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Multisensory self-motion encoding in parietal cortex

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Navigation through the environment requires the brain to process a number of incoming sensory signals, such as visual optical flow on the retina and motion information originating from the vestibular organs. In addition, tactile as well as auditory signals can help to disambiguate the continuous stream of incoming information and determining the signals resulting from one's own set of motion. In this review I will focus on the cortical processing of motion information in one subregion of the posterior parietal cortex, i.e., the ventral intraparietal area (VIP). I will review (1) electrophysiological data from single cell recordings in the awake macaque showing how self-motion signals across different sensory modalities are represented within this area and (2) data from fMRI recordings in normal human subjects providing evidence for the existence of a functionally equivalent area of macaque area VIP in the human cortex.

MOTION-SENSITIVE AREAS IN THE MACAQUE VISUAL CORTICAL SYSTEM

Self-motion through the environment generates a variety of sensory input signals. In the macaque more than half of the cortical tissue is dedicated to the processing of visual signals. This indicates the importance of the incoming visual information for the processing of self-motion information and implies its

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dominance over the other sensory signals. In the parietal cortex the different sensory signals converge. In recent experiments we could show that individual cells within a functional subdivision of the posterior parietal cortex (PPC), i.e., the ventral intraparietal area (VIP), process these signals originating from different sensory modalities. By summarizing these studies, we will describe the visual motion processing in area VIP and, thereafter, we will show how self-motion information originating from other sensory modalities (vestibular, tactile, and auditory) is processed in this area. Yet, we will start our description of the cortical motion processing by briefly illustrating, how the preceding stages process the relevant visual motion signals.

VISUAL MOTION PROCESSING IN THE M-PATHWAY

In primates, visual information processing is segregated into parallel channels already within the retina and the preprocessed signals are transmitted via the thalamus towards area V1 of the visual cortex. Signals related to the motion of a stimulus are predominantly processed and forwarded within the fast ''M-pathway''. Information is sent directly from area V1 or via a further processing stage (area V2) to the middle temporal area (MT). Area MT (or V5) is located in the posterior bank of the superior temporal sulcus (STS). It is retinotopically organized, i.e., neighbouring cells within area MT represent neighbouring parts within the visual field (Shipp & Zeki, 1989; Ungerleider & Desimone, 1986a, 1986b). Many cells in area MT are tuned for the direction and speed of a moving visual stimulus (Albright, 1984; Mikami, Newsome, & Wurtz, 1986a, 1986b). Furthermore, a considerable proportion of cells in area MT increase their discharge in relation to smooth eye movements (for review see, e.g., Ilg, 1997).

The visual field representation in area MT is mostly contralateral. Although visual receptive fields of MT cells are larger than those in striate cortex, they are still small compared to the large field motion across the whole visual field typically occurring during self-motion. Area MT thus can only be considered a relay station for visual motion processing necessary for the encoding of self-motion.

Two major output structures of area MT are the medial superior temporal area (MST) in the anterior bank of the STS and the ventral intraparietal area (VIP) in the depth of the intraparietal sulcus (IPS). It is known for many years now, that MST neurons respond selectively to optic flow stimuli mimicking self-motion in 3-D space (Duffy & Wurtz, 1991a, 1991b, 1995; Graziano, Andersen, & Snowden, 1994; Lappe, Bremmer, Pekel, Thiele, & Hoffmann, 1996; Saito, Yukie, Tanaka, Hikosaka, Fukada, & Iwai, 1986; Tanaka, Hikosaka, Saito, Yukie, Fukada, & Iwai, 1986). Over the years, these and other studies have established the view of an involvement of area MST in heading perception.

Further evidence for this functional role comes from studies showing responses of single MST neurons to real compared to visually simulated motion (Bremmer, Kubischik, Pekel, Lappe, & Hoffmann, 1999; Duffy, 1998; Froehler & Duffy, 2002). In these studies, vestibular responses were observed during linear movement in light (i.e., combined visual and vestibular stimulation) as well as in darkness (i.e., pure vestibular stimulation). Usually, vestibular responses were smaller than visual responses. Only a weak if any correlation was found between preferred visual and vestibular directions. As an example, a cell preferring visually simulated forward motion might prefer pure vestibular stimulation directed backwards or into any other direction. The expected response scheme of identical preferred directions in the visual and vestibular domain, i.e., a synergistic signal convergence, was observed only for a small proportion of cells.

HEADING ENCODING IN AREA VIP

As mentioned above, area MST is not the only major output structure of area MT. Based on anatomical data (Maunsell & Van Essen, 1983; Ungerleider & Desimone, 1986a), the ventral intraparietal area (VIP) was originally defined as the MT projection zone in the intraparietal sulcus (IPS). Studies on the functional properties of VIP cells showed sensitivity for the direction and speed of moving visual stimuli (Colby, Duhamel, & Goldberg, 1993; Duhamel, Colby, & Goldberg, 1991). Follow-up studies suggested an involvement of area VIP in the processing of self-motion information (Bremmer, Duhamel, Ben Hamed, & Graf, 1995, 1997; Schaafsma & Duysens, 1996; Schaafsma, Duysens, & Gielen, 1997).

In the experiments reviewed here, we went one step further and tested neurons in area VIP for their capability to encode the direction of self-motion (Bremmer, Duhamel, Ben Hamed, & Graf, 2002a). In our studies, we presented optic flow stimuli simulating straight-ahead (expansion) or backward (contraction) motion, i.e., with the singularity of the optic flow (SOF) at the screen centre. During the experiment, the head fixed animal was facing a translucent screen subtending the central 80° by 70° of the visual field. Computer generated visual stimuli as well as a fixation target were back-projected by a liquid crystal display system. During visual stimulation, the monkey had to keep the eyes for 4500 ms within the tolerance window always at straight-ahead position ([x, y] = [0°, 0°]) to receive a liquid reward. Visual stimuli were random dot patterns, consisting of 240 dots, each individual dot 0.5° in size. Expansion and contraction stimuli were presented interleaved in pseudorandomized order.

About two thirds of the neurons in area VIP responded selectively to optic flow stimuli simulating forward or backward motion. Activity often encompassed strong phasic responses to the onset of the simulated movement, which then decreased to a weaker tonic discharge level. One such example is shown in

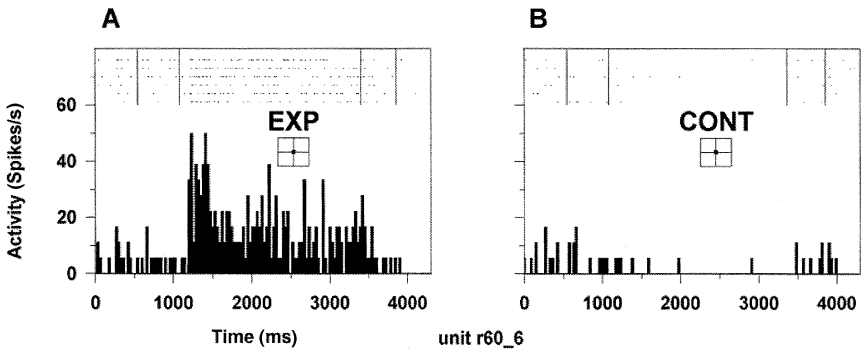

Figure 1. Optic flow responses in area VIP. The two histograms show the responses of a single VIP neuron to an expansion stimulus (left) and a contraction stimulus (right). Raster displays (spike trains) indicate the response on a single trial basis. The tick marks in the spike trains indicate stimulus onset (1st tickmark), motion onset (2nd tickmark), motion offset (3rd tickmark), and stimulus offset (4th tickmark). This cell responded to the expansion stimulus but was inhibited by the contraction stimulus.

Figure 1. The panel on the left shows the responses of a cell for simulated forward motion (expansion), while the right panel shows the cell's response for simulated backward motion (contraction). The cell revealed a clear preference for forward motion. At the population level, the majority of cells preferred expansion over contraction stimuli (72%). In addition, the average response of the population of neurons for an expansion stimulus was significantly stronger compared to the response for a contraction stimulus (Wilcoxon Signed Rank Test, $p < .001$).

Optic flow stimuli with central singularities mimic a particular situation: gaze direction and movement direction are either co- or antialigned. In other words: in such a case forward directed gaze is combined with either forward (i.e., coaligned) or backward (i.e., antialigned) self-motion. During natural navigation, however, gaze direction and movement direction most often are not aligned. Thus, we were interested in the question, whether the neuronal response strength might be influenced by the location of the singularity of the optic flow on the retina. Accordingly, we tested a subset of neurons for their response to nine different focus locations, one central focus and eight foci shifted 25° into the periphery. The vast majority of neurons (95%) showed a significant influence of the location of the SOF with regard to their responses. An example is shown in Figure 2. Mean discharges for the nine different focus locations are shown in the 3-D plots. Variation of the focus location had a significant influence on the neuronal discharges (ANOVA, $p < .001$). Expansion responses increased for focus locations further downward in the visual filed, while contraction responses decreased for these focus locations. Such kind of negative

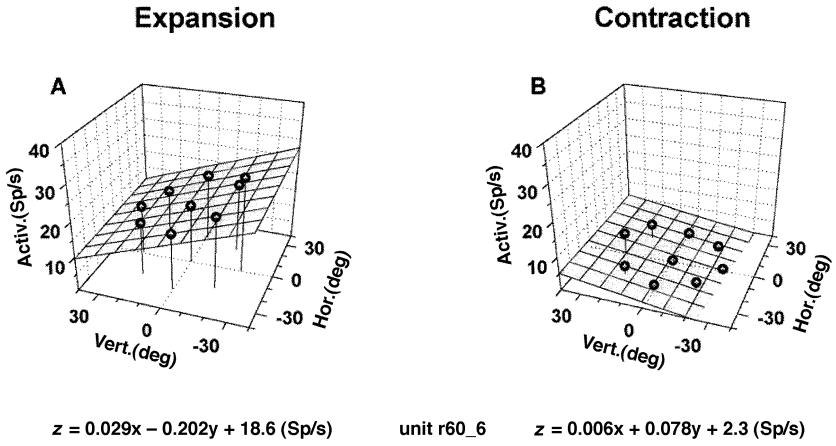

Figure 2. Modulation of cell activity by shifting the location of the singularities of the optic flow (SOF). The figure shows the responses of the cell from Figure 1 for stimuli with shifted SOFs. Each shaded plane represents the two-dimensional linear regression to the mean discharge. The x–y plane in these plots represents the central 80 by 80 degrees of the visual field. The base point of each drop line depicts the SOF location on the screen, and the height of each line depicts the mean activity value for stimulation with the SOF at this location.

correlation between the tunings for expansion and contraction responses was observed for the majority of cells.

We used a two dimensional linear regression analysis to quantify the modulatory influence on the cell's response. A regression plane could be approximated significantly to the discharges of the neuron to expansion ($p < .001$) and contraction ($p < .02$) stimuli.

At the population level, the modulatory influence of the SOF location on the discharge was balanced out, as implicitly shown in Figure 3. The panel on the left (right) shows the distribution of horizontal and vertical slopes and intercepts of the regression planes for the individual expansion (contraction) responses. Slopes were normally distributed along the horizontal and vertical axis, respectively. This result is similar to our data obtained previously in area MST (Lappe et al., 1996). By using a recently introduced population code, which we named the isofrequency coding, we could show that an ensemble of VIP neurons is capable of encoding the heading direction (Bremmer et al., 2002a).

VESTIBULAR STIMULATION

Vestibular sensory signals can indicate rotational and translational self-motion. In two very recent studies we could show that many neurons in area VIP signal not only visually simulated self-motion but rather real physical displacement

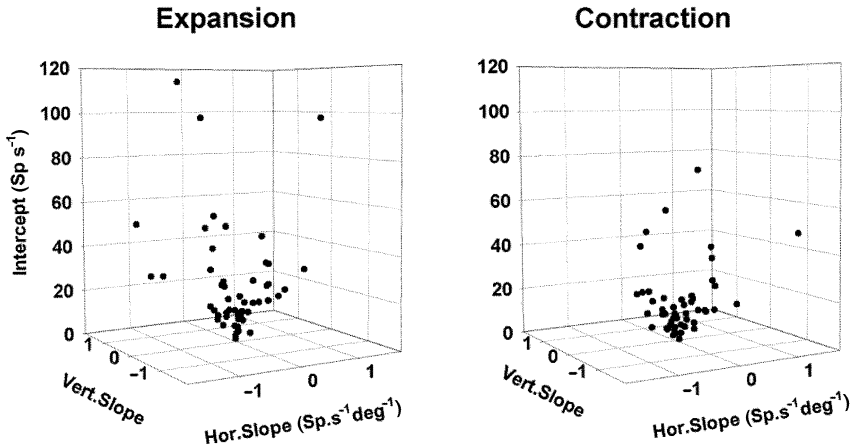

Figure 3. Population response to optic flow stimuli with shifted SOFs. The scatter plot shows the distribution of the regression parameters (slope along the horizontal and vertical axis, intercept) for expansion (left) and contraction (right) responses. Slopes along the horizontal and vertical axis are normally distributed.

(Bremmer, Klam, Duhamel, Ben Hamed, & Graf, 2002b; Schlack, Hoffmann, & Bremmer, 2002).

In a first study (Bremmer et al., 2002b), neurons were tested for rotational vestibular responsiveness in light (first column of Figure 4) and in total darkness, i.e., with all lights shut off and the animals' eyes covered with light-tight material (middle column of Figure 4). During these experiments, animals performed reflexive, compensatory eye movements (optokinetic reflex [only in light] and vestibulo ocular reflex). In order to test for possible influences of these compensatory eye movements, some neurons were tested during VOR suppression. To this end, animals fixated a chair mounted LED while being rotated in otherwise darkness (right column of Figure 4). As can be seen from Figure 4, this individual VIP cell preferred real rotational displacement towards the right, regardless of whether this rotation was performed in light or in darkness or with or without compensatory eye movements. Like in this example, all neurons kept their selectivity for vestibular stimulation across the different experimental conditions.

All neurons with vestibular responses also were directionally selective for optic flow stimuli simulating translational movements in the frontoparallel plane. The ''circular pathway'' paradigm was used to map this directional selectivity (for a detailed description of this stimulus see, e.g., Bremmer et al., 2002a, 2002b). In this paradigm the speed of the stimulus is kept constant throughout a stimulus trial (cycle), but stimulus direction changes continuously (0–360°) within a complete stimulus cycle. Thus, each pattern element moves

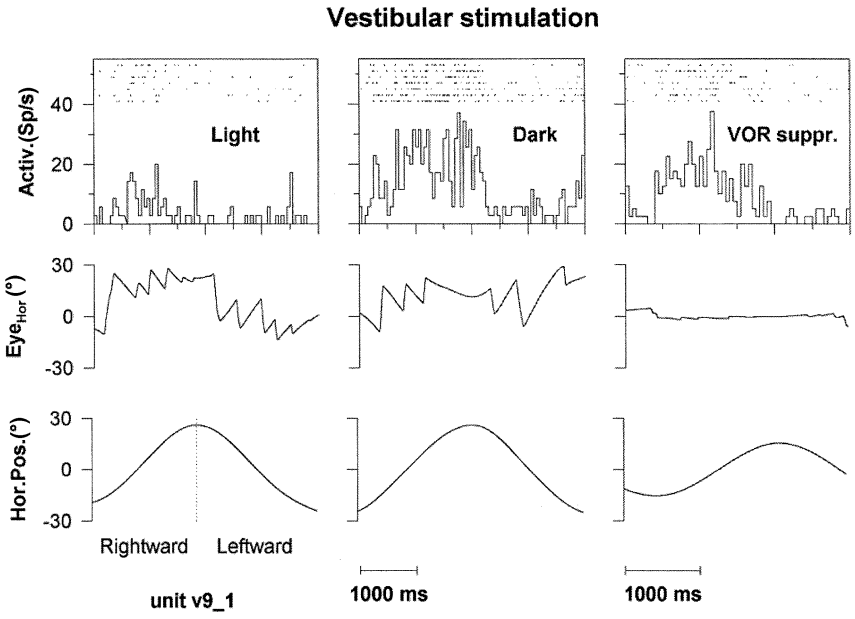

Figure 4. Vestibular responses in area VIP. The top row shows the responses of a single VIP neuron to vertical axis rotation in light (left), in darkness (middle), and during VOR suppression (right). Sample eye position traces are shown in the middle row for the respective conditions. The chair positions during these movements are shown in the bottom row. This cell preferred rightward movement in all three conditions.

with the same speed (typically 27°/s or 40°/s) around its own centre of motion. Accordingly, this paradigm allows for covering the full frontoparallel stimulus space during a single trial.

Interestingly, preferred directions for visual and for vestibular stimulation were always co-aligned. In other words: In case a VIP neuron preferred real rotational movement to the right the horizontal component of the preferred direction was also directed to the right and vice versa (Figure 5). This is opposite to what one would expect and what one finds, e.g., in vestibular brain stem neurons. This is because the net retinal flow during vestibular driven compensatory eye movements for rotations in light is opposite to the rotation direction. Yet, all VIP neurons investigated in our study showed this nonsynergistic response characteristic. Considering geometrical properties (Bremmer et al., 2002b), we showed earlier that such a coalignment of visual and vestibular on-directions was necessary to encode the retinal image motion of objects in near-extrapersonal space during goal directed forward motion. A recent study indeed revealed such an overrepresentation of the encoding of motion in near-extra personal space in area VIP (Bremmer & Kubischik, 1999).

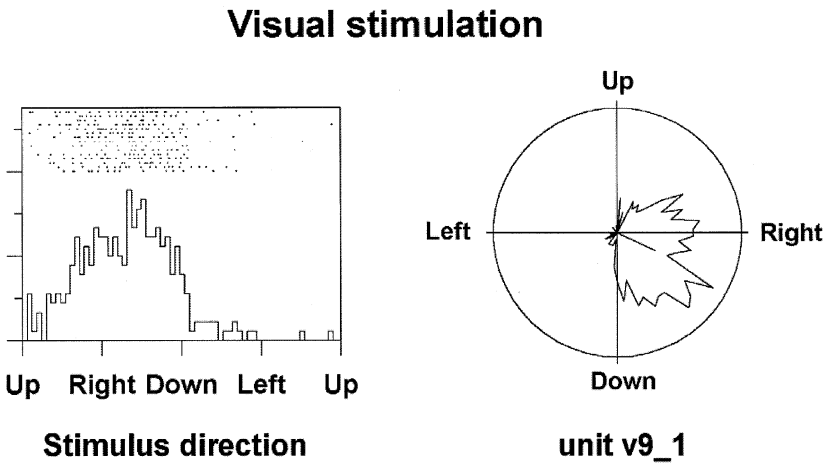

Figure 5. Directional selectivity for visual stimulation. The left panel indicates the directional selectivity of a cell to optic flow simulation movement within the frontoparallel plane. The right panel shows the very same response in a polar plot. It becomes immediately obvious that this cell preferred frontoparallel motion to the right and slightly downward.

In a second study, VIP neurons were tested for their responsiveness to linear translation (Schlack et al., 2002). Again, experiments were performed either in light or in total darkness. Monkeys were moved sinusoidally on a parallel swing with the eyes covered with a light-tight windshield during experiments in darkness. Three quarters of the neurons responded to pure vestibular stimulation, i.e., linear forward or backward translation in darkness. Responses were often tuned for the direction of the movement. Yet, preferred directions for the vestibular stimulation coincided with the preferred direction for visually simulated self-motion (expansion vs. contraction stimuli) only in about half of the cases. For those cells with opposite visual and vestibular on-directions, preferred directions during bimodal stimulation were dominated equally often by the visual and vestibular modality. This response characteristic for linear translational movements is somewhat similar to the one described for area MST (Duffy, 1998).

TACTILE AND AUDITORY RESPONSES

In addition to visual and vestibular information, also somatosensory and auditory signals can be used as to signal self-motion. Interestingly, many neurons in area VIP are responsive to tactile stimulation (Colby et al., 1993; Duhamel et al., 1991; Duhamel, Colby, & Goldberg, 1998). Most VIP cells that have a somatosensory RF respond well to stimulation of restricted portions of the head. Tactile and visual RFs are organized in an orderly manner. Central visual RFs

are matched to small tactile RFs around the lips and nose and large peripheral visual RFs are associated with large tactile RFs on the side of the head or body. Importantly, the matched tactile and visual RFs often demonstrate coaligned or antialigned direction selectivity.

Finally, a recent study demonstrated VIP responses to auditory stimuli (Schlack, Sterbing, Hartung, Hoffmann, & Bremmer, 2000). In these experiments, single unit activity was recorded during exposure to auditory and visual stimuli. Receptive fields in the two sensory domains tended to be spatially congruent, i.e., a neuron with an RF located, e.g., in the upper left quadrant was very likely to respond to auditory stimuli in the upper left part of space.

The function of such multisensory responses is only partially understood. There may be an advantage of representing together sensory patterns that are strongly correlated because they are likely to have a common origin in the external world. As an example, congruent optical and tactile/auditory flow arises when the animal navigates in dense vegetation. Based on this enlarged set of sensory information, self-motion could be guided more reliably.

HUMAN BRAIN AREAS INVOLVED IN THE PROCESSING OF SELF-MOTION INFORMATION

Neuropsychological studies of patients with inferior parietal cortex lesions often reveal strong impairments of attentive sensorimotor behavior (for review see, e.g., Driver & Mattingley, 1998; Vallar, 1998). Such patients frequently show symptoms like hemispatial neglect or extinction. Interestingly, these behavioural deficits occur across different sensory modalities and are often organized in head- or body-centred coordinates (for review see, e.g., Halligan, Fink, Marshall, & Vallar, 2003).

We considered these neuropsychological data as potential evidence for the existence of a polymodal area in human parietal cortex representing visual spatial information in a nonretinocentric frame of reference. As shown above, area VIP in the macaque contains many neurons that show multisensory directionally selective discharges, i.e., these neurons respond to moving visual, vestibular, tactile, or auditory stimuli. Many of these neurons also encode sensory information from different modalities in a common, probably head-centred, frame of reference (Duhamel, Bremmer, BenHamed, & Graf, 1997). We therefore tested for the existence of a functional equivalent of the macaque area VIP in normal human subjects by means of functional MRI measurements.

The test for the existence of ‘‘human area VIP’’ was based on the above described responses to multisensory motion stimuli (Bremmer et al., 2001). In this functional MRI experiment subjects experienced visual (large random dot pattern), tactile (airflow), or auditory (binaural beats) motion stimuli or a stationary control.

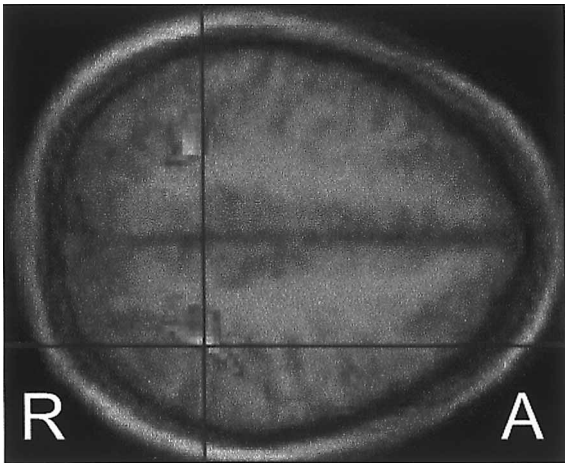

Figure 6. Identification of a parietal region activated by visual, tactile, and auditory motion. The bilaterally activated region in the depth of the intraparietal sulcus is shown in a horizontal section. ''R'' indicates the right hemisphere (A: anterior). Significance of activation is colour coded, with yellow/white corresponding to highest significance values. The anatomical image is the average anatomical MRI from the eight subjects involved in this study.

Spatially circumscribed, strong cortical activation ($p < .05$, corrected) was found for each individual stimulus condition. Conjunction analysis revealed cortical structures activated by all three modalities, i.e., vision, touch, and audition. Bilateral activation was found in three circumscribed cortical regions, one of which was located in parietal cortex (Figure 6). By superimposing the functional images on the average anatomical brain originating from the eight subjects it was possible to identify the activated region as the depth of the intraparietal sulcus. Accordingly, it is suggested that this area constitutes the human equivalent of monkey area VIP.

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