The Kinetic Occipital Region in Human Visual Cortex

In the present study we showed that the kinetic occipital (KO) region, located laterally in occipital cortex –20 mm behind human MT/V5, can be strongly and bilaterally activated under passive viewing conditions. We used continuous, randomly changing visual stimulation to compare kinetic gratings to uniform motion and kinetic gratings to luminance defined gratings. The KO activations under these passive conditions are stronger than those observed when the two types of gratings are compared under active conditions, i.e. while subjects perform a task (counting gratings of a given orientation). Region KO was shown to process both shape and motion information, the conjunction of which is typically present in kinetic contours. Area MT/V5 also processes these two aspects of visual stimulation but favors motion signals. Clear segregation of shape and motion processing was observed only in occipito-temporal and parietal regions respectively. Although neurons with properties similar to those derived from the conditions activating the KO region have been documented in the macaque monkey, their location seems inappropriate for them to correspond to the KO activation observed in humans.

Kinetic contours are generated by differences in motion. They can be created by differences in direction or speed of motion on either side of the contour as well as by the juxtaposition of coherent and noncoherent motion or motion and nonmotion. All these types of contours are computationally important because they allow the visual system to disambiguate luminance edges and separate object boundaries from shadows and surface markings. Here we restrict ourselves to kinetic boundaries created by differences in direction, because their extraction requires the processing of the direction of motion rather than the mere processing of motion per se or the coherence of that motion. Furthermore, this type of kinetic boundary excludes any contribution from nonmotion cues, such as blur or temporal frequency, to the contour generation. Such contours are probably very important for breaking camouflage when the subject is moving, such as when a predator is pursuing its prey, and are the only cues available when color, luminance and stereo cues are absent. Humans are very accomplished at using such contours for different aspects of spatial vision, including vernier acuity, orientation discrimination, contour localization, shape perception and letter recognition (Regan, 1986, 1989; Regan and Hong, 1990; Regan and Hamstra, 1991, 1992; Säry et al., 1994; Rivest and Cavanagh, 1996).

Some progress has been made into our understanding of the processing of kinetic contours in the primate brain. Recent evidence has shown that these contours are processed in the ventral pathway (Ungerleider and Mishkin, 1982) together with luminance defined contours. Indeed, neurons selective for orientation of luminance and motion defined contours have been reported in areas V2 and IT (Marcar et al., 1992, 1994; Säry et al., 1995), and TE shape selective cells are selective both for kinetic and luminance defined shapes (Säry et al., 1993). Similar mechanisms might operate in humans, since the activation of human visual cortex obtained by comparing orientation discrimination to a passive viewing control was very similar whether kinetic or luminance defined gratings were used (Orban et al., 1995). On the other hand, it is not as clear where the initial motion preprocessing of the kinetic contours occurs, i.e. the extraction of motion direction necessary for the creation of the kinetic boundary. Initially Marcar and Cowey (1992) had suggested that this preprocessing was accomplished in area MT/V5, which is known to project to areas V2 and V4 (Maunsell and Van Essen, 1983; Ungerleider and Desimone, 1986). In these two ventral areas the direction signals could then be used to extract orientation selectivity for kinetic boundaries. Marcar and Cowey (1992) observed deficits in kinetic shape perception after lesions of area MT/V5 and the surrounding areas. The lack of selectivity for the orientation or position of kinetic boundaries in the MT neurons themselves (Marcar et al., 1995) is not contradictory to the view that area MT/V5 plays a role in the preprocessing of the kinetic contours. However, lesions restricted to area MT/V5 (Lauwers et al., 1995) only mildly impair orientation discrimination of kinetic boundaries, suggesting that other early cortial areas might also contribute to the motion preprocessing required for the extraction of kinetic contours. Indeed, Orban et al. (1995) described a motion area in human lateral occipital cortex which could play this role. This area was differentially activated when subjects counted the kinetic gratings of a given orientation compared with when they performed the same task for luminance defined gratings.

The present experiments were undertaken to obtain further evidence that this lateral occipital region is indeed specialized in the processing of kinetic contours. In the original experiment in which kinetic gratings and luminance gratings were contrasted, there was a possible confounding factor, in that motion is present between the kinetic boundaries in the kinetic grating stimuli. Thus the differential activation observed in the subtraction kinetic gratings minus luminance gratings might be due to the local motion rather than to the kinetic boundaries. In the original study (Orban et al., 1995) we argued that this was unlikely since the difference between kinetic and luminance grating conditions in the KO region was maximal when subjects counted the orientations of the gratings. Yet there is a straightforward way to eliminate this confounding factor: namely to show that the KO region is also differentially active when kinetic gratings are compared with uniform motion. The first aim of the present experiments was to compare these two conditions. Since it is impossible to find contour-related attributes which subjects could use in a task performed with the kinetic gratings as well as with the uniform motion, we resorted to passive stimulation. Thus we compared kinetic gratings with
uniform motion while the subjects performed a fixation task and remained passive to the stimuli. We also repeated the comparison of kinetic and luminance gratings under the same conditions. All three types of stimuli were generated with randomly textured patterns and were presented continuously. For the grating stimuli the four main orientations were presented in random order, to match the presentation of motion along the four main axes in the uniform motion conditions (Zeki et al., 1991; Watson et al., 1993; Dupont et al., 1994).

In the three conditions (uniform motion, kinetic and luminance gratings) motion and shape cannot easily be disentangled since comparing kinetic gratings with luminance gratings isolates motion and comparing kinetic gratings with uniform motion isolates shape. The addition of a fourth condition, a static randomly textured pattern, allows the study of the main effects of motion and shape as well as their interactions. The addition of this fourth condition also enabled us to locate MT/V5 (Zeki et al., 1991; Watson et al., 1993; Dupont et al., 1994) and compare it with the kinetic occipital region in the same group of subjects, something we could not do in the initial publication (Orban et al., 1995). Finally, we replicated the two conditions which defined the kinetic occipital region in the original experiment (Orban et al., 1995), counting gratings of a given orientation for kinetic and luminance defined gratings. This allowed us to compare the differential activation strength of region KO when the subjects performed a task with a visual stimulus and when they remained passive during continuous and randomly changing stimulation. These experiments demonstrate the existence of a lateral occipital region which is specialized for the processing of kinetic boundaries, and which is distinct from area MT/V5.

Materials and Methods
Ten young (mean age ± SD, 22.5 ± 2 years) male subjects participated in the study which was approved by the Ethical Commission of the KU Leuven Medical School. All were right-handed, had normal vision and no neurological history, were not on any medication and had a normal MRI scan. They were trained in two sessions prior to the PET scanning. Fixation was controlled by EOG, and all subjects fixated steadily.

Stimulus Characteristics and Tasks
Six stimulus conditions were used: two in which the subjects performed the same task (counting) with the visual stimulus while fixating, as in Orban et al. (1995), and four conditions in which the subject remained passive to the visual stimulus and only fixated. Each condition lasted 2 min.

In the active trials (counting tasks) series of 9, 10 or 11 gratings were presented for 200 ms at a rate of 3/s: 4, 5 or 6 gratings were vertical and the others slightly oblique (orientation difference 5.8 ± 1.4° for luminance defined and 14 ± 2° for kinetic gratings). The task of the subjects was to count the nonvertical stimuli and press the right or left key depending on whether or not this number was 5. This task was performed both with luminance defined (CLUM) and kinetic gratings (GKN).

Stimuli were exactly the same as those used in our previous study (Orban et al., 1995). Rectangular gratings were created on an Atari computer at 70 Hz. The stripe width was 0.66°, the diameter was 3° and mean luminance was 47.5 cd/m². Stimuli were centered on the fixation point. They were generated by modulation of random textured patterns (50% white and dark pixels of 1 arc min) and the stripes differed either in luminance (28.8 versus 66.1 cd/m²) or in motion direction. In the kinetic and uniform motion stimuli, pixels moved at 4°/s. In the conditions in which subjects judged the orientation of kinetic gratings, motion was upward and downward and the nearly vertical orientation of the kinetic boundary was manipulated independently of the defining cue. In the passive conditions, the direction of motion was always parallel to the kinetic boundary.

The four passive conditions (Fig. 1) included presentation of kinetic (GKN) and luminance defined gratings (GLUM), of uniform motion (UNIFORM) and of a static randomly textured pattern (STATIC). The kinetic gratings and uniform motion were presented with pixels moving along horizontal, vertical and both oblique (45 and 135°) axes. In these stimuli the pixels moved backward and forward along a single axis for a total of 856 ms before switching randomly to another axis. In the static condition the same random textured pattern remained stationary throughout the entire 2 min period. In the kinetic and luminance defined gratings vertical, horizontal and both oblique orientations were presented. These stimuli switched to another randomly chosen orientation every 856 ms, in the kinetic gratings this change was coupled to the change in motion axis since the pixels always moved parallel to the kinetic boundary. It should be noted that locally (over a diameter smaller than the stripes of the kinetic stimuli) the motion was exactly the same in the kinetic and uniform motion condition; the rate of change in motion direction was also exactly the same in these two types of stimuli and the rate of change in orientation was exactly the same in luminance defined and kinetic gratings.

Data Acquisition
During the PET session, the subject had to perform the tasks while lying in the PET scanner (Siemens-CTI 931/8/12). The subjects viewed the stimuli in a dimly lit room at a distance of 114 cm. The order of conditions was randomized according to a Latin square design. The head of the subject was immobilized with a foam headholder (Smither Medical Products, Akron, OH). The start of the task coincided with the start of the injection of 40 mCi (1.48 Gbq) H 2 15O. The injection lasted 12 s and the scan began when activity reached the brain, which was clearly marked by a sharp rise in counts (~30 s post-injection). Scanning lasted 40 s and occupied the middle third of the period during which the subjects performed the task. Each subject underwent six emission scans while performing one of the six tasks. Scans were separated by a 15 min time interval for decay of the tracer.

The PET scanner measured 15 planes (slice thickness 6.75 mm) parallel to the inferior orbito-meatal line. Prior to the emission scans, a transmission scan was acquired which was used to correct for
attenuation. The (attenuation corrected) images were reconstructed using filtered back projection with a Hanning filter of cut-off frequency 0.5 cycles/pixel. Each reconstructed image represents the activity distribution during the measurement which is related to the regional cerebral blood flow (rCBF).

After the PET scanning, each subject underwent a magnetic resonance imaging (MRI) scan. The MRI images were acquired using a three-dimensional Magnetization-Prepared Rapid Gradient Echo (MPRAGE) sequence (Mugler and Brookeman, 1990). Acquisition parameters were: repetition time 10 ms, echo time 4 ms, flip angle 8°, field of view 256 mm, acquisition matrix 256 × 256. The 3-D volume had a thickness of 160 mm, partitioned into 128 sagittal slices.

**Data Analysis**

The data were analyzed with statistical parametric mapping (SPM95, software from the Wellcome Department of Cognitive Neurology, London, UK) implemented in MATLAB (Mathworks Inc., Sherborn, MA). Statistical parametric maps are spatially extended statistical processes that are used to characterize regionally specific effects in imaging data. Statistical parametric mapping (SPM) combines the general linear model (to create the statistical map of SPM) and the theory of Gaussian fields to make statistical inferences about regional effects (Friston et al., 1991, 1994; Worsley et al., 1992).

**Spatial Realignment and Normalization**

The scans from each subject were realigned using the first scan as a reference. The six parameters of this rigid body transformation were estimated using a least squares approach (Friston et al., 1995a). Following realignment, all images were transformed into a standard space (Talairach and Tournoux, 1988). This normalizing spatial transformation matches each scan (in a least squares sense) to a reference or template image that already conforms to the standard space. As a final pre-processing step the images were smoothed using a Gaussian kernel (20 × 20 × 12 mm full width at half maximum).

**Statistical Analysis**

After specifying the appropriate design matrix, the condition, subject and covariate effects were estimated according to the general linear model at each voxel (Friston et al., 1995b). The design matrix included global activity as a confounding covariate and this analysis can therefore be regarded as an ANCOVA (Friston et al., 1990). To test hypotheses about regionally specific condition effects the estimates were compared using linear contrasts. The resulting set of voxel values for each contrast constitute a statistical parametric map of the t-statistic SPM(t).

The SPM(t) were transformed to the unit normal distribution [SPM(Z)] and thresholded at 3.09 (P < 0.001 uncorrected) and at 4.10 (P < 0.05 after the correction for multiple comparisons as used in SPM95).

MRI images of each subject were registered, after segmenting the brain (ANALYZE, Mayo Clinic USA), to the corresponding PET images using automatic image registration (Woods et al., 1993). Then the same transformations into the standard space as those used for the PET images were applied to the resampled (and registered) MRI images. An averaged (for the group of subjects) MRI image in the standard space was already conforms to the standard space. As a final pre-processing step the images were smoothed using a Gaussian kernel (20 × 20 × 12 mm full width at half maximum). These regions must match statistical inferences about regional effects (Friston et al., 1991, 1994; Worsley et al., 1992).

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In this and subsequent tables all differential activation regions reaching P < 0.001 uncorrected are tested. Gdm: medial occipital gyrus, Gdi: inferior occipital gyrus, Lpi: inferior parietal lobule, Lps: superior parietal lobule; GPC: precentral gyrus.

*Distance laterally from the midline (x) with right positive, anterior–posterior distance (y) from anterior commissure (AC) with forward positive and distance (z) above (positive) and below (negative) the anterior–posterior commissure line.

*P < 0.05 after correction.

**Comparison of Static and Uniform Motion: Passive Viewing**

This comparison provides background information regarding the location of human MT/V5 in the subjects of the present study. The results are shown in Table 1 and Figure 2A. The most significant differences were observed over regions which correspond to right and left human MT/V5. Another very significant activation was observed in right Brodmann area (BA) 40. Weaker activations reaching only a significance of P < 0.001 (uncorrected) were observed in the left lateral occipital cortex, presumably corresponding to the kinetic occipital (KO) region, right lateral sulcus, left BA7 and right precentral gyrus (Table 1).

**Comparison of Uniform Motion and Kinetic Gratings: Passive Viewing**

The result of subtracting uniform motion from kinetic gratings is given in Table 2 and Figure 2B. Only two regions in the lateral inferior occipital cortex yielded a significant difference when corrected for multiple comparisons. These regions must correspond to region KO, since kinetic contours are present in the kinetic gratings but not in uniform motion. This designation is supported by the location of the two activations: the one in the left hemisphere lies close to the region defined by the active task in the present study and the one in the right hemisphere near the coordinates of the kinetic region observed by Orban et al. (1995). Weaker activations were observed in the right fusiform gyrus, close to the border with the lingual gyrus and in the left lingual gyrus (Table 2).

**Comparison of Kinetic and Luminance Defined Gratings: Passive Viewing**

Although this comparison is similar to that originally used to define the kinetic occipital region, there might be a difference between active conditions and passive conditions. Indeed, in the
active conditions, subjects must use the boundary information to solve the task. This probably explains why the differential activation of KO in the Orban et al. (1995) study was stronger in the active than in the passive conditions.

The results of subtracting luminance defined from kinetic gratings are given in Table 3 and Figure 2C. The three major differentially active regions are the left and right MT/V5 and left KO. As can be seen from the comparison of Figure 2A and C, activation of the right KO is fused with the right MT/V5. A weaker activation was observed in the left BA7 (Table 3). The fact that these activations are very similar to those observed in the subtraction uniform-static strongly suggests that in the passive conditions it is mainly the presence or absence of motion which produces the differential activation in the kinetic versus luminance defined gratings comparison. It is noteworthy that the right parietal BA40 region was not activated in the kinetic versus luminance defined grating comparison but was activated in the uniform motion versus static comparison. This might...
Region KO is Distinct from Area MT/V5
The present results indicate that the right and left KO regions defined by the subtraction of uniform motion from the kinetic gratings correspond to the region defined originally by the orientation counting tasks. These two regions are clearly distinct from the MT/V5 areas. The locations of these areas in coronal section are shown in Figure 3. On average, region KO is located 25 mm more posterior than MT/V5, with average (over right and left) coordinates of 31, -91, -2 for KO and 40, -66, 0 for MT/V5. Hence they are clearly distinct areas, even taking into account the low resolution of the average subject PET technique. This is amply confirmed by the difference of the activation profiles of the two areas, shown in Figures 4 and 5 respectively. The profiles of the right and left KO areas are clearly very similar: both regions are more strongly activated by kinetic gratings than by uniform motion or luminance defined gratings, and static random textured pattern is the weakest stimulus. The profiles of areas MT/V5 are clearly different from those of regions KO, the main difference being that uniform motion is almost as effective a stimulus in activating MT/V5 as is a kinetic grating, and is clearly better than either the static randomly textured pattern or luminance defined gratings.

These activation profiles also demonstrate the robustness of the differential activation of region KO in the two main subtractions. In the subtraction GKin - GLUM the mean percent change in rCBF is 5.5% in left KO and 5.7% in right KO. In the subtraction GKin - UNIFORM the values were 5.5% in left KO and 7.1% in right KO. In contrast, in the subtraction CKin - CLUM the mean percent change in rCBF was only 1.3% in left KO and 0.5% in right KO. The differential activations obtained in the passive conditions in KO region compare favorably with the mean percent change in MT/V5 yielded by the subtraction UNIFORM - STATIC: 8% in left MT/V5 and 6.8% in right MT/V5.

Main Effects of Motion and Shape
Given the activation profiles of KO and MT/V5, it is not surprising that the main effect of motion defined as (GKin + UNIFORM) - (GLUM + STATIC) was significant in both right and left MT/V5 and in left KO (Table 4). In contrast, the main effect of shape defined as (GKin + GLUM) - (UNIFORM + STATIC) was significant in right and left KO and in several inferior occipital regions (Table 5). The interaction between the motion and shape effects failed to reach significance anywhere (Tables 4 and 5), although there was a trend towards a positive interaction in the right KO region (z = 1.55, P < 0.12). Thus region KO is only marginally more strongly activated when shape is defined by motion than when defined by luminance. These data support the view that area MT/V5 is activated by motion more than by shape, while region KO is activated equally by both. This is also clearly shown in Figure 6, where the regions activated by motion and shape are shown in coronal sections. Posteriorly in the occipital lobe, the motion and shape effects overlap considerably, including at the level of region KO. As one moves forward the two effects tend to become dissociated, particularly in the right hemisphere. Motion dominates in the parietal regions and the middle temporal gyrus, whereas shape dominates in the fusiform gyrus.

Discussion
Comparison with Our Previous PET Study (Orban et al., 1995)
Our results show that very robust activations of the KO region...
can be obtained under passive conditions. This was true for the subtraction of uniform motion from kinetic gratings and to a slightly lesser degree for the subtraction of luminance defined gratings from kinetic gratings. In the present experiment the differential activation in the active condition (counting the nonvertical gratings) was weaker than in the previous study and located in the opposite hemisphere. The number of subjects was smaller in the present study than in the previous study and the task was slightly easier, which might account to a certain extent for the weaker activation. Both experiments taken together suggest that the counting of nonvertical gratings task is a less optimal way of activating region KO. This fact, together with interindividual differences in KO activation strength and lateralization which we have documented in our subsequent fMRI study (Van Oostende et al., 1996a,b), combined with inherent limitations in the sensitivity of the PET technique, might explain the variability in lateralization observed between the two studies.

Another apparent discrepancy between the two studies is that the comparison of kinetic with luminance defined gratings under passive viewing yielded a stronger differential activation than the active comparison in the present study, while the opposite was true in the previous study. There are, however, two major differences between the passive conditions of the two studies. Here subjects were stimulated continuously compared with 60% of the time in the previous study. More importantly, multiple orientations of kinetic gratings and hence multiple shapes and speeds were provided, comparison with our results provide some enlightenment in this respect. Subjects could base their judgements only on the kinetic boundaries in the active conditions and thus the task dependent increase in activation in region KO in that experiment could be considered as evidence that region KO is involved in the processing of kinetic boundaries. Our subsequent fMRI experiment definitively resolved the issue in favor of kinetic boundaries (Van Oostende et al., 1996a,b).

Although at present the subtraction ‘kinetic grating minus uniform motion’ is the optimal comparison with which to visualize region KO, we do not imply that KO is the only region active in this subtraction. What really defines region KO is its functional profile based on a set of comparisons. In our opinion, this represents the counterpart for functional imaging of using the functional properties of neurons as a criterion for distinguishing monkey visual cortical areas, along with architectonics, connections and topographical organization. Indeed, the functional profile of region KO was clearly different from that of area MT/V5.

**Definition and Selectivity of Region KO**

We refer to the region selectively activated by kinetic boundaries as the kinetic occipital area. This is used in a descriptive sense since the three subtractions which yield differential activation in this region all rely on a kinetic grating presentation as the experimental condition. However, the kinetic boundaries were always produced by pixels moving in opposite directions. Hence we do not know whether the kinetic boundaries themselves or the pixels moving in opposite directions are the critical aspect of the stimulus. The initial experiment (Orban et al., 1995) might provide some enlightenment in this respect. Subjects could base their judgements only on the kinetic boundaries in the active conditions and thus the task dependent increase in activation in region KO in that experiment could be considered as evidence that region KO is involved in the processing of kinetic boundaries. Our subsequent fMRI experiment definitively resolved the issue in favor of kinetic boundaries (Van Oostende et al., 1996a,b).

**Comparison with Other PET Studies of Form-from-Motion**

Zeki (1993) briefly reported a PET experiment in which form-from-motion was compared with (the average of) uniform motion and form-from-luminance. The stimulus was somewhat similar to ours in that stripes of different widths were used, but as no details concerning stimulus size, element density or speed of motion were provided, comparison with our results is difficult. Judging from the figure provided, it is likely that

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**Table 4.**

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*Note: All values are significant at the .05 level. KO = kinetic occipital area; L = left hemisphere; R = right hemisphere.*
region KO was included in the region of activation. Furthermore, from the subtraction used by Zeki it is difficult to know whether it is the motion, the shape of the kinetic contour stimulus or both that caused the activation observed. Our experiment clearly shows that both motion and shape activate region KO.

Gulyás et al. (1994) also studied form-from-motion by comparing a form discrimination (using a form defined by motion) with a motion discrimination (in a shape defined by motion). Although many regions were activated in this subtraction, none were near region KO. Several regions were located ventrally in the fusiform gyrus, some of them close to the inferior occipital/fusiform regions in which we observed a shape effect (Table 5). This study only underscores the difficulty of comparing kinetic shape and uniform motion in a paradigm other than a passive fixation paradigm. The two dimensions to be discriminated in the Gulyás et al. (1994) experiment were very different: degree of coherence of motion and squareness of a shape. It is difficult to see how comparison of these two dimensions could isolate the processing of kinetic contours. There is, however, agreement between the Gulyás et al. study and ours in that form-from-motion is processed further along the ventral pathway (Haxby et al., 1994). Our experiments show that for these ventral regions form-from-motion is not different from form-from-luminance, since interactions between motion and shape main effects were absent.

**Location of Region KO with Respect to Other Visual Areas in the Human Brain**

Our results clearly show that region KO is distinct from area MT/V5, which is usually considered the most prominent motion area in human cortex (Zeki et al., 1991; Tootell et al., 1995b; Ungerleider, 1995), although many regions of the human brain in fact process motion, as shown by the present results, as well as those of Dupont et al. (1994), Dale et al. (1995) and Sunaert et al. (1996). Another brain region responding to motion is area V3A (Tootell et al., 1995a). The central vision representation in area V3A is located higher and more medially than region KO.
Region LO defined by Malach et al. (1995) is located posteriorly and ventrally to area MT/V5. Region KO thus seems to be located dorsally and posteriorly to region LO. Finally, region KO lies in front of the tier of three retinotopically defined areas, V1, V2 and V3 (Seraf et al., 1995; Shipp et al., 1995). However, comparisons across group studies are difficult and further work is required to clarify the relationships of region KO with areas V3 and V5A and region LO. Such experiments using fMRI to map region KO and the other areas in a single subject have shown that region KO is distinct from all three areas (Van Oostende et al., 1995a,b). However, the present study allows us only to conclude that region KO is selective for kinetic boundaries and we must leave open the possibility that this represents a new selectivity of an existing area rather than a new, separate area of the human brain.

Dissociation of Visual Cortical Regions Processing Shape and Motion

Although the functional profiles of area MT/V5 and region KO are clearly different, both areas still process motion and shape information. Thus in these posterior, middle occipital regions the segregation of motion and shape is incomplete, although in human area MT/V5 motion is clearly the dominant effect. This latter observation is in good agreement with the monkey single cell data as MT/V5 neurons are best driven and are most selective for moving stimuli but also react to static luminance patterns and are orientation selective (Albright, 1984; Marcar et al., 1995). In this respect it is worth noting that when mapping the dorsal and ventral occipito-temporal streams in human cortex, using attention to locations and to faces respectively (Hazeltin et al., 1994), the segregation was incomplete in posterior occipital regions surrounding striate cortex.

Our results also show that beyond the middle occipital areas there is a clear segregation, at least in the right hemisphere, between ‘motion’ and ‘shape’, as more dorsal parietal areas are significantly activated only by motion and more ventral occipito-temporal areas are significantly activated only by shape. This again is in agreement with the monkey data, which have shown that in inferotemporal cortex and in V4 neurons can be selective for orientation or shape irrespective of whether the defining cues are motion or luminance differences (Sáry et al., 1993, 1995; Logothetis and Charleis, 1990). The strongest ventral activation by shape occurred in a region (46, –78, –12) corresponding relatively well to region LO (Malach et al., 1995), the branching point of which was located at 45, –73, –18. It is noteworthy that activation in this region was recently reported by Goebel et al. (1996) in the comparison of letters defined by motion and uniform motion. Again our results show that this region is not exclusively involved in processing of kinetic boundaries (the conjunction of shape and motion) but rather of form, whether defined by motion or luminance.

Comparison with Lesion Studies

It has been reported that both cortical lesions (Regan et al., 1992) and multiple sclerosis (Regan et al., 1991) affect the perception of kinetic shapes much more than the perception of luminance defined shapes. However, the widespread nature of the lesions in both studies make a comparison with our results difficult. Although at first glance the preferential impairment of kinetic shape perception over that of luminance defined shapes suggests that the motion preprocessing is affected in these lesions, this need not necessarily be the case. Kinetic shape perception might be more vulnerable to neuronal damage since the proportion of neurons in the ventral pathway which are shape selective for kinetic defined shapes is small compared with those selective for luminance defined shapes (Sáry et al., 1993, 1995).

Comparison with Monkey Data

It is well established that area MT neurons in monkeys respond less vigorously to kinetic grating stimuli than to uniformly moving random dot and random textured patterns (Snowden et al., 1991; Marcar et al., 1995). Hence it may seem surprising that in our experiments area MT/V5 is slightly more activated by kinetical gratings than by uniform motion. However, during the kinetical grating presentation, the MT neurons will be driven by both forward and backward motion, while during the uniform motion presentation they will be driven only by a single direction. Thus, during a given presentation, twice as many MT neurons respond to the kinetical gratings than to uniform motion. Since the response of individual cells to kinetic gratings is more than half that of uniform motion (Marcar et al., 1995), one would expect a slightly larger population response to the kinetic gratings than to the uniform motion.

Since kinetic gratings drive twice as many neurons as uniform motion, it is sufficient that KO neurons simply respond equally well to uniform motion and to kinetic gratings to explain the profile of region KO we observed. Their response to local motion would suffice to explain the KO activation in the subtraction of luminance defined gratings from kinetic gratings. We cannot, however, exclude the possibility that KO neurons are selective for the orientation of kinetic boundaries. The results of Snowden et al. (1991) suggest that KO neurons should have to be nondirection selective to respond as much to kinetic gratings as to uniform motion. Sensitivity to the motion discontinuities similar to those which have recently been reported for orientation discontinuities in V1 (Sillito et al., 1995) would further accentuate the difference in the population response to kinetic gratings compared with uniform motion. Preliminary experiments in our laboratory have shown that some neurons in areas V2 and V4t, which are not direction-selective, show an enhanced and direction-selective response to a foreground stimulus moving in the direction opposite to a slowly moving background (Orban et al., 1989).

As in humans, an area other than MT/V5 also appears to preprocess the kinetic grating motion signals in monkeys, since lesions of area MT/V5 only mildly impair the discrimination of kinetic grating orientation discrimination (Lauwers et al., 1995). Which other areas of the monkey visual cortex may perform this function is presently unclear. Both of the areas suggested by the preliminary physiological recordings are unlikely choices. V2 is located too posteriorly to correspond to region KO. Area V4t is also unlikely, since it was probably included in the lesions of the Lauwers et al. (1995) study. Thus this still leaves us with no clear indication of which monkey cortical area contains neurons with the properties accounting for the selectivity for kinetic gratings, displayed by region KO in the human brain. Further experiments both in humans and in monkeys are presently being undertaken to address this question.

Notes

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