Salient AT3000) graphics card. For the retinotopic mapping, the stimuli were made in advance in bitmap format and were reconstructed on-line at the time of the scanning session. In the PET experiment, stimuli were displayed on a color monitor (Philips Brilliance 201B, 640 × 480 pixels), which was mounted above the scanner bed at an angle of 52° relative to the horizontal. Subjects viewed the stimuli from a fixed distance of 114 cm. In the fMRI experiments, stimuli were projected by means of a LCD projector (Barco Reality 6300, 640 × 480 pixels) onto a translucent screen, positioned in the bore of the magnet at 30 cm from the subject’s eyes. Subjects viewed the stimuli by means of a mirror angled 45° to their line of sight. In all experiments, the monitor or the projector was the only source of light in an otherwise dark room. The color monitor (PET) and the projector (fMRI) were calibrated (Shepherd, 1997) and were warmed up for 45 min before each session, because preliminary measurements have shown that these devices are not completely stable within the first 30–40 min. The monitor was also degaussed prior to scanning. The chromaticity and luminance measurements were obtained using a Minolta CS-100 colorimeter. A small white (main and control experiments) or red (retinotopic mapping) fixation point was continuously present at the center of the screen.

PET and fMRI Study: Main Experiment

The stimulus was a 4° circular colored patch (mean luminance PET, 4.80 cd/m²; fMRI, 5.82 cd/m²), presented in the central visual field on a gray background (PET, 16.98 cd/m²; fMRI, 101.2 cd/m²). The stimuli were shades of brown, to avoid subjects using verbal labels (Boytont and Olson, 1987).

We used in-house software to step through the color and luminance spectrum of the monitor (PET) and the projector (fMRI) and to select those points within this spectrum that appeared brown. This was done by two persons independently. The set of brown shades (n = 13 586) that was selected on the monitor used in the PET experiment is projected onto the CIE (Commission Internationale de l’Eclairage, 1931) chromaticity diagram in Figure 1. The brown color with chromaticity coordinates (x = 0.355, y = 0.370) was chosen as the center (black cross, Fig. 1a,b) of the reference region. This region was defined by a radius of 0.003 CIE units from the center (circle in solid line, Fig. 1b). A second annular region within the group of selected browns was delineated using a radius ranging between 0.010 and 0.021 CIE units from the center (circles in dashed line, Fig. 1b). The distance in CIE color space, between a color belonging to the reference region and a color within the annular region, was varied to obtain color pairs with different degrees of distinguishability.

To obtain equiluminant pairs of brown stimuli, heterochromatic flicker photometry (15 Hz; Wagner and Boynton, 1972; Kaiser, 1991) was used inside the scanner, for each subject and for each session. The stimulus contained four white points (0.15° diameter) surrounding the central fixation point at a distance of 1.33°. The default luminance (PET, 35.55 cd/m²; fMRI, 202.0 cd/m²) of these points was decreased at random times to a luminance ranging between 15.47 and 4.03 cd/m² in the PET study and between 64.83 and 53.95 cd/m² in the fMRI experiment.

Figure 1. Properties of the monitor used in the PET experiment and composition of the color pairs. (a) The chromaticities of the red, green and blue phosphors of the monitor are plotted over the whole of their operating ranges. The range of colors that our screen is capable of displaying is depicted by the black triangle. The group of brown shades (n = 13 586) that was selected on the monitor is presented in the CIE chromaticity diagram. The brown color with chromaticity coordinates x = 0.355 and y = 0.370 was chosen as the center (black cross). (b) Magnification of the area surrounding the center. To compose the color pairs, a reference region at a radius of 0.003 CIE units (circle in solid line) and an annular region with inner and outer radii of 0.010 and 0.021 CIE units (circles in dashed line) were defined around the center.
fMRI Study: Retinotopic Mapping

The five stimuli used for the retinotopic mapping were designed to stimulate the horizontal and vertical visual field meridian, the upper and lower visual field and the foveal representation in visual cortex. The horizontal (HM) and vertical (VM) meridian stimuli were horizontally and vertically oriented wedges extending 15° into each hemifield, resulting in a total width of 30° for the vertical meridian stimulus. The maximum eccentricity of the meridian stimuli and the upper (UPPER) and lower (LOWER) visual field stimuli was 12.5°. The foveal (FOV) stimulus was a 3° diameter central patch.

All retinotopic stimuli were checkerboards that consisted of black, white and colored checks, which alternated at 4 Hz. The check size was scaled such that cortical representation was approximately equal at all eccentricities tested, resulting in checks that were smaller toward the center of the stimulus and larger peripherally.

Task Configuration

In the main experiment subjects performed two tasks, a successive color discrimination or TSD task (Orban et al., 1997; Cornette et al., 2001; Fig. 2a) and a DIM task (Fig. 2b). The retinal input in TSD and DIM was identical. During every trial, two stimuli, each lasting 500 ms, were presented in succession, with a fixed interstimulus interval of 300 ms. The color of the first stimulus was chosen pseudo-randomly, that of the second one was the same in half of the trials. One of the four points dimmed for 300 ms at a random moment in each trial or during the ensuing intertrial interval.

In TSD, subjects decided whether or not the second stimulus had the same color as the previous stimulus of that trial. Within 600 ms after the onset of the second stimulus, the participants had to press the right-hand key if it had the same color as the first stimulus or the left-hand key if it had a different color. In DIM, subjects were...
presented with the same display as in TSD, but had to attend to a change in the luminance of one of the four points, rather than to the color of the stimulus. In DIM, they pressed both keys simultaneously within 400 ms of the onset of each dimming event.

In order to match the number of decisions made in each TSD condition with that in the corresponding DIM condition, the number of dimmings was half that of the stimulus presentation rate. Thus, the number of decisions across the corresponding TSD and DIM conditions was equalized, but twice as many key presses were made in DIM compared to TSD because both keys had to be pressed in DIM.

Differences in visuospatial attention were reduced by using small stimuli in central vision, while participants continuously fixated the central fixation point. During the TSD task subjects presumably attend to most of, if not the entire colored stimulus. In an attempt to equalize attentions was equalized, but twice as many key presses were made in DIM for the slowest rate to 414 ms at the fastest rate. To avoid rhythmic key pressing, especially at the higher rates, the duration of the TSD intertrial interval was randomly varied, plus by minus half the mean interval. An exception was made for the TSD condition at the fastest rate (70 ms/min), in which the intertrial interval varied randomly between 564 and 644 ms (i.e. mean 614 ms ± 50 ms). Preliminary test sessions had shown that shorter intertrial intervals created difficulties in distinguishing the successive stimulus pairs. In DIM, the interstimulus delay was randomly varied to avoid subjects performing a TSD task. In addition, verbal instructions were given before each scan in the PET and before each epoch in the fMRI study.

As a baseline task, we used a fixation-only condition (FIX), in which only a central fixation point was presented and no motor response was required.

Training Sessions
Prior to the scanning sessions of the PET and fMRI main experiment, subjects were trained in two separate 2.5 h sessions in the scanner, but without making measurements. In the training sessions, differences in the shading of the color pairs (TSD) and the size of the luminance change (DIM) were individually adapted, for each condition, until a stable performance level of 82% was reached for all experimental and control conditions. These parameters were then used in the training sessions to obtain equal performance levels for every subject over all conditions. No auditory feedback was given during training or during scanning sessions.

Image Acquisition
In the PET experiment, subjects were immobilized using a foam head holder (Smither Medical Products, Akron, OH), whereas an individually molded bite-bar was used in the fMRI experiments. The subjects had to fixate the central fixation point continuously throughout the entire experiments. Fixation was controlled using electro-oculography in the PET camera and a MR compatible eye movement tracking device (Ober2; Permobil Meditech, Timra, Sweden) in the MR scanner. The susceptibility effect of the Ober2 device was reduced by using only a single goggle, on the left side (Sunaert et al., 1999).

PET Study
Images were acquired with a high-resolution PET scanner (Siemens-CTI, ECAT Exact HR+, 3D mode), using the H215O method (Fox et al., 1986). At the beginning of each task, subjects received an injection of 300 MBq H215O over a period of 20 s through a catheter inserted in the left brachial vein. The emission scan was started when radioactivity reached the brain (∼40 s after injection) and lasted 60 s. In all subjects, 14 emission scans (TSD and DIM each at six different rates and FIX repeated once) were taken, with an interval of 10 min to allow the H215O tracer to decay (half-life is 125 s). The order of the conditions was randomized within and between the subjects.

fMRI Study: Main Experiment
This experiment complemented the PET study, by providing more anatomical detail with its higher spatial resolution and by permitting more scans and single subject analyses.

Each functional time series consisted of 190 whole-brain, gradient-echo echoplanar images or scans (GE EPI; repetition time (TR)/echo time (TE) = 3000/40 ms, flip angle 90°, field of view (FOV) = 200 × 200 mm², 64 × 64 matrix, 4 mm slice thickness, 0.5 mm slice gap, 32 sagittal slices), using a 1.5 T MR scanner (Siemens Vision). The experiment was run in a block design format. Within one time series (duration 9 min 41 s), the five TSD and DIM conditions were each presented twice in blocks of 21.4 s (seven scans) and were interleaved every two blocks with the FIX condition for 15.3 s (five scans). At the beginning of each epoch the subjects were given verbal instructions about the task they had to perform. These time series were repeated 14 times in two scanning sessions, with the conditions in different order, yielding a total of 196 images per TSD or DIM condition (seven scans per epoch × two epochs per series × 14 time series) and 700 images for the fixation condition (five scans per epoch × 10 epochs per series × 14 time series).

Sagittal anatomical images were acquired before each functional imaging session by three-dimensional magnetization prepared rapid gradient echo (MPRAGE; Mugler and Brookeman, 1990), with T1/T2 = 11.4/4.4 ms, inversion time (TI) = 300 ms, FOV = 256 × 256 mm², 256 × 256 matrix, 160 mm slab thickness, 128 sagittal partitions.

fMRI Study: Retinotopic Mapping
The six passive conditions, which include the five retinotopic stimuli and a fixation-only condition, were alternated every 10 images and were presented twice during each time series (duration 6 min 7 s). In all subjects, 13 time series were taken in two sessions, yielding a total of 260 images per condition. In total, four high-resolution anatomical scans (MPRAGE) were taken. The acquisition parameters of the functional and anatomical scans were identical to those described for the main experiment.

In one fMRI subject (S1), three additional scanning sessions were performed using a higher spatial resolution for the functional images (voxel size 2.2 × 2.2 × 2.5 mm instead of 5.0 × 5.0 × 4.5 mm). Four conditions (HM, VM, UPPER, LOWER) alternated every 10 images and were presented three times during each time series. Nineteen functional time series, each consisting of 120 GE EPIs (TR/TE = 4200/40 ms, flip angle 90°, FOV = 141 × 141 mm², 64 × 64 matrix, 2.5 mm slice thickness, 48 coronal slices) were taken of the posterior part of the brain, yielding 570 images per condition.

Furthermore, in one fMRI subject (S3), two additional time series were acquired, in which passive viewing of a uniformly moving (7° diameter, 6°/s, eight random directions) random texture pattern alternated every 10 images with the viewing of the same, but stationary pattern. These conditions were used to localize motion responsive areas (Sunaert et al., 1999), more specifically the human MT/V5 complex (hMT/V5+). This was done in only one participant, because the average location of hMT/V5+ is relatively well known from many studies, including some of our own laboratory (Zeki et al., 1991; Dupont et al., 1994; Tootell et al., 1995; Sunaert et al., 1999; Orban et al., 2003).

Data Analysis
The imaging data were analyzed with Statistical Parametric Mapping version SPM99 (Wellcome Department of Cognitive Neurology, London, UK). The functional scans were coregistered with the anatomical image, realigned and stereotactically normalized into the Montreal Neurological Institute template in Talairach space (Talairach and Tournoux, 1988), using affine and nonlinear transformations. The data were spatially smoothed with an isotropic Gaussian kernel (PET, 16 mm full width at half maximum; fMRI studies, 7 mm; fMRI retinotopic mapping, 3 mm)

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The different fMRI conditions were modeled as a box car function convolved with the hemodynamic response function. ANCOVA was used to remove global changes in cerebral blood flow for PET data and in blood oxygenation level dependent (BOLD) contrast for fMRI. Low frequency drifts in the fMRI data were removed by using an appropriate high-pass filter. Statistical analysis was performed on a voxel-by-voxel basis using the general linear model (Friston et al., 1995). Condition effects were tested by applying appropriate linear contrasts to the parameter estimates for each condition, resulting in a t-statistic for every voxel, which constituted the statistical parametric maps (SPM). The SPM(t) values were transformed to SPM(Z) for display and tabulation.

Group analyses were performed using random effect models (Holmes and Friston, 1998; Friston et al., 1999) for both the PET and fMRI data, in order properly to account for intersubject variance across all subjects and, consequently, to allow us to make population inferences. Unless otherwise stated, the threshold was set at \( P < 0.05 \) corrected for multiple comparisons in the PET analysis and \( P < 0.01 \) uncorrected in the fMRI random-effect group analysis. A lower threshold in the fMRI group analysis is justified because of the presence of a priori information in the PET random-effect analysis, a study that included a larger number of subjects. Voxels that survived this threshold were considered to be significant in the analysis and only these voxels are further reported.

Single subject analyses were performed on the data of the fMRI main and control experiments. A threshold of \( P < 0.001 \) uncorrected was used for the single subject analyses of the retinotopic mapping and of the control experiments. To display the retinotopic maps, an average image was made of the four anatomical high-resolution, three-dimensional scans of each subject. The occipital pole of this average image was unfolded and flattened (Dale and Sereno, 1993; Sereno et al., 1995; Tootell et al., 1997) after making cuts in the calcarine sulcus, the postcentral gyrus and across the temporal lobe, using the FreeSurfer2000 software (Cortechs, MGH NMR Center, Boston, MA). The individual data of the retinotopic mapping and of the fMRI main study, obtained with SPM, were then realigned with and superimposed on the two-dimensional flat map of the occipito-parietal/temporal cortex of each subject.

In addition to the group analysis plotting the MR changes relative to fixation for the most significant voxel, we also calculated activity profiles using a region of interest (ROI) approach. In this ROI analysis, fMRI signals are averaged over all voxels that are active above baseline during specified tasks for each visual region and for each subject. These voxels are defined by the contrast (5TSD + 5DIM) - 10FIX and are delineated on the individual flat maps. Signals are then averaged across all subjects. This analysis was performed for ventral and dorsal areas V1, V2 and V3, area V3A, the color-responsive region (CRR), hMT/V5+ and the lateral occipital sulcus (LOS). The borders of the retinotopic regions were delineated from the individual flat maps. The borders from the functionally defined regions (CRR, hMT/V5+, LOS) are not well-known and therefore in each of those regions an area comprising all voxels active in the contrast (5TSD + 5DIM) - 10FIX was delineated.

**Planned Analyses**

To identify the regions involved in successive color discrimination, we performed a conjunction analysis between the main effect of task, given by the subtraction of all TSD conditions minus all DIM conditions, and the parametrically increasing rate effect. We used a conjunction analysis since a significant effect in the conjunction implies the effect to be significant in each of its two elements, i.e. task effect and rate effect (Price and Friston, 1997). The advantage of using a conjunction instead of a simple task effect is to exclude differences between tasks due to changes within the intertrial interval. Figure 3 shows that any trial-related neuronal activity will yield a MR activity that increases with the rate at which the task is performed. The regions involved in dimming detection were identified by a conjunction analysis between the reverse main effect of task and the increasing rate effect. Since the number of motor responses in DIM was double that in TSD in the main experiment, the latter analysis also revealed regions involved in motor execution.

The second reason for parametrically varying the stimulus presentation rate was to investigate the type of attentional modulation in the activation sites revealed by the conjunction analysis (Rees et al., 1997; Cornette et al., 1999). Two different modulatory effects of attention can be distinguished (Rees et al., 1997). First, attention can increase neuronal activity in TSD relative to DIM equally across the entire epoch (tonic, Fig. 3a). This results in a differential MR activity independent of the rate: the intercept of the linear MR activity-rate function is changed but not its slope (\( x = \) constant, Fig. 3b). Secondly, attention can increase the visual response within each trial, but without altering the baseline neuronal activity (phasic, Fig. 3c). Since increasing the rate will include more visual responses in each epoch, the differential activity will increase with rate. This will result in an increase in both the intercept and the slope of the MR activity–rate relationship in TSD (\( y > x \), Fig. 3d). Notice that the same effect will result whenever the task increases neuronal activity during a limited portion of the trial, e.g. before the motor response. To differentiate between these two types of attentional/task modulation, we tested the interaction between task and rate (Rees et al., 1997) within the activation sites obtained in the conjunction analysis. The interaction was considered to be significant at \( F_{\text{corr}} < 0.05 \) or \( Z(\text{int}) > 4.51 \).

In the retinotopic mapping, the contrasts HM – VM and VM – HM were used to map the horizontal and vertical meridians in the brain. The upper and lower visual fields were mapped by the contrasts UPPER – LOWER and LOWER – UPPER. To map the fovea, FOW was contrasted with UPPER + LOWER, which together represent the peripheral visual field.

**Control Experiments: Psychophysics and MRI**

The control experiments were designed to eliminate two possible confounds in the study: differences in visuospatial attention and differences in motor responses between TSD and DIM conditions.
Visual Stimulus: Psychophysical Control Study

First, a psychophysical experiment (subjects 2 and 3) was performed to study the deployment of visuospatial attention during the TSD and DIM tasks. The original 4° color disk with its central fixation point and four dimming points was divided into two distinct stimulus regions (Fig. 2c): the central 2.81° of the original disc extended to just beyond the four dimming points and the outer annulus (with inner and outer radii of 1.26 and 2°) of the original disc had its inner border located just inside the four dimming lights. Thus, the dimming and fixation points were visible in both parts of the stimulus. Additionally, to test whether or not subjects were using both halves of the original disc to perform the TSD task, only the upper or lower half of the original stimulus was presented.

Visual Stimulus: fMRI Control Study 1

In the first fMRI control study (subjects 2 and 3), visuospatial attention between the experimental and control conditions was equilized, based on the results of the psychophysical control study (see below). The original color disc was used, but the four dimming points were positioned at the edge of the 4° disc (Fig. 2c). In this manner, subjects were compelled to attend the entire 4° stimulus in performing the DIM task, as they did in the TSD task (see below).

Visual Stimulus: fMRI Control Study 2

In the second fMRI control experiment (subjects 1 and 3), we addressed the question of whether a residual differential allocation of attention might still exist between the two tasks due to the use of a single large dot (TSD) versus four small dots (DIM) (McMain and Somers, 2002). Therefore we used a small 1° radius color disc without the presence of the four dimming points (Fig. 2d) in which dimming occurred over the entire disc. In this experiment visuospatial attention was perfectly matched between tasks.

Tasks: fMRI Control Studies 1 and 2

In the fMRI control studies, subjects had to press both keys in TSD if the second stimulus had a different color from the first and no key if it had the same color. In DIM, they pressed both keys in the case of a change in luminance of one of the four points (control 1) and of the 1° radius disc (control 2). In the second control study, dimming occurred randomly before/after the presentation of a pair of color stimuli. Due to the impossibility of maintaining isoluminant color stimuli during the dimming of the whole disc, the timing of the dimming was not exactly coincident with the presentation of the color disks (Fig. 2d). No dimming occurred within the interstimulus interval or small periods (100 ms at rate 70 stim/min; 300 ms at 10 stim/min) immediately before and after each pair of color stimuli (Fig. 2d). Dimming lasted 300 ms (control 1) and 100 ms (control 2), while the response window in DIM was left at 400 ms in control study 1, but equaled that in TSD (600 ms) in control study 2. Furthermore, in both control studies, the number of key presses was equalized in TSD and DIM by halving the number of dimming events: dimming occurred only once every two trials, in a random fashion. Thus in the control experiments the number of decisions and also the number and type of motor responses were equal. In the second fMRI control study, only two stimulus rates (10 and 70 color stimuli/min) were used for both tasks. The acquisition of the images and data analysis in both fMRI control studies and the number of images per condition and subject in control study 1, were identical to those in the original experiment. In control study 2, 280 images were acquired per condition and per subject, which is greater than in the previous studies. However, the total number of images in the conjunction analysis of the second control study is lower (only two rates per task instead of five).

Results

Behavioral Data

During scanning, mean performance in TSD conditions ranged from 83.3 to 85.1% correct in the PET experiment and from 79.0 to 84.4% in the fMRI main experiment. In DIM conditions, mean performance ranged from 83.5 to 85.6% correct in the PET experiment and from 77.0 to 81.3% in the fMRI main experiment. This was similar to the performance at the end of the second training session, indicating that no additional learning occurred during scanning. Mean performance did not differ significantly across TSD [ANOVA; PET, F(5,60) = 0.18, P > 0.9; fMRI, F(4,12) = 0.92, P > 0.4] or DIM [ANOVA; PET, F(5,60) = 0.19, P > 0.9; fMRI, F(4,12) = 1.48, P > 0.2] conditions in either experiment. Moreover, no significant difference in mean performance was observed between TSD and DIM tasks in the PET [ANOVA; F(11,132) = 0.16, P > 0.9] and fMRI [ANOVA; F(9,27) = 0.99, P > 0.4] main experiment.

The mean reaction times were statistically equivalent among TSD conditions in the PET [ANOVA; F(5,55) = 2.01, P > 0.1] and in the fMRI study [ANOVA; F(4,12) = 2.29, P > 0.1]. In the DIM conditions of the two studies, there was a significant decrease in reaction times with increasing rate [ANOVA; PET, F(5,55) = 34.58, P < 0.0001; fMRI, F(4,12) = 34.98, P < 0.0001]. In the two experiments, the mean color distances increased with increasing rate, but changes failed to reach significance [ANOVA; PET, F(5,55) = 2.26, P > 0.07; fMRI, F(4,12) = 0.56, P > 0.7]. The increase in mean amplitude of dimming with increasing rate did prove significant [ANOVA; PET, F(5,55) = 14.82, P < 0.0001; fMRI, F(4,12) = 34.74, P < 0.0001]. Subjects maintained fixation well during scanning. The average frequency of saccades was one per minute in the PET experiment and one per condition for each time series in all fMRI studies. The frequency of eye movements did not differ significantly among conditions for any experiment (Friedman ANOVAs; all P > 0.2).

PET Experiment

The regions involved in successive color discrimination were revealed by the conjunction between the main effect of task (TSD–DIM) and the increasing rate effect. In the PET experiment, significant activation sites were observed in the right calcarine sulcus, right lingual gyrus, left dorsal intraparietal sulcus, left superior precentral sulcus, medial frontal gyrus and bilaterally in the lateral cerebellum (Fig. 4, Table 1). A detailed description of the cerebellar involvement has been given elsewhere (Claeys et al., 2005). Furthermore, activation at Puncorr < 0.001 was observed in the collateral sulcus bilaterally. Given the a priori hypothesis, this was considered significant. Weak activation sites were observed in left lingual gyrus, in right superior precentral sulcus and bilaterally in superior frontal sulcus and inferior frontal gyrus.

The conjunction between the reverse main effect of task (DIM–TSD) and the increasing rate effect was used to reveal regions involved in dimming detection and in motor output. Significant activation sites were observed in the right middle occipital gyrus, left inferior temporal gyrus, in bilateral precentral gyrus and right precentral sulcus (Fig. 4, Table 2). Furthermore, weak bilateral activation sites were seen in the middle and inferior occipital gyri and in the right superior parietal lobule. Finally, weak activation sites were observed in the medial superior frontal gyrus and in the medial cerebellum.

fMRI Main Experiment: Group Analysis

In successive color discrimination, revealed by the conjunction between the main effect of task (TSD–DIM) and the increasing rate effect, significant activation sites were observed in early visual areas, particularly right calcarine sulcus and bilateral lingual gyrus, and in bilateral posterior fusiform gyrus (Fig. 5,
Table 1). Bilateral activation sites were observed dorsally in the anterior and middle part of the intraparietal sulcus (IPS). The anterior dorsal IPS region is located more laterally than the dorsal IPS anterior (DIPSA) region described by Sunaert et al. (1999). Furthermore, an activation site was observed in the right inferior parietal lobule and bilaterally in the postcentral gyrus. The latter activation could possibly be related to somatosensory feedback (Rausch et al., 1998). In the frontal cortex, activation sites were observed bilaterally in dorsal premotor cortex (dPMC), superior frontal sulcus, inferior frontal gyrus and medially in the pre-supplementary motor area (pre-SMA). Bilateral activation sites were also seen in the lateral cerebellar hemispheres.

Activity profiles plot the percentage adjusted MR signal change relative to the baseline fixation condition, as a function of the different stimulus presentation rates for the two tasks. The functional profiles of the visual regions will be described once they have been identified by the retinotopic mapping.

The main effect of task, given by the subtraction TSD – DIM, revealed significant activation sites in right calcarine sulcus, lingual gyrus, posterior fusiform gyrus and inferior temporal gyri, in right inferior parietal lobule, bilateral anterior dorsal IPS and left middle dorsal IPS. In the frontal lobe, sites were seen in bilateral dPMC, superior frontal sulcus, inferior frontal gyrus, medially in pre-SMA and in the lateral cerebellum. Additional bilateral activation sites were revealed in the dorsolateral prefrontal cortex (BA 9/46). With the exception of these latter sites, the pattern of activation was very similar to that obtained in the conjunction analysis. MR activity in dorsolateral prefrontal cortex was rate-independent in both tasks.

Activation sites related to dimming detection and motor output were revealed by the conjunction between the reverse main effect of task (DIM–TSD) and the increasing rate effect. Significant activation sites observed using this conjunction included bilateral sites in middle and inferior occipital gyri and in inferior temporal gyri (Table 2). In parietal cortex, a bilateral activation site was seen along the dorsal lips of the IPS, corresponding to the motion responsive region DIPSM/L (dorsal intraparietal sulcus medial/lateral; Sunaert et al., 1999; Peuskens et al., 2001). This region was located posterior to the anterior and middle dorsal IPS activation sites observed in successive color discrimination. Activations were also seen in bilateral primary motor cortex (M1), in left precentral gyrus.
### Table 1
PET and fMRI main study: conjunction between main effect of task (TSD–DIM) and increasing rate effect

<table>
<thead>
<tr>
<th>Brain region</th>
<th>fMRI group (RFX)</th>
<th>ss</th>
<th>Z-score</th>
<th>PET group (RFX)</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Z-score</th>
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<td></td>
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<td></td>
</tr>
<tr>
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<td>vV1</td>
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<td>−78</td>
<td>−14</td>
<td>2.43</td>
<td>4*</td>
<td>1.84</td>
<td>6</td>
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<td>4.80</td>
<td>18</td>
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<td>−78</td>
<td>−20</td>
<td>2.97</td>
<td>4*</td>
<td>3.46</td>
<td>−14</td>
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<td>4.46</td>
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<td>4.96</td>
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<td>24</td>
<td>4.55</td>
<td>4</td>
<td>6.92</td>
<td>58</td>
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<td>19 L inf. frontal gyrus (44)</td>
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<td>2.46</td>
<td>3</td>
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<td>−60</td>
</tr>
<tr>
<td>20 Medial frontal gyrus (8/6)</td>
<td>Pre-SMA</td>
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<td>48</td>
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<td>−30</td>
<td>3.44</td>
<td>4</td>
<td>1.60</td>
<td>−38</td>
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All activation sites in PET and fMRI group random-effect analyses (RFX) reaching \( P_{\text{corr}} < 0.05 \) (bold), \( P_{\text{uncorr}} < 0.001 \) (normal), or \( P_{\text{uncorr}} < 0.01 \) (italic). R, right; L, left; ant., anterior; inf., inferior; mid., middle; post., posterior; sup., superior; () = Brodmann area; vV1, ventral primary visual cortex; VP, ventral posterior area; CRR, color-responsive region; dors. IPS, dorsal intraparietal sulcus; dPMC, dorsal premotor cortex; pre-SMA, pre-supplementary motor area; ss, frequency of occurrence in fMRI single subjects (\( n = 4 \)); *determined by retinotopic mapping; Z(int), Z-score in interaction analysis of fMRI group study.

and in the supplementary motor area (SMA). Finally, the medial cerebellum was activated.

The activity profile of DIPSL shows that differential activity remained relatively constant with increasing stimulus presentation rate (Fig. 6a). The functional profile of DIPSL is clearly distinct from the dorsal IPS regions engaged in successive color discrimination.

### Comparison between Analyses
In successive color discrimination, there was a good agreement in the activation sites revealed by the group and single subject fMRI studies, except within some of the parietal sites (Table 1). In the conjunction between the reverse main effect of task and the increasing rate effect, a high degree of single subject-group conformity was also observed (Table 2). The global pattern of activation in the fMRI main experiment was very similar to the PET study for both conjunction analyses. However, more sites were activated in the fMRI study, especially in parietal cortex for the conjunction between the main effect of task and increasing rate effect.

### fMRI Retinotopic Mapping Experiment
The retinotopic cortical regions were mapped to identify the occipital activation sites involved in successive color discrimination or dimming detection. In our study, the borders of V1, V2 and V3/VP matched earlier descriptions (Sereno et al., 1995; DeYoe et al., 1996; Engel et al., 1997), but some variability was observed in the representation of the horizontal meridian(s) anterior to the vertical meridian represented at the anterior border of area VP (Fig. 7). To clarify the topography in this region, we mapped the upper and lower visual field, because previous studies have disclosed a more anteriorly located, color-responsive region with a continuous representation of the entire contralateral hemifield (McKeefry and Zeki, 1997; Hadjikhani et al., 1998; Bartels and Zeki, 2000). We observed such a topographic organization in the color-respon-
sive region (CRR), located in the posterior fusiform gyrus (FG; Fig. 7). The border between the upper (green plus sign) and lower (green minus sign) visual fields of this area is shown in green. In almost all cases (6/8 hemispheres), this border corresponded to a horizontal meridian activation (Figs 7 and 8). The upper visual field in CRR was mapped anteriorly and medially compared to the lower visual field. Our results consistently showed a foveal representation at the anterior end of this border (green asterisk) in all hemispheres. An additional mapping experiment in subject 1, with higher spatial resolution and a much larger number of images confirmed our original maps.

The activation sites involved in successive color discrimination were superimposed onto the corresponding retinotopic map of each subject and the local maxima of these sites are presented as pink squares in Figure 7. This comparison, considered over all subjects, allowed us to identify the sites involved in successive color discrimination and attention to color (group analysis, Table 1): those in the calcarine sulcus as area V1, in lingual gyrus as area VP and in posterior fusiform gyrus as CRR. In single subjects, activation of area V2 was also observed. The frequency with which the retinotopic visual areas V1, V2, VP and CRR were activated is listed by hemisphere and subject in Table 3a. The frequency of activation is similar for areas V1 and V2, but less than that of areas VP and CRR. Overall, the activation sites are symmetrical in the two hemispheres and there are no clear left-right differences.

A ventral/dorsal asymmetry was, however, observed in the early visual areas V1, V2 and VP/V3. Since the most strongly asymmetric activation pattern was seen in area V3/VP, we quantified this asymmetry by measuring the differential activity between TSD and DIM at the fastest rate (70 stim/min), within a 1 cm diameter region positioned symmetrically in ventral V3 (VP) and dorsal V3 for all hemispheres in the original experiment. In 7/8 hemispheres, differential activity was significantly larger in area VP (average MR signal change = 0.20%, SEM = 0.033%) compared to dorsal V3 (0.026%, SEM = 0.010%). The results remained unaltered by shifting the 1 cm diameter ROI within the same retinotopic area over a total distance of 2.5 cm on the flat maps. This shows that area VP is preferentially involved in the color discrimination task, whereas dorsal area V3 is equally activated in both TSD and DIM tasks.

### Table 2
PET and fMRI main study: conjunction between reverse main effect of task (DIM–TSD) and increasing rate effect

<table>
<thead>
<tr>
<th>Brain region</th>
<th>fMRI group (RFX)</th>
<th>PET group (RFX)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>x</td>
<td>y</td>
</tr>
<tr>
<td>Occipitotemporal</td>
<td></td>
<td></td>
</tr>
<tr>
<td>a R mid. occipital gyrus (18/19)</td>
<td>V3A</td>
<td>30</td>
</tr>
<tr>
<td>b L mid. occipital gyrus (18/19)</td>
<td>V3A</td>
<td>−34</td>
</tr>
<tr>
<td>c R inf. occipital gyrus (18)</td>
<td>LOS</td>
<td>32</td>
</tr>
<tr>
<td>d L inf. occipital gyrus (18)</td>
<td>LOS</td>
<td>−36</td>
</tr>
<tr>
<td>e R inf. temporal gyrus (37)</td>
<td>NMT/V5+</td>
<td>56</td>
</tr>
<tr>
<td>f R mid. occipital gyrus (19/37)</td>
<td>NMT/V5+</td>
<td>44</td>
</tr>
<tr>
<td>g L inf. temporal gyrus (37)</td>
<td>hNMT/V5+</td>
<td>−40</td>
</tr>
<tr>
<td>Parietal</td>
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<td></td>
</tr>
<tr>
<td>h R sup. parietal lobule (7)</td>
<td>DIPSL</td>
<td>28</td>
</tr>
<tr>
<td>l L sup. parietal lobule (7)</td>
<td>DIPSM/L</td>
<td>−16</td>
</tr>
<tr>
<td>Frontal</td>
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<tr>
<td>j R precentral gyrus (4)</td>
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</tr>
<tr>
<td>k L precentral gyrus (4)</td>
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<td>−46</td>
</tr>
<tr>
<td>m L precentral gyrus (6)</td>
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<td>n R precentral sulcus (6)</td>
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<td>o Medial sup. frontal gyrus (6)</td>
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<tr>
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<td>−52</td>
</tr>
<tr>
<td>q L medial cerebellum</td>
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<td>−58</td>
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<td></td>
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<tr>
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<td>−74</td>
</tr>
<tr>
<td>v R medial cerebellum</td>
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<td>−86</td>
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All activation sites in PET and fMRI group random-effect analyses (RFX) reaching $P_{uncorr} < 0.05$ (bold), $P_{corr} < 0.001$ (normal), or $P_{corr} < 0.01$ (italic). R, right; l, left; inf., inferior; mid., middle; sup., superior; ( ), Brodmann area; LOS, lateral occipital sulcus region; hMT/V5+, human middle temporal/V5 complex; DIPSM/L, dorsal intraparietal sulcus medial/lateral; M1, primary motor cortex; SMA, supplementary motor area; ss, frequency of occurrence in fMRI single subjects ($n = 4$); *determined by retinotopic mapping; Z (int), Z-score in interaction analysis of fMRI group study.
contrasts with the CRR, in which differential activity was very similar in the ventral (average = 0.196%, SEM = 0.028%) and dorsal (0.194%, SEM = 0.025%) divisions.

The local maxima of the visual cortical activation sites, obtained in the conjunction between the reverse main effect of task and the increasing rate effect, are indicated by a white square in the retinotopic maps of dorsal occipital cortex (Fig. 8). The retinotopic organization of human V3A matched the description of Tootell et al. (1997). A bilateral activation site was consistently seen in V3A and the motion-selective hMT/V5 complex (purple contour, Fig. 8), comprising human area MT and its satellites (Zeki et al., 1991; Tootell et al., 1995; Sunaert et al., 1999; Peuskens et al., 2001). Activation at this site is not surprising, since a change in luminance or dimming within a very short period of time is equivalent to flicker, which has been shown to activate hMT/V5+ and several other motion-sensitive regions such as human area V3A (Tootell et al., 1995; Sunaert et al., 1999). Furthermore, activation sites were observed bilaterally in a region beyond the retinotopically organized areas in our maps (Fig. 8). This activation site was located near the lateral occipital sulcus (LOS), laterally and dorsally to CRR and posteriorly to hMT/V5+. It corresponds to the most posterior part of the lateral occipital complex or LOC (Malach et al., 1995; Grill-Spector et al., 1999, 2000; Denys et al., 2002; James et al., 2002), which has a crude or non-existent retinotopy (Tootell and Hadjikhani, 2001). Recent results (Vanduffel et al., 2002) suggest that this region might correspond to dorsal area V4 in the monkey.

**Functional Profiles of Visual Areas in the fMRI Main Study (Region of Interest Analysis)**

In a region of interest analysis, fMRI signals of all voxels active during the tasks within a given visual area were averaged across hemispheres and subjects (Fig. 9). The activity profiles obtained in the ROI analysis were very similar to those obtained for the local maxima generated by the group conjunction analysis (see, for example, ventral area V1 in Fig. 9), although the former showed a higher percentage of MR signal change relative to the baseline fixation condition, due to the averaging of MR signals measured in single subjects. In the ventral portions of area V1, V2 and V3 (=VP) activity is higher in TSD compared to DIM. In the dorsal portions of area V1, V2 and V3, however, activities were equal in both TSD and DIM conditions. This confirms that the ventral halves of the early visual areas V1, V2 and V3, however, activities were equal in both TSD and DIM conditions. Activities in the ventral and dorsal portions of the color-responsive region were averaged (Fig. 9), because differential activity between TSD and DIM was very similar in the two divisions of the CRR (see above).

Interestingly, the activity profiles of ventral area V1, VP and CRR show that differential activity in those regions depends on rapid visual stimulation and decreases at slower rates (Fig. 9, thick black frames). There is a clear interaction between the task and the stimulus presentation rate in all three areas (Fig. 9), although the interaction is clearly stronger in CRR (Fig. 9;
The interaction between rate and task was significant in pre-used and are therefore not shown. Numbers and characters correspond to the sites DIM conditions. The standard errors of the mean (SEM) are smaller than the symbols study). The solid lines indicate the TSD conditions and the dashed lines represent the conjunction between the main effect of task and increasing rate effect (fMRI group study). In the control experiments only single subject analyses were performed. Therefore, in the following results sections, we will emphasize the consistencies in activation pattern between subjects. In the first fMRI control study (subjects 2 and 3), activation sites were observed in ventral area V1, ventral V2, VP and in the color-responsive region in both hemispheres of subject 3 (Fig. 10b), replicating the original results (Fig. 10a; Table 3). In subject 2, the control experiment showed activation sites in area V1, V2, VP and CRR of the right hemisphere, and in area VP and CRR of the left, similar to the original experiment. In both the original and first control experiment, mainly the ventral part of the early visual areas V1, V2, and ventral area VP were activated. Parietal activation sites were consistently located in the anterior and middle part of the dorsal intraparietal sulcus in both hemispheres of both subjects and were even more robust than in the original experiment (Fig. 10b). Overall, the activation pattern and the topography of activation sites observed in the control study is very similar to that in the original experiment (Fig. 10a,b). Furthermore, the functional profiles of area V1, CRR and anterior dorsal IPS (averaged across hemispheres and subjects) were also very similar in the original and control study (Fig. 10d).
In the second fMRI control study (subjects 1 and 3), significant activation sites were observed in parietal cortex. Similar to the previous studies, the parietal activation sites were consistently located in the anterior and middle part of the dorsal intraparietal sulcus in both hemispheres of the two subjects (Fig. 10c). These sites were even more significant in some hemispheres compared to our original and first control studies. The foveal representation of the color-responsive region is consistently activated in both hemispheres of our two subjects (Fig. 10c). In subject 3, two additional activation sites were observed: one located more anteriorly than foveal CRR, in the inferior temporal sulcus/gyrus posterior to hMT/V5+ and another situated more anteriorly in the fusiform gyrus (Fig. 10c). However, these latter two activations were not present in either hemisphere of subject 1. In all four hemispheres, the early visual areas V1, V2 and VP showed considerably less activity than in the original and first control study, due to a much smaller stimulus. For the same reason, the functional profiles of CRR, middle and anterior dorsal IPS (averaged across hemispheres and subjects) all displayed lower MR signal changes for both tasks. However, the differential activity between TSD and DIM and the modulatory effects in those regions were very similar to those in the original study (Fig. 10e).

In both fMRI control experiments, equalizing the number and type of motor responses resulted in the disappearance of the activation sites in primary motor cortex and SMA in the conjunction between DIM–TSD and the increasing rate effect.

**Table 3**

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<th>S2</th>
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<th>S3</th>
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<td>VP</td>
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<td>R, L</td>
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</tbody>
</table>

Activation sites at $P_{\text{uncorr}} < 0.001$; tiles at $P_{\text{uncorr}} < 0.01$. S, subject; R, right; L, left; v, ventral; italic *, results from control experiment 1; Freq., frequency of significant activations in original experiment on a total of eight hemispheres. For other abbreviations, see Tables 1 and 2.

**Figure 7.** Mapping of the activation sites in ventral visual cortex involved in successive color discrimination. Retinotopic maps ($P_{\text{uncorr}} < 0.001$) on a flattened occipitotemporal surface representation of four individual hemispheres are shown. The horizontal (HM) and vertical (VM) meridian representations are shown in yellow/red and blue respectively. Area V1 is located along the line cutting the calcarine sulcus (CS) and is characterized by a representation of the horizontal meridian, only the ventral part of which is shown. The borders of the retinotopically organized areas are localized at the site with the highest activity, in the middle of the meridian representations, and are indicated by white solid lines (HM) and white dotted lines (upper VM). The border between the upper and lower visual field maps in the color-responsive region (CRR) is shown in green. The upper and lower visual fields of this region are indicated by a green plus and minus sign respectively and its foveal representation is indicated by a green asterisk. The local maxima of the individual activation sites (fMRI single subject analysis) involved in the conjunction analysis between the main effect of task (TSD–DIM) and the increasing rate effect are indicated by a pink square. Gyrual cortex from the original brain is presented in light gray and sulcal cortex in dark gray. Scale bar: 1 cm. R, right; L, left; S, subject; CS, calcarine sulcus; CoS, collateral sulcus; FG, posterior fusiform gyrus; LG, lingual gyrus; OP, occipital pole.

**fMRI Control Experiment 2**

In the second fMRI control study (subjects 1 and 3), significant activation sites were observed in parietal cortex. Similar to the
Furthermore, activity in area V3A, hMT/V5+, LOS and DIPSM/L remained higher for DIM than for TSD across the two control experiments.

Discussion
Using an active successive color discrimination task, our study revealed a distributed network of activated cortical regions, which included the ventral occipitotemporal pathway up to the color-responsive region, but also dorsal occipitoparietal pathway regions, particularly anterior dorsal IPS regions, and the dorsal premotor region. These regions will be discussed in turn, after considering some methodological issues of the study.

Methodological Considerations
In the current study, retinal input and oculomotor behavior were identical in all experimental and control conditions. In addition, the performance levels were equalized across all conditions. Colored stimuli can be discriminated by differences in color and/or in luminance. In our study, any differences in the luminance of the stimuli were carefully eliminated using heterochromatic flicker photometry. Equiluminance was obtained in the scanner for each subject individually and for each session. To avoid subjects using verbal labels while performing the successive color discrimination task, the stimuli were presented in different shades of brown. The brown color was chosen because a previous psychophysical study (Boynton and Olson, 1987) has demonstrated that brown is the most difficult color to verbalize. Thus, subjects performed a successive discrimination using the feature color exclusively.

The purpose of parametrically varying stimulus presentation rate was to specify the modulatory effects of attention in the brain regions revealed by the conjunction analysis. Experiments were not designed to investigate the effect of an increasing judgement load, since performance and thus also load, were kept identical across all conditions at the different presentation rates. This was done by individually adjusting the stimulus parameters (color in TSD and luminance in DIM). It is noteworthy that a previous study of our group has shown little effect of increasing the load in visual regions engaged by featural attention (Sunaert et al., 2000). The attentional effects in our study were featural in nature since in the original experiment the differences in visuospatial attention between the tasks were very small (psychophysical control experiment) and results were not altered by eliminating these differences in the fMRI control experiments.

Early Visual Regions
During successive color discrimination, the early visual areas V1, V2 and VP were activated. The activity in these early visual regions, particularly in area V1, was less strongly modulated than in the color-responsive region. Another difference between the early visual regions and CRR is that in areas V1, V2 and VP the activation sites are located mainly in their ventral divisions, whereas in CRR the activation site is observed in both its upper and lower visual field representations. This latter observation combined with the results of our psychophysical control study in which only half of the original stimulus was presented, suggests that CRR is more important to the perceptual aspects of the color discrimination task than the earlier visual regions. Since our psychophysical control study showed that the presence of both the upper and lower half of the color disc are necessary to correctly perform the color discrimination task and since both upper and lower visual fields are activated in CRR, the predominant ventral activation in areas V1, V2 and VP is not due to the use of only the upper part of the stimulus, but can most likely be explained by a preference for color of the ventral parts of these areas compared to their corresponding dorsal parts (Wade et al., 2002). This func-

Figure 8. Mapping of the activation sites in the visual cortex involved in the conjunction between the reverse main effect of task (DIM–TSD) and the increasing rate effect. The retinotopic maps \( P_{uncorr} < 0.001 \) are shown on a flattened surface representation of the occipitotemporal/parietal cortex in two hemispheres. The local maxima of the individual activation sites (single subject analysis) are indicated by a white square. The purple contour indicates the hMT/V5+ activation in the motion localizer scans. ITS, inferior temporal sulcus; LOS, lateral occipital sulcus; TOS, transverse occipital sulcus. For other conventions see Figure 7.
tional dorsal/ventral asymmetry in color processing in human dorsal/ventral area V3 is in agreement with single cell studies in the monkey (Burkhalter and Van Essen, 1986).

Previous human functional imaging studies have also shown activity in V1 during passive (Kleinschmidt et al., 1996; McKeefry and Zeki, 1997; Hadjikhani et al., 1998; Bartels and Zeki, 2000) and active color tasks (Corbetta et al., 1991; Beauchamp et al., 1999). In the latter studies, however, confounding differences in retinal input or luminance were not controlled, while these were specifically excluded in the

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present study. Functional imaging studies in humans also provide evidence for color selectivity in area V2 (Hadjikhani et al., 1998; Bartels and Zeki, 2000).

Our results are consistent with electrophysiological evidence in monkeys, that some neurons in V1 are color-selective and show precise color tuning (Dow and Gouras, 1973; De Monasterio and Schein, 1982; Livingstone and Hubel, 1984; Conway, 2001; Landsman and Ts'o, 2002; Wachtler et al., 2003). Single cell studies in the macaque monkey have also shown color-selective cells in ventral area V2, including cells with narrow chromatic tuning (Burkhalter and Van Essen, 1986; Gegenfurtner et al., 1996; Kiper et al., 1997; Moutoussis and Zeki, 2002) and in area VP (Burkhalter and Van Essen, 1986). Metabolic mapping studies in primates have also revealed color selectivity in V2 (Tootell and Hamilton, 1989). Furthermore, single cell studies have shown a clear effect of featural attention as early as areas V1 and V2 in color and brightness discrimination tasks (Mehta et al., 2000) and in a bar orientation discrimination task (Motter, 1993).

The early visual areas V1, V2 and VP are known to be anatomically connected with each other and with area V4 and TEO in monkeys (Felleman and Van Essen, 1991; Distler et al., 1993).

**Human Color-responsive Region**

During the successive color discrimination task, we consistently observed a ventral bilateral activation site located in the posterior fusiform gyrus (fMRI) or more medially in the collateral sulcus (PET), corresponding with the findings of previous human imaging studies using different chromatic stimuli (Lueck et al., 1989; Zeki et al., 1991; Sakai et al., 1995; Clark et al., 1997; McKeefry and Zeki, 1997; Hadjikhani et al., 1998; Bartels and Zeki, 2000). The relatively small difference in localization of this color-responsive region in the PET and fMRI study can be explained by the differences in spatial resolution.
between these two techniques. In all cases, CRR was located a short distance anterior to the upper vertical meridian that constitutes the anterior border of area VP. It showed a complete representation of the contralateral hemifield, in which the upper visual field was represented medially and anteriorly with respect to the lower visual field. The foveal representation in CRR was consistently localized at the anterior end of the border between the visual field maps. The color-responsive region observed in our study corresponds to the posterior area V4 of the human V4-complex, described previously (McKeefry and Zeki, 1997; Bartels and Zeki, 2000), and to the human retinotopic color-selective area in the inferior occipitotemporal cortex, deemed area V8 by Hadjikhani et al. (1998).

In our study, the horizontal meridian, which is located anterior to the anterior border of area VP and which separates ventral area V4 from area V8, could not be clearly identified. Consequently, we were not able to define ventral area V4 with certainty. Others have also found this horizontal meridian to be subtle in humans (Tootell and Hadjikhani, 2001). Similarly, the retinotopic organization anterior to the anterior border of dorsal area V3 could not be clearly established. Consequently, dorsal area V4 could not be explicitly identified in our study. It is noteworthy, however, that dorsal area V3A could easily be identified by means of the delineation between its upper and lower visual field representation, separated by a small portion of the horizontal meridian representation.

Our results revealed activity related to attention to color in CRR, in agreement with earlier less well-controlled studies (Corbetta et al., 1991; Beauchamp et al., 1999; Chawla et al., 1999). Furthermore, the activation in CRR in the main and the two control experiments was consistent with the size of the stimuli and the retinotopic organization of this region.

Attentional modulation was stronger and more phasic (i.e. linked to the processing of the stimuli) in CRR than in the early visual areas V1 and VP. Our results agree with the findings of Mehta et al. (2000), who reported that the degree of modulation due to featural attention was low in area V1 but high in area V4 in monkeys. Furthermore, single cell studies in monkeys showed that V4 cell responses increase and become more selective as a color discrimination task becomes more difficult and requires more attention (Spitzer et al., 1988). In our study, where the performance level was kept constant across all conditions, we observed an interaction with rate, indicating a fixed increment in the visual response (Fig. 3) in CRR with attention to color.

According to Bartels and Zeki (2000), human V4 is active when subjects passively viewed dynamically illuminated versus statically illuminated achromatic Mondrians. One might therefore suspect the CRR to be active in both the color discrimination and the dimming detection. Yet in our study, the CRR was two and a half times more active when subjects discriminated color than when they detected the dimming at fast rates. The only region which came close to being active in both tasks was LOS where the activity at fast rates was nearly equal in the two conditions.

Dorsal Intraparietal Sulcus

The next areas involved in the successive color discrimination task are the anterior and middle dorsal intraparietal sulcus. Our results are in agreement with another human functional imaging study that showed the involvement of the IPS in an active task using color as the attribute (Beauchamp et al., 1999). Our data are also in agreement with human lesion studies, e.g. Meadows (1974) identified the dorsal parietal cortex as one of the three cortical regions (besides area V1 and CRR) which are each important in specific aspects of color vision. The function of dorsal parietal cortex was described as the association of colors with other types of information, e.g. in visuomotor tasks. The parietal activity revealed by our study cannot be explained by the occurrence of saccades (Petit et al., 1996; Corbetta et al., 1998; Kimmig et al., 2001), since eye positions recorded during the PET and fMRI scanning sessions showed that all subjects fixated very well. Dorsal intraparietal sulcus regions have also been shown to be involved in the control of visuospatial attention (Corbetta et al., 1993, 1998, 2000; Vandenberghe et al., 1996, 1997, 2000; Nobre et al., 1997; Hopfinger et al., 2000). In our control experiments, however, in which visuospatial attention was matched between experimental and control conditions, we have demonstrated that the activation sites in the intraparietal sulcus remained present and were even more robust. Consequently, we can conclude that the parietal activity in our study was not related to visuospatial attention. Furthermore, it has been shown in primates that motor planning is encoded in posterior parietal cortex (Andersen et al., 1997; Snyder et al., 1998, 2000). In our initial experiment motor preparation was clearly different between the tasks (pressing left/right versus pressing both keys). However, the parietal activation sites survived the matching of motor response number and type in our control experiments. Peuskens et al. (2001) have obtained similar results using a visual heading task. Human imaging studies have suggested the involvement of parietal cortex in decision-related processes (Deiber et al., 1991; Leonards et al., 2000; Faillenot et al., 2001; Peuskens et al., 2001). In each of these studies, the result of the sensory processing had to be linked with a motor response, i.e. a decision has to be made, just as in our study.

Comparison with the other studies from our group using the same dimming control task reveals a systematic rostro-caudal organization along the IPS. Faillenot et al. (2001) reported activation sites in the anterior and lateral dorsal IPS bilaterally, during successive orientation discrimination of gratings and objects. The anterior dorsal IPS activation sites revealed by our study were located a little more laterally, but very close to their anterior IPS activations (Fig. 11, –34 mm). Our middle dorsal IPS sites corresponded to their lateral dorsal IPS activation sites (Fig. 11, –48 mm). The other parietal activation sites observed in the study of Faillenot et al. (2001) were located more posteriorly compared to the middle dorsal IPS sites revealed by our study (Fig. 11, –60, –72 mm). Bilateral activation sites in dorsal IPS were observed in a visual heading task (Peuskens et al., 2001) and in a successive direction discrimination task (Corbetta et al., 1998). While the heading region was clearly located more posteriorly than our parietal activation sites involved in the color discrimination task (Fig. 11, –60, –72 mm), the direction sites were located at the antero-posterior level of our middle IPS activation sites (Fig. 11, –48 mm), but more inferiorly.

Finally, a recent PET study (Fias et al., 2002), in which the task consisted of a visual quantification of a grating orientation, revealed anterior and posterior parietal activation sites. Their anterior sites were situated inferior to the anterior dorsal IPS sites observed in our study (Fig. 11, –34 mm). Their posterior...
parietal activations were located at the most posterior level of all the parietal activation sites described here (Fig. 11, –72 mm).

In summary, using active visual tasks that are similar but with different attributes, we identified three distinct antero-posterior levels of activation sites along the dorsal IPS. The parietal sites involved in successive color discrimination were located at the anterior and middle level, while those involved in a heading task (Peuskens et al., 2001) and in an orientation quantification task (Fias et al., 2002) were situated at the posterior level. The intraparietal sulcus region involved in the DIM task (DIPSM/L; Table 2) was also located at the posterior level (Fig. 11, –60 mm). This activation site, which remained significant after equalizing the number of motor responses, most likely reflects the decision making process in the DIM task.

In monkeys there is also growing evidence for the involvement of parietal cortex, particularly area LIP, in decision processes (Shadlen and Newsome, 1996, 2001; Platt and Glimcher, 1999). Furthermore, a substantial fraction of LIP neurons in monkeys are selective for color, when color is behaviorally relevant (Toth and Assad, 2002). Area LIP has major inputs originating in the extrastriate visual cortex, including area V4 (Andersen et al., 1990; Lewis and Van Essen, 2000) and TEO (Andersen et al., 1990; Blatt et al., 1990; Distler et al., 1993; Webster et al., 1994). These connections provide the substrate for linking dorsal IPS and ventral regions. Thus, area LIP in monkeys is a potential homologue of the regions in the human intraparietal sulcus that the current study has shown to be involved in color discrimination. Using spatiotopic mapping, Sereno et al. (2001) have described a region in the human parietal cortex, just beyond the medial end of the intraparietal sulcus, that is also a potential homologue for macaque area LIP. Their region is localized 35 and 19 mm posterior to our anterior and middle dorsal intraparietal sulcus sites. Furthermore, the parietal region described by Sereno et al. (2001) is situated 17 mm more medial than our anterior area and 19 mm below our middle dorsal IPS regions. Thus, their parietal area cannot correspond to the sites observed in the current study. A possible explanation could be that the activation sites in these two studies represent different parts of the same area, or that macaque area LIP has evolved into multiple, spatially distinct areas in human parietal cortex. A recent fMRI study (Vanduffel et al., 2002) has shown considerable differences in activation patterns in human and macaque parietal cortex. Hence, to solve this issue, a direct comparison of color discrimination in humans and monkeys will be necessary. This, however, is beyond the scope of the current study.

Dorsal Premotor Cortex

The dorsal premotor cortex was also bilaterally activated in the successive color discrimination task (Fig. 11, –4 mm). Several recent human functional imaging studies have reported a similar coactivation of dorsal parietal cortex and dorsal premotor cortex (Cornette et al., 1998; Peuskens et al., 2001; Fias et al., 2002). As in dorsal IPS, these activation sites in dorsal premotor cortex show a systematic organization, mirroring that in dorsal IPS. While the dorsal premotor activation in heading was located anterior to our activation sites (Fig. 11, 0 mm), those involved in successive direction discrimination and orientation quantification were located at the same antero-posterior level but more inferiorly (Fig. 11).

These data suggest that the connections between the dorsal IPS and the dorsal premotor cortex may be arranged topographically, in a manner related to the attribute used in the task. Similarly, it has been shown in monkeys that the corticocortical connections between dorsal parietal cortex and frontal motor areas, such as the dorsal premotor cortex, are arranged in multiple, highly specific, parallel circuits (Tanné et al., 1995; Johnson et al., 1996; Wise et al., 1997; Rizzolatti and Luppino, 2001), each of which is involved in specific sensory-motor transformations (Rizzolatti and Luppino, 2001).

It is noteworthy that in premotor regions, unlike parietal regions, task and rate interact strongly. This probably reflects an effect of the task on the preparatory motor activity rather than on the visual response. Indeed, in monkeys, premotor neuronal activity has been shown to be affected not only by the action to be taken, but also by events guiding that action (Boussaoud and Wise, 1993; Wise et al., 1997). Thus, dorsal premotor cortex might be considered a final link in a parieto-premotor visuomotor pathway, related to the transformation of visual information, extracted in the color-responsive region and transmitted further to dorsal IPS regions, into motor schemes.

Conclusion

Our results clearly showed that even with color as the attribute, successive visual discrimination involves both ventral and dorsal visual stream areas. We showed that the intraparietal sulcus is involved in decisions whose perceptual basis is in the ventral stream. This demonstrates a cooperation between the two visual streams when decisions about visual attributes have to be made explicit through motor responses. Furthermore, depending on the attribute, distinct dorsal parieto-frontal circuits seem to be active. Further studies are required, however, to confirm the existence of multiple visual decision processes.

Notes

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