RESEARCH NOTE

J. K. Hietanen · D. I. Perrett

A comparison of visual responses to object- and ego-motion in the macaque superior temporal polysensory area

Abstract The responses of visual movement-sensitive neurons in the anterior superior temporal polysensory area (STPa) of monkeys were studied during object-motion, ego-motion and during both together. The majority of the cells responded only to the image of a moving object against a stationary background and failed to respond to the retinal movement of the same object (against the same background) caused by the monkey's ego-motion. All the tested cells continued responding to the object-motion during ego-motion in the opposite direction. By contrast, most cells failed to respond to the motion of an object when the observer and object moved at the same speed and direction (eliminating observer-relative motion cues). The results indicate that STPa cells compute motion relative to the observer and suggest an influence of reference signals (vestibular, somatosensory or retinal) in the discrimination of ego- and object-motion. The results extend observations indicating that STPa cells are selective for visual motion originating from the movements of external objects and unresponsive to retinal changes correlated with the observer's own movements.

Key words Visual ego-motion · Object-motion · Superior temporal polysensory area · Macaque monkey

Introduction

It has long been recognised that the visual system must distinguish object-motion characteristics, which help define object identity and actions of other animate objects, from self-induced visual motion, which helps define the actions of the observing organism (von Helmholtz 1911; von Holst and Mittelstaedt 1950; Gibson 1966). The di-

J. K. Hietanen[1] · D. I. Perrett (✉)
School of Psychology, University of St Andrews, Scotland, KY16 9JU, UK

Present address:
[1] Department of Psychology, P.O. Box 607, FIN-33101 University of Tampere, Finland

chotomy between the ego- and object-motion types of image motion characteristics is reflected in the organisation of the visual motion processing system. Neurophysiological single-unit recordings using artificial stimulus displays have provided evidence that visual cues relating to ego-motion and object-motion are processed by separate visual systems. The dorsal part of the medial superior temporal area (MSTd) of primates has been shown to contain cells that prefer the movement of a wide field of elements to movement of a small object, suggesting thus a functional role in visual detection of ego-motion (Tanaka et al. 1986; Saito et al. 1986; Tanaka and Saito 1989; Duffy and Wurtz 1991a, b). Neurons particularly suitable for signalling object-motion have been described in the superior colliculus (Bender and Davidson 1986), middle temporal area (MT) and ventral part of the medial superior temporal area (MSTv; Allman et al. 1985; Saito et al. 1986; Tanaka et al. 1986; Sugita et al. 1990) in monkey. These cells exhibit response preferences for a local stimulus movement in one direction against a stationary background.

In natural three-dimensional environment the visual attributes typifying ego-motion and object-motion are, however, far from clearly separated. For example, local discontinuities in the velocity field at the edges of objects are not produced solely by the movement of the objects but also by the movement of the observer. When a stationary object and background elements are located at different distances from the observer, then any ego-motion (translation) will produce motion of the object's image relative to that of the background elements. These configurational changes in the retinal image are called object-relative motion cues. Observer-relative motion cues are based on image displacement across the retina and smooth pursuit eye movements made in tracking the moving object. A pure form of observer-relative motion can be achieved in darkness by witnessing movements of a luminous spot of light. The observer's own egocentre is used as a frame of reference in attributing the motion. Observer-relative motion cues (i.e. retinal image displacement) can be identical, independent of whether the

image motion results from object-motion or from the movements of the observer's eyes with a stationary object. In natural conditions, of course, the visual system is frequently affected by situations in which it must be able to detect object-motion during simultaneous ego-motion.

The present study investigates the response properties of the cells in the anterior region of the dorsal bank of the macaque superior temporal sulcus (STPa) during object-motion, ego-motion and both occurring concurrently. The general response properties, directional tuning of the motion-sensitive cells and the relationship of STPa to other cortical motion processing areas have been described previously (Oram et al 1993).

Materials and methods

Extracellular single-unit activity was recorded from four rhesus monkeys (*Macaca mulatta*; two females and two males). The basic methods for recording extracellular single-unit activity and horizontal and vertical eye movement have been described elsewhere (Hietanen and Perrett 1993a; Oram et al. 1993). Quantitative measurements of cell responses were collected, based on the neuronal spike activity during a 250-ms time period collected 100 ms after the onset of the visual stimulation. The data were usually collected from five stimulus presentation cycles (in pseudo-random order) in each condition, and these data were analysed by using one-way ANOVA and post-hoc tests (protected least-significant difference, PLSD; Snedecor and Cochran 1980).

After isolating a cell, its response to various (static and moving) visual stimuli was tested using a large-field shutter (rise time <15 ms) through which the stimuli were presented. Only cells with responses to motion in the horizontal plane (left, right, towards or away from the monkey) were selected for further testing. After the cell's response for stimulus movement was established, neuronal responses were collected in a testing protocol which comprised the following stimulus conditions (see Fig. 1): (a) moving an object in the cell's preferred direction (monkey stationary); (b) moving the monkey in the opposite direction (object stationary); (c) moving the object in the cell's preferred direction while moving the monkey in the same direction and same speed (minimizing/eliminating relative movement between the monkey and the object); (d) moving the object in the cell's preferred direction while moving the monkey in the opposite direction; and (e) presenting a static object to a stationary monkey. The monkey's movement (ego-motion) was produced by moving the primate chair in which the monkey was sitting during experiments. The primate chair was located on top of a mobile trolley, which made it possible to move the monkey smoothly either to the left and to the right or forwards and backwards.

Responses were collected by presenting the stimuli through a shutter for 1 s.The onset of the stimulus movement or the monkey's movement was synchronized with the onset of the tone signal, which preceded the shutter opening by 500 ms, and the movement continued for the whole period of time while the shutter was open. The moving (or static) stimulus used in the majority of tests was the experimenter's head and upper body (for ease of matching conditions a-d). To produce an object motion, the experimenter translated his head/upper body at a distance of approx. 1 m in front of the monkey. At this proximity the monkey could not see the experimenter's lower body through the shutter aperture. This ensured that the appearance of the stimulus was the same for object-motion and self-motion conditions. In the testing condition c, this arrangement also provided a simple and accurate way of eliminating relative movement between the monkey and the object, as the experimenter could easily move the trolley while keeping the distance between his body and the monkey unchanged. In other conditions the trolley was moved by an assistant with a speed comparable with that of the object (experimenter) movement. The
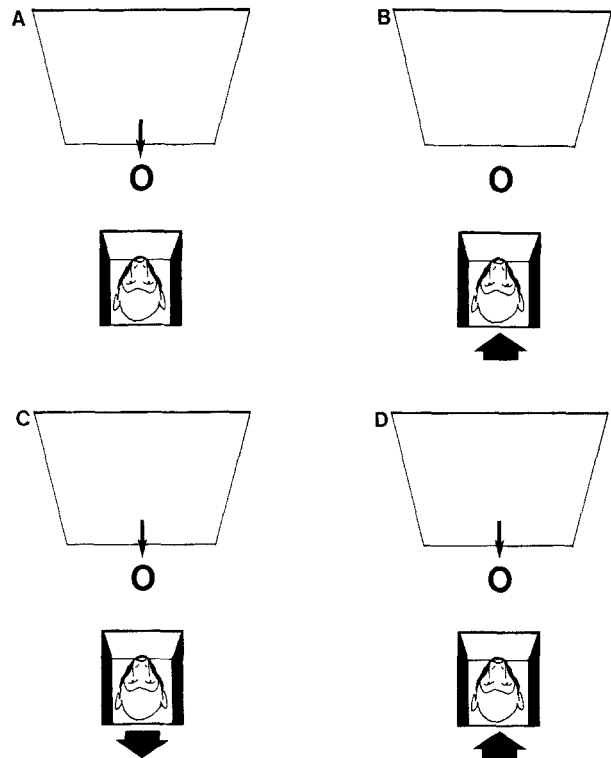

Fig. 1 An example of the different stimulus conditions used for testing a cell which prefers approaching movement of an object. The *trapezoid shape* indicates an object (*O*) which moves relative to the monkey's head. *Small arrows* indicate the direction of object movement, and *big arrows* indicate the movements of the monkey. Absence of an arrow indicates a stationary object or monkey. See text for a more detailed description of the conditions

velocity of the object motion or monkey's ego-motion was approximately 1 m/s in all the experiments.

Results

Nineteen movement-sensitive cells were tested for their response to the image motion resulting from object-motion and from ego-motion. Sixteen out of nineteen cells exhibited statistically stronger responses to the sight of an object movement than to the sight of visual motion that resulted from the monkey's ego-motion. In fact, for the 16 cells, the responses to an objectively stationary object during ego-motion never exceeded those observed during the presentation of a static object to a stationary monkey. Figure 2 depicts the results of experiments with one cell which discriminated between object-motion and visual ego-motion. Three out of the nineteen cells failed to show any discrimination between object-motion and visual self-motion in their responses; these 3 cells exhibited comparable responses in both conditions.

An important question was whether the cells continued responding to the object-motion during concomitant ego-motion. Nine out of the sixteen cells which discriminated between object-motion and ego-motion were also tested with the object moving in the cell's preferred di-

Fig. 2 Responses of one cell to the sight of a retreating object. The cell failed to respond to visual motion, which was achieved by moving the monkey away from a static object with the same speed. The response to the object-motion was significantly stronger (PLSD; $P<0.0005$) than the responses during self-motion or during static object presentation. There was no difference in responses in between the two latter stimulus conditions ($P>0.3$). (ANOVA $F_{2,12}=124.4$, $P<0.0005$, $n=5$ in each condition.) The peristimulus rastergrams present the neuronal spike activity collected from five interleaved trials and the histograms above each show an averaged activity from these trials (bin width 20 ms). The *arrowheads* below the time axes denote the onset of visual stimulation. *Scale bars* at the *lower right* scale the response (spikes/second) and time (milliseconds)
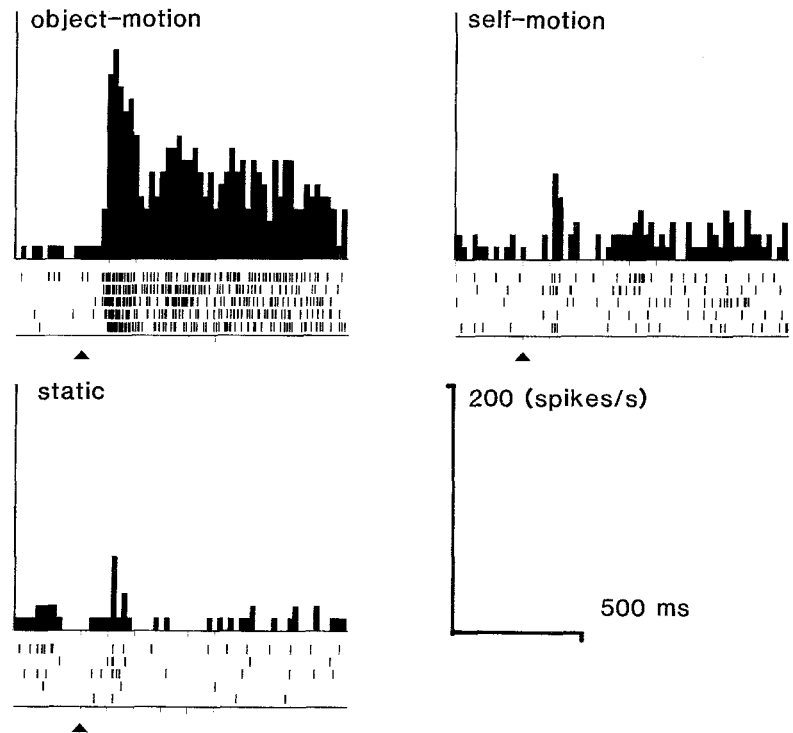
rection while the monkey was moved simultaneously in the opposite direction. So, for example, if a cell was found to be responsive to object movement to the left (and not responding when the object was static but the monkey was moved right), the cell was tested with the object moving to the left while the monkey was moved to the right at the same time. All nine tested cells continued to be responsive to the object-motion during ego-movement in the opposite direction In seven of the nine cells tested this way, the responses were indistinguishable from those obtained during object-motion only.

Thirteen cells were tested for object-motion together with movement of the monkey in the same direction. Ten cells failed completely to respond in this condition. For example, a cell which responded strongly to the sight of a retreating object did not respond, however, when the monkey was moved together with the object while keeping the distance between the object and the monkey fixed. This indicated that the cell was not driven by the object-relative motion cues (uncovering of the background texture elements, for example) but by the motion relative to the observer. This hypothesis was further confirmed with one cell tested in the darkness. Despite the elimination of the background, the cell responded to object-motion but not ego-motion. The remaining 3 cells (of the 13 tested) exhibited indistinguishable responses in the object-motion and combined object-ego-motion conditions, suggesting thus that the cells were driven by the cues resulting from the relative motion between the object and its background. For one of these cells this hypothesis was also supported by the results from tests carried out in a darkened room by moving an illuminated object in the cell's preferred direction. In this situation,

the elimination of the object-relative motion cues abolished the responses to object-motion in the cell's preferred direction.

For all of the cells recorded, inspection of the eye movement records and cell responses never suggested that the cell responses were linked with the occurrence of saccades, smooth pursuit movements or fixation onsets. Typically, the eye movement recordings revealed that the monkey did not execute systematic pursuit movements tracking the object on every trial during object-motion or ego-motion. Despite comparable variation in eye movements across stimulus conditions, neural responses were reliably different.

Discussion

The main result of the present experiment was that STPa differentiates between visual motion that results from movements of external (animate or inanimate) objects and movements of self. To our knowledge, this is the first experiment to study visual responsiveness in cortical motion processing areas to stimulus motion which results from *actual* movements of the animal.

The results showed that all the tested cells continued responding to the object-motion during simultaneous ego-motion *when relative motion between the object and monkey was also present*. By contrast, the majority of the tested cells which discriminated between object-motion and ego-motion did not exhibit responses to the object-motion when the observer-relative motion was eliminated by moving the monkey together with the object in the same direction. Admittedly the object-relative cues differ

slightly in these two testing situations. This difference, however, should not have produced any significant effect on the cell responses, as the responses were found (Oram et al. 1993) to be tolerant for the variation in stimulus speed within a range that well exceeded the differences present in object-relative velocity fields between the two testing conditions.

The interesting question is what kind of information is used for the observed response discrimination between object-motion and ego-motion? The results showed that the motion-sensitive STPa cells are driven by the observer-relative motion visual cues. The observer-relative cues do not differ, however, between object-motion and ego-motion. How, then, is the discriminative response capacity between object-motion and ego-motion realized? It is suggested that the response discrimination in STPa must be based in part on extraretinal factors. Under natural environmental conditions the visual system does not work in isolation, but interacts with other sensory systems active during ego-motion. Neurophysiological single-unit studies have shown that ego-motion signals from different sensory systems combine in vestibular nuclei (Waespe and Henn 1977), thalamus (Büttner and Lang 1979), area 2v in the anterior parts of the intraparietal sulcus (Büttner and Lang 1979), areas 7a and 7b in the posterior parietal cortex (Pause and Schreiter 1980; Kawano et al. 1984) and parieto-insular vestibular cortex (PIVC) in the upper bank of the lateral sulcus (Grüsser et al. 1990). STPa has been shown to receive direct projections from areas 7a and 7b (Seltzer and Pandya 1984; Morel and Bullier 1990).

The results from previous experiments (Hietanen 1993, Hietanen and Perrett 1993a, b) suggested that motor/proprioceptive input inhibits responses to visual stimulation that results from the monkey's own actions (i.e. the sight of the monkey's own arm movements or arbitrary patterns moved by the monkey). In the present experiments, the possibility of motor input influencing cell responses can be ruled out quite confidently, whereas the vestibular-visual and/or somatosensory-visual interactions seem potential candidates for providing a physiological mechanism for the response discrimination between visual responses to object-motion and ego-motion. It should be remembered that, in natural conditions when the animal is actively locomoting, motor (corollary discharge) signals could have an additional influence on this discriminative neural capacity. However, in conditions with adequate illumination, the retinal signals may well contribute to the response discrimination as well. Wertheim (1994) has recently suggested that the concept of "extraretinal signal" should be displaced by the term "reference signal", which is a compound signal including an efference copy, a vestibular and a visual component. Thus in the present experiment the visual whole-field flow during ego-motion may have provided a reference signal against which the observer-relative object motion signals were evaluated.

In conclusion, the present experiments suggest that the direction of motion is predominantly represented in an egocentric frame of reference in STPa and that one of the major functions of this area in motion processing is to detect object-motion that is not caused by the animal's own body movements. The cell responses seem to be a product of a two-step computation. The cells respond if (1) there are observer-relative visual motion cues present, and (2) the presence of these cues cannot be explained by the reference signals accompanying the ego-motion. These results provide further evidence for STPa's role in processing preferentially "unexpected" stimulation and ignoring "expected" sensory consequences which result from one's own actions (Mistlin and Perrett 1990; Hietanen and Perrett 1993a, 1996).

References

Allmann J, Miezin F, McGuinness E (1985) Stimulus specific responses from beyond the classical receptive field: neurophysiological mechanisms for loco-global comparison in visual neurons. Ann Rev Neurosci 8: 407–430

Bender DB, Davidson RM (1986) Global visual processing in the monkey superior colliculus. Brain Res 38: 372–375

Büttner U, Lang W (1979) The vestibulocortical pathway: neurophysiological and anatomical studies in the monkey. Prog Brain Res 50: 581–588

Duffy CJ, Wurtz RH (1991a) Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. J Neurophysiol 65: 1329–1345

Duffy CJ, Wurtz RH (1991b) Sensitivity of MST neurons to optic flow stimuli. II. Mechanisms of response selectivity revealed by small-field stimuli. J Neurophysiol 65: 1346–1359

Gibson JJ (1966) The senses considered as perceptual systems. Houghton Mifflin, Boston

Grüsser O-J, Pause M, Schreiter U (1990) Vestibular neurones in the parieto-insular cortex of monkeys (Macaca fascicularis): visual and neck receptor responses. J Physiol (Lond) 430: 559–583

Helmholtz H von (1911) Physiological optics. (Translation edited by J.P.C. Southall, 1962) Dover, New York

Hietanen JK (1993) Unpublished Ph.D thesis, St Andrews University, Scotland

Hietanen JK, Perrett DI (1993a) Motion sensitive cells in the macaque superior temporal polysensory area. I. Lack of response to the sight of the animal's own limb movement. Exp Brain Res 93: 117–128

Hietanen JK, Perrett DI (1993b) The role of expectation in visual and tactile processing within temporal cortex. In: Ono T, Squire LR, Raichle ME, Perrett DI, Fukuda M (eds) Brain mechanisms for perception and memory: from neuron to behaviour. Oxford University Press, Oxford, pp 83–103

Hietanen JK, Perrett DI (1996) Motion sensitive cells in the macaque superior temporal polysensory area: response discrimination between self-generated and externally-generated pattern motion. Behav Brain Res. (in press)

Holst E von, Mittelstaedt H (1950). Das reafferenzprinzip (Wechselwirkungen zwischen zentralnervensystem und peripherie). Naturwissenschaften 37: 464–476

Kawano K, Sasaki M, Yamashita M (1984) Response properties of neurons in posterior parietal cortex of monkey during visual-

vestibular stimulation. I. Visual tracking neurons. J Neurophysiol 51: 340–351

Mistlin AJ, Perrett DI (1990) Visual and somatosensory processing in the macaque temporal cortex: the role of expectation. Exp Brain Res 82: 437–450

Morel A, Bullier J (1990) Anatomical segregation of two cortical visual pathways in the macaque monkey. Vis Neurosci 4: 555–578

Oram MW, Perrett DI, Hietanen JK (1993) Directional tuning of motion sensitive cells in the anterior superior temporal polysensory area of the macaque. Exp Brain Res 97:274–294

Pause M, Schreiter U (1980) Neurons in the parietal cortex (area 7b) of behaving monkeys activated by vestibular stimulation (abstract). Neurosci Lett [Suppl] 5: S281

Saito H, Yukie M, Tanaka K, Hikosaka K, Fukada Y, Iwai E (1986) Integration of direction signals of image motion in the superior temporal sulcus to the macaque monkey. J Neurosci 6: 145–157

Seltzer B, Pandya DN (1984) Further observations on parieto-temporal connections in the rhesus monkey. Exp Brain Res, 55: 301–312

Snedecor GW, Cochran WG (1980) Statistical methods, 7th edn. Iowa State University Press, Ames, Iowa

Sugita Y, Tanaka K, Saito H (1990) Analysis of object motion in the macaque ventral MST area. In: Iwai E, Mishkin M (eds) Vision, memory and the temporal lobe. Elsevier, New York, pp 341–346

Tanaka K, Hikosaka K, Saito H, Yukie M, Fukada Y, Iwai E (1986) Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. J Neurosci 6: 134–144

Tanaka K, Saito H (1989) Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. J Neurophysiol 62: 626–641

Waespe W, Henn V (1977) Neuronal activity in the vestibular nuclei of the alert monkey during vestibular and optokinetic stimulation. Exp Brain Res 27: 523–538

Wertheim AH (1994) Motion perception during self-motion: the direct versus inferential controversy revisited. Behav Brain Sci 17: 293–355