'Real-motion' cells in area V3A of macaque visual cortex

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Summary. The stability of visual perception despite eye movements suggests the existence, in the visual system, of neural elements able to recognize whether a movement of an image occurring in a particular part of the retina is the consequence of an actual movement that occurred in the visual field, or self-induced by an ocular movement while the object was still in the field of view. Recordings from single neurons in area V3A of awake macaque monkeys were made to check the existence of such a type of neurons (called 'real-motion' cells; see Galletti et al. 1984, 1988) in this prestriate area of the visual cortex. A total of 119 neurons were recorded from area V3A. They were highly sensitive to the orientation of the visual stimuli, being on average more sensitive than V1 and V2 neurons. Almost all of them were sensitive to a large range of velocities of stimulus movement and about one half to the direction of it. In order to assess whether they gave different responses to the movement of a stimulus and to that of its retinal image alone (self-induced by an eye movement while the stimulus was still), a comparison was made between neuronal responses obtained when a moving stimulus swept a stationary receptive field (during steady fixation) and when a moving receptive field swept a stationary stimulus (during tracking eye movement). The receptive field stimulation at retinal level was physically the same in both cases, but only in the first was there actual movement of the visual stimulus. Control trials, where the monkeys performed tracking eye movements without any intentional receptive field stimulation, were also carried out. For a number of neurons, the test was repeated in darkness and against a textured visual background. Eighty-seven neurons were fully studied to assess whether they were real-motion cells. About 48% of them (42/87) showed significant differences between responses to stimulus versus eye movement. The great majority of these cells (36/42) were real-motion cells, in that they showed a weaker response to visual stimulation during tracking than to the actual stimulus movement during steady fixation. On average, the reduction in visual response during eye movement was 64.0 ± 15.7% (SD). Data obtained with a uniform visual background, together with those obtained in darkness and with textured background, indicate that real-motion cells receive an eye-motion input, either retinal or extraretinal in nature, probably acting presynaptically on the cell's visual input. In some cases, both retinal and extraretinal eye-motion inputs converge on the same real-motion cell. No correlation was observed between the real-motion behaviour and the sensitivity to either orientation or direction of movement of the visual stimulus used to activate the receptive field, nor with the retinotopic location of the receptive field. We suggest that the visual system uses real-motion cells in order to distinguish real from self-induced movements of retinal images, hence to recognize the actual movement in the visual field. Based on psychophysical data, the hypothesis has been advanced of an internal representation of the field of view, stable despite eye movement (cf. MacKay 1973). The real-motion cells may be neural elements of this network and we suggest that the visual system uses the output of this network to properly interpret the large number of sensory changes resulting from exploratory eye movements in a stable visual world.

Key words: Visual cortex – Area V3A – Motion analysis – Visual stability – Objective map – Macaque

Introduction

The perception of movement in the visual world may be the result of the movement of images on the retina but this is certainly not always the case. It is so when the head and eyes are still, but not so when either the head or eyes, or both, are moving. Visual tracking of a moving object, for example, gives a sensation of movement of the followed object despite the stillness of its image on the retina. Hence, a question arises: what does the visual system take into account in order to give a proper evaluation of motion in the visual field? Many experimental data suggest that it must take into account at least two different

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kinds of inputs: the retinal image movement and the
eye/head movement (the movement of "gaze").

Striking evidence that the visual system uses a gaze-
movement signal to evaluate actual motion in the visual
field comes from psychophysical experiments on afterim-
ages. It has been reported that a long-lasting afterimage
appears motionless when it is viewed in complete darkness
and the eyes are still, or moved passively, but as moving
when the eyes move actively, either during saccadic or
slow pursuit movements (Mack and Bachant 1969;
Grüsser and Grüsser-Cornehls 1973). Further evidence
comes from the work of Brindley and Lewin (1968), who
used occipital electrodes in a blind woman to generate
phosphene movements which were perceived as spots of light having a
well-defined external location. The subject reported that
the phosphene seemed to move with her eyes whenever
she made an eye movement, just as afterimages did in the
above described experiments. Finally, it has been reported
that if the eyes are mechanically (Mach 1886; Brindley
and Merton 1960), pharmacologically (Kornmuller 1931;
Hammond et al. 1956) or pathologically (Helmholtz 1909;
Hughlings Jackson 1932) immobilized, the attempt to
move them gives a sensation of movement of the objects
present in the visual field.

In all the cases described above, there is a retinotopic-
ally "stable" neural stimulation associated with a percep-
tion of movement in the visual field. It is evident that in all
these cases the perceptive process does not depend on a
retinal image movement, which is in fact lacking, but on
performing an active ocular movement, or even the inten-
tion to make it. The perception of visual movement in such
situations also suggests that the perceptive process does
not depend on the stimulation of spatially separated
receptive fields in a temporal sequence. Indeed, the stimu-
lation of the same retinal locus, when associated with an
active ocular movement or the intention to make one,
gives the sensation of movement in the visual field. This
means, we believe, that the visual system has particular
"sensors" for detection of the actual movement in visual
space, uniformly distributed to cover the whole extent of
the visual field. These neural elements, in order to work as
sensors of the actual movement, must receive at least the
two inputs previously mentioned, one relative to the
movement of the retinal image impinging upon their
receptive field, and the second carrying information about
the movement of gaze. Neurons of this type should be able
to recognize whether a movement of an image occurring in
a particular part of the retina has been the consequence of
an actual movement in the visual field, or self-induced by
an ocular movement, while the object was still in the field of
view. Cells of this type, which we have called "real-
motion" cells, have been found in a small percentage
(10–15%) in both areas V1 and V2 of macaque visual
cortex (Galletti et al. 1984, 1988). Results reported here
show that in area V3A (a prestriate area of the monkey
visual cortex, see Van Essen and Zeki 1978), more than 40%
of the neurons are real-motion cells, and receive a
signal of gaze movement which can be either retinal or
extraretinal in nature. Brief reports on these results have
previously appeared (Aicardi et al. 1987).

Material and methods

Experiments were carried out on five juvenile macaque monkeys
(Macaca fascicularis) whose weight ranged from 2.5 to 3.5 kg.
Extracellular recordings were made in the visual cortex of seven
hemispheres. The behavioural and electrophysiological methods
used are described in detail elsewhere (Galletti et al. 1984). Briefly,
animals sat in a primate chair facing a tangent screen, 80 °x 80 deg
in extent, 57 cm in front of their eyes. They learned to fix a small (0.2 deg)
spot of light (fixation spot), delivered for 0.5 to 5 s either stationary,
or moving all over the screen, without taking into account any other
visual stimulus concurrently presented on the same screen. When
well trained, they were preanesthetized with ketamine hydrochlor-
ide i.m. and then deeply anaesthetized with sodium pentobarbital i.v.
A metal holder device for subsequent head restraining was implanted
on the skull, and a search coil was implanted under the conjunctiva
of one eye, in order to record eye movement using the technique
described by Robinson (1963) and improved as suggested by Judge
et al. (1980). After recovery from surgery, animals were retrained
with the head restrained and were, then reanaesthetized to implant a
stainless steel recording chamber on the skull. Recording sessions
began after complete recovery from surgery and were performed 5
days/week for several months. Once recordings in one hemisphere
were finished, a second chamber was implanted on the other side and
recording sessions restarted. Aspetic precautions were observed
throughout, and monkeys were returned to their home cages after
each experimental session.

Single unit activity was recorded by glass-coated Eligiloy micro-
electrodes (Suzuki and Azuma 1976) guided into the visual cortex
through the intact dura by a remote controlled electrical microdrive
mounted daily on the recording chamber. Once a neuron was
isolated, its receptive field was carefully mapped by visual stimuli
back-projected on to the screen. Circular and rectangular di-
aphragms were used to produce spots of light of different size, and bars
of light of different length, width and orientation. The light intensity of
the stimuli, which was usually 1 Log unit above the level of a white
uniform background of 1 to 2 cd/m², could be varied by neutral
density filters. Coloured stimuli, matched for brightness, were pro-
duced by broadband filters to which appropriate neutral density filters
had been added. The fixation spot and the visual stimuli used to
map receptive fields were obtained using two separate optical
systems, so both could be positioned anywhere on the screen by
mirror galvanometers and moved in any direction at speeds up to
about 1000 deg/s.

The collection, storage and analysis of data, together with the
control of the sequences of visual stimulation during both training
and recording sessions, were performed with a personal computer.
The sample rate for action potential was 0.5 ms, that for eye position
5 ms. The computer automatically discarded trials where the animals
performed inaccurate behavioural operations, while trials where the
animal's fixation or eye tracking was inadequate were discarded by
the operator. Details about data collection and storage procedures
have been described elsewhere (Battaglini et al. 1984).

In order to test whether a neuron was a real-motion cell, a
standard visual stimulation was used. It consisted of three blocks of
10–20 trials each. In the first, the animal gazed at the fixation spot,
motionless at the center of the screen, while a visual stimulus of
suitable form, colour, orientation, direction and velocity of move-
ment swept across the cell receptive field. The velocity of the stimulus
was selected on the basis of the neuron's sensitivity to this parameter
(see Results). Generally, speeds of 1 or 10 deg/s were used. In the
second block of trials, the stimulus was motionless on the screen
while the animal tracked the fixation spot which moved at the same
velocity as the stimulus previously did, but in the opposite direction,
so that velocity and direction of the relative movement between
stimulus and receptive field were the same in the two cases. Even
though retinal stimulation was the same in the two blocks, an actual
movement in the visual field occurred only in the first. In the third
block, the animal tracked the fixation spot which moved on the
screen as in the second block, but the visual stimulus was not projected on the screen in order to test whether the ocular movement alone affected cell activity. In several cases, the standard stimulation was repeated in darkness and/or against a textured visual background consisting of thousands of black spots (each about 0.2 deg in size) uniformly distributed over the white screen, in order to test the influence on cell activity of retinal input from outside the receptive field.

Particular attention was paid to possible variation in the time of spike amplitude and/or cell excitability, sometimes repeating one, two or even all three blocks of stimulation. Moreover, we randomly changed the sequence of the blocks of trials for each unit studied and, at the end of standard stimulation, again checked receptive-field position and size, as well as orientation sensitivity of the cell.

Neuronal responses were calculated as the best peak frequency on ten BINS of 20 ms, by subtracting the background activity recorded before visual stimulation from the total activity during visual stimulation.

When recordings were finished, microelectrode penetrations were carried out at known coordinates and electrolytic lesions were made to locate them after histology. The animals were then deeply anaesthetized, pins were inserted into the brain at known coordinates and animals were killed with an overdose of pentobarbital. Brains were removed, sectioned and stained with cresyl-violet. Unmarked penetrations were reconstructed on the basis of their positions with respect to electrolytic lesions and pin tracks. More detailed information about surgery, histological technique and reconstruction of microelectrode penetrations have been reported in a previous paper (Galletti et al. 1984).

Results

General remarks

Neurons whose data are reported here were located in the annulare gyrus, which is buried within the lunate sulcus and occupies part of its floor. According to Van Essen and Zeki (1978), area V3A occupies most of this gyrus, while a little part of it is occupied by area V3. To decide whether neurons recorded from the annulare gyrus belonged to area V3 or V3A a series of data were taken into account: penetration coordinates within the chamber, shifts of receptive field location along the penetration, receptive field size and scatter as well as location of the penetration with respect to the markers (electrolytic lesions and pin tracks; see Material and Methods). A detailed description of this methodology has been reported elsewhere (Galletti and Battaglini 1989).

The total number of neurons taken into account for the present study is 119, all belonging to area V3A, with receptive field centers within 16 deg from the fixation point in the inferior contralateral quadrants of the visual field. Some of these neurons are the same as those reported in a previous study (Galletti and Battaglini 1989), to which the reader is directed for the analysis of relationship between receptive field size and eccentricity.

Almost all neurons turned out to be sensitive to the orientation of the visual stimulus. They gave strong, sustained responses to correctly oriented visual stimuli, no matter whether they were stationary on the receptive field or entered the receptive field from anywhere outside it. From this aspect, they looked like a sort of ‘form detector’, and this behaviour was a striking feature of V3A neurons. An attempt was made to quantify the range of orientation sensitivity of these neurons by testing, for each neuron, the range of stimulus orientation still evoking a neural response. The result was that, on 119 neurons tested, the mean range was ±42.6 deg (±18.3 SD) with respect to the preferred orientation. The same procedure was applied to the samples of orientation-sensitive neurons previously recorded from areas V1 and V2 (Galletti et al. 1984, 1988). The values obtained for these two areas were 50.4 deg ±24.8 SD and 50.1 deg ±24.8 SD, respectively. The ranges were not statistically different, as if the cells of the two areas belonged to the same neuronal population (Student’s t test: degrees of freedom = 188; t = 0.09). In contrast, the orientation sensitivity of these two areas was statistically very different from that of area V3A (degrees of freedom = 311; t = 2.97; p <0.005).

All V3A neurons were very sensitive to moving stimuli during animal’s steady fixation. About half of them (51%) were not sensitive to the direction of movement, but a quarter (26%) were direction-selective cells, in that they responded when the stimulus moved in one direction but not when it moved in the opposite one. As far as velocity sensitivity is concerned, almost all V3A neurons were well activated by stationary stimuli as well as by stimuli moving at various speeds, even at high speeds, faster than 50 deg/s. In several cases, neurons were still activated by speeds of hundreds of deg/s, so another striking feature of these neurons was to have a large range of speed sensitivity (more than 2 Log units). Detailed results concerning the velocity sensitivity of V3A neurons will be described in a later paper.

Real-motion cells

Out of the 119 neurons taken into account in this study, 87 were fully studied with the standard pattern of visual stimulation previously described in order to assess whether they were real-motion cells. For the remaining 32 cells either the real-motion test was not completed, or data had to be discarded off-line due to the occurrence of changes in excitability and/or characteristics of the cells before the end of the test (see Material and Methods), or because of inaccuracy in tracking eye movements.

About 48% of the tested neurons (42/87) showed significant differences between responses to stimulus versus eye movement. Figure 1 shows one of these cells. This neuron had a receptive field 3 deg × 4 deg in size, located at 8 deg from the fovea in the contralateral inferior quadrant of the visual field. It was an orientation selective cell, in that it showed a narrow range of orientation sensitivity (±35 deg with respect to the preferred orientation), and responded to both directions of stimulus movement. The responses in the two directions were both very weak when the receptive field was moved (by tracking) across the stationary visual stimulus. The reduction of the visual response during eye movement was 86% when the receptive field moved in one direction and 70% when it moved in the other. On average, this type of neuron showed
response reductions of $64.0 \pm 15.7\%$ (SD) during eye movement.

In many cases, as in that shown in Fig. 1, the animal first performed ten trials with the stimulus moving during steady fixation (the first ten trials shown in raster dots on the left), then twenty trials with the stimulus motionless during tracking eye movement (all the trials shown at the centre) and, finally, a further ten trials with the stimulus moving during steady fixation (the second ten trials on the left). Results were consistent in all the trials. Control trials (on the right) showed that in this case, as in the great majority of those studied, eye movement alone did not significantly alter the spontaneous activity of the cell.

Figure 2 shows a cell whose response to the actual stimulus movement was weaker than that to the receptive field movement across the stationary visual stimulus, that is just the opposite behaviour with respect to that shown in Fig. 1. Only six cells (7%) in our sample showed this behaviour. On average, their visual responses during steady fixation were reduced by $54.0 \pm 26.1\%$ (SD) with respect to those evoked during eye movement. The neuron shown in Fig. 2 had a receptive field 4 deg x 5 deg in size, located at 8 deg from the fovea, and was sensitive to the orientation of the stimulus but not to the direction of its movement, in that it gave about the same response for both directions. Control trials showed that, in this case, eye movement increases the spontaneous discharge rate of the cell.

About half of the tested neurons (45/87) were equally well activated either by the actual stimulus movement or
by the receptive field movement across the motionless stimulus. The mean difference between the visual responses in the two situations was $-1.8 \pm 16.3\%$ (SD), with the responses to stimulus movement considered equal to 100%. Figure 3 shows one of these neurons. It was sensitive to orientation of the stimulus and was direction selective, in that it gave a strong response to the stimulus moving in the preferred direction and no response at all to the stimulus moving in the opposite one. The receptive field was 6 deg $\times$ 6 deg in size, located 14 deg from the fovea. Control trials showed that, also in this case, eye movement increased the spontaneous discharge rate of the cell.

In the great majority of tested neurons (68/87) the spontaneous discharge rate was not affected by tracking eye movement alone, performed against a white, uniform visual background, as in the case shown in Fig. 1. About 15% of the neurons (13/87) increased their discharge rate during ocular movement, as shown in Figs. 2 and 3, while just about 7% of them (6/87) showed a decrease during eye movement.

Several V3A neurons which were tested for real-motion behaviour in the light, against a white and uniform visual background, were also tested in complete darkness. All neurons which were not real-motion in light also maintained the same behaviour in darkness. Some of the cells which were real-motion in light no longer showed this behaviour in darkness, although some others did. Figure 4 illustrates two examples of real-motion cells tested both in light and darkness. Unit 08147 maintained its real-motion behaviour also in darkness, while unit 08126 did not. In order to obtain the same visual response to the actual stimulus movement in the two experimental situations, the light intensity of the visual stimulus (and that of the

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**Fig. 3.** Response of a non-real-motion cell to the visual stimulation of its receptive field during steady fixation (STIMULUS MOVEMENT), visual tracking (EYE MOVEMENT) and during tracking eye movement without any visual stimulation on the receptive field (CONTROL). Other explanations as in Fig. 1.

**Fig. 4.** Responses of two real-motion cells to the visual stimulation of their receptive fields during steady fixation (STIMULUS MOVEMENT), visual tracking (EYE MOVEMENT) and during tracking eye movement without any visual stimulation on the receptive fields (CONTROL). Both units were tested against a uniform visual background (LIGHT) and in complete darkness (DARK). Markers under peristimulus time histograms indicate the beginning and end of stimulus (STIMULUS MOVEMENT) or fixation point (EYE MOVEMENT and CONTROL) movements.
Fig. 5. Responses of three different neurons to the visual stimulation of their receptive fields during steady fixation (STIMULUS MOVEMENT), visual tracking (EYE MOVEMENT) and during tracking eye movement without any visual stimulation on the receptive fields (CONTROL). Unit 08109 was a real-motion cell, unit 08094 showed just the opposite behaviour and unit 08108 was a non-real-motion cell (it is the same as the unit shown in Fig. 3). All three units were tested against a uniform visual background (UNIFORM) and a textured one (TEXTURED). Markers under peristimulus time histograms as in Fig. 4.

fixation spot) was decreased by neutral density filters in the dark series. In spite of this, a slight difference in visual responses between the two series may be observed (see in particular unit 08147).

Several V3A neurons tested for real-motion behaviour against a white and uniform visual background were also tested against a textured visual background consisting of thousands of black points uniformly distributed over a white surface. As shown in Fig. 5, the three types of cells we found with the above described standard stimulation maintained the same behaviour when tested against the textured visual background, although texture did affect their excitability in at least three different ways. First, a reduction in visual response was observed in about half of the studied neurons when using texture, both for actual stimulus movement and for receptive field movement across the stationary visual stimulus (see Fig. 5). Second, in several cases, the weakening of the visual response that real-motion cells show when the eyes move and the stimulus is still, was further increased when the test was performed against a structured visual background (Fig. 5, unit 08109). The same phenomenon was also seen when the cell response was weakened during actual stimulus movement instead of during eye movement. This time, it was the response to the actual movement that was further reduced (Fig. 5, unit 08094). Third, in about half of the studied neurons the change of visual background from uniform to textured increased the spontaneous activity of the cells, no matter whether they were real-motion or not.

No correlation at all was observed between real-motion behaviour and sensitivity to either orientation or direction of movement of the visual stimulus used to activate the receptive field. No correlation was observed with the retinotopic location of receptive field either: real-motion and non real-motion cells had receptive fields located throughout the inferior contralateral quadrant, from vertical to horizontal meridian and from 1 to 16 deg from the fovea. Finally, nothing can be said about a possible grouping of real-motion cells inside area V3A since our cell population is too small to permit an analysis of their laminar or columnar distribution.

Discussion

V3A neurons are highly sensitive to the orientation of visual stimulus, on average more sensitive than V1 and V2 neurons, and respond to properly oriented stimuli, entering the receptive field from anywhere outside it, with a strong, sustained discharge of action potentials. About half of them are sensitive to the direction of motion of the stimulus (a quarter are even direction selective). Almost all are sensitive to a large range of velocities of stimulus movement and more than 40% are real-motion cells, in
that they give a good response to actual movement in the visual field and a weaker response to equivalent movement of the retinal image, self-induced by eye movement. In addition to all these characteristics, we have recently found that the visual responsiveness of about one half of V3A neurons was influenced by the direction of gaze (Galletti and Battaglini 1989). All these data suggest that area V3A is involved in the analysis of form, as well as in visual motion detection and in the process of encoding spatial locations of the visual environment (see Galletti and Battaglini 1989). On this basis, area V3A cannot be allocated along a single functional stream (cf. Maunsell and Newsome 1987) because it seems to perform visual transformations that would be proper for at least three of them, namely form analysis, motion detection and space location. Instead, our data agree with the view of multiple segregation inside each prestriate area, which would allow the generation of separated visual "constructs" and their multistage integration, to be used for the process of perceptual categorization (Zeki and Shipp 1988).

**Neural mechanism for real-motion behaviour**

More than 40% of V3A neurons were real-motion cells. It might be that the different neuronal responses observed for stimulus versus eye movement were due to differential difficulty and/or attention required by the visual fixation and the tracking tasks. However, our monkeys performed equally well both tasks and had to pay constant visual attention on both of them in order to be rewarded. Hence, we believe that the real-motion behaviour can not be due to changes in difficulty and/or level of visual attention.

More reliably, the real-motion behaviour may be the result of either an inhibition of the visual response by an 'eye-motion' signal during eye movement, or a cellular facilitation due to a 'fixation' signal which enhances the visual response during steady fixation (hence when there is an actual stimulus movement in our experimental conditions). The same reasoning may be applied, although reversed, for the few cells showing the opposite behaviour with respect to the real-motion one.

Both 'eye-motion' and 'fixation' signals are widely represented ("tracking" and 'fixation' neurons, respectively) in cortical as well as subcortical targets of the visual system (Bizzi 1968; Lynch et al. 1977; Noda and Suzuki 1979; Suzuki et al. 1981; Schlag-Rey and Schlag 1984; Sakata et al. 1985; Komatsu and Wurtz 1988; Mustari et al. 1988; Thier et al. 1988). Since anatomical inputs to area V3A are still largely unknown at present, there is no reason to rule out the possibility that these signals can really reach V3A neurons.

Data from the literature may help to understand which of the two inputs at issue, eye-motion or fixation, may be the critical one in modulating real-motion cell responses. Fixation neurons are sensitive to the direction of gaze and/or to the depth of fixation point in the visual field, regardless of whether the target of gaze is stationary or moving in the field itself (Bizzi 1968; Lynch et al. 1977; Noda and Suzuki 1979; Schlag-Rey and Schlag 1984; Sakata et al. 1985). Hence, when the subject intentionally looks toward a particular part of the visual scene, a tonic discharge should be evoked by a number of fixation neurons both during steady fixation and tracking eye movement. It follows that the output from fixation neurons cannot be responsible for the real-motion behaviour, even though it might be responsible for other processes like the encoding of visual space in the field of view (Andersen et al. 1985; Galletti and Battaglini 1989). Real-motion behaviour should then be due to an eye-motion signal, which inhibits real-motion cells during pursuit eye movements.

Actually, in some cases we noted a decrease in the discharge rate of V3A neurons when the eye started to move in a tracking task (see, in particular, 'control' series). But this phenomenon involved a few V3A neurons (about 7%), and these cells were either real-motion or non-real-motion in nature. Most real-motion cells did not change their spontaneous activity during pursuit, and in some cases their activity was even increased during ocular movement. This suggests that the eye-motion signal responsible for real-motion behaviour does not directly act on real-motion cells; rather, it seems to selectively act on the visual input reaching that neuron. It might be a presynaptic modulation of the visual input to real-motion cells. Alternatively, the interaction between eye-motion and visual inputs might take place, pre- or post-synaptically, on upstream neurons which, in turn, project to real-motion cells. Real-motion cells were found in areas V1 and V2 (Galletti et al. 1984, 1988), where it was also found that eye-motion signal selectively inhibited the visual input. Cells with real-motion behaviour, although tested with saccadic instead of tracking eye movements, have also been found in the superior colliculus (Robinson and Wurtz 1976) and in the pulvinar (Robinson and Petersen 1985), but nothing can be said about the pre- or post-synaptic nature of the interaction at those levels.

The results obtained when the test for real-motion cells was performed in darkness or against a textured visual background allow some conclusions about the source of the eye-motion signal to real-motion cells. As a matter of fact, some cells which had real-motion responses in the light, did not show this behaviour in darkness. This implies that those cells received a retinal signal, responsible for their real-motion behaviour. In paralyzed animals, it has been found that neurons of several structures of the visual system have receptive fields with opponent centre-surround organization for directional selectivity (see Allman et al. 1985 for a review of this subject; see also Tanaka et al. 1986). These neurons show a strong inhibition of the response evoked by visual stimulation when motion in the surround is in the same direction as motion in the centre. During tracking eye movement in our experimental conditions, the relative movement of retinal images of both surround and visual stimulus are in the same direction, therefore the visual response might be reduced by this centre-surround mechanism. Certainly, a white and uniform visual background has no strong effect on the visual response of these neurons; as a matter of fact, the response was never completely suppressed when cells were tested in light. However, the fact that the use of textured background further decreases the visual response during eye
movement supports the view that these real-motion cells have a centre-surround mechanism for directional selectivity.

There were also real-motion cells in the light which remained so in darkness. In these cases, the signal responsible for real-motion behaviour had to be extraretinal in nature, but no direct evidence about the source of this input can be obtained from the present experiments. It is probable that some real-motion cells receive both retinal and extraretinal eye-motion inputs, as suggested by cells which were real-motion in darkness and, in addition, showed an even weaker visual response during eye movement against a textured visual background.

It has been reported that retinal eye-motion input may influence the visually evoked activity of retinal ganglion cells and lateral geniculate neurons (shift-effect, cf. Krüger and Fischer 1973; Fischer and Krüger 1974), while extraretinal eye-motion input affects the responses of superior colliculus and pulvinar cells (Robinson and Wurtz 1976; Robinson and Petersen 1985). It is tempting to speculate that the real-motion cells modulated by retinal eye-motion input are connected together along the geniculo-cortical pathway, while those modulated by extraretinal eye-motion input along the extra-geniculo-cortical pathway. Present data show that at the level of area V3A, but possibly before, convergence of the two streams on the same real-motion cell has already occurred.

> Functional role of real-motion cells

Real-motion cells are very peculiar neural elements in the visual system in that they couple visual information coming from the receptive field with information on eye movement. Their response to a self-induced movement of the retinal image is on average 64% weaker than that evoked by the same retinal image displacement, due to an actual movement in the visual field. It may be suggested that the visual system uses neurons of this type in order to distinguish real from self-induced movements of retinal images, hence to recognize the actual movement in the visual field. One would expect that such real-motion detectors should discharge whenever an actual movement occurs in the field of view, while they should be silent if the retinal image movement has been self-induced by an eye movement. In fact, we rarely observed real-motion cells completely silent during eye movement, while the stimulus was stationary in the visual field. But we often noted that the presence of a visual background further decreased the visual response during eye movement; in some cases the response completely disappeared when the real motion test was performed against a textured background. It may be suggested that several types of inputs may modulate the visual response of real-motion cells. Among these, a visual one relative to the movement of the surround, an extraretinal eye-motion input and, possibly a vestibular input, which could be useful in accounting for head movements. Each of these inputs might weaken the visual response during eye/head movement with a mutual, synergic action, resulting in a complete inhibition of the response of real-motion cells in certain circumstances.

Psychophysical data from the literature strongly support the hypothesis that both extraretinal and retinal inputs are important for detection of actual movement in the visual world. It has been reported, for example, that when subjects attempt to move their paralyzed eyes, they have a sensation of movement of the objects in the visual field (Kornmüller 1931; Hammond et al. 1956), but this sensation is much clearer, or present only, if a certain degree of retinal slip is concurrently present (Siebeck 1954; Brindley et al. 1976; Stevens et al. 1976). Again, in a series of adaptation experiments in which the self-induced displacements of retinal images due to eye movement were altered by the experimenter, it has been demonstrated that the stability of the visual world despite eye movement is clearly due to two distinct processes of compensation, one of them using visual cues, the other based on extraretinal signals tied to the eye movement itself (see Wallace 1985 for a review on this subject).

> Stability of visual perception despite eye movements

The stability of visual perception despite eye movements is a process which has been studied for a long time by Psychophysicists and whose physiological basis is still unknown. It has been assumed, and accepted by most authors in the field, that visual stability is due to an accounting mechanism, which matches the size of an eye movement with the simultaneously occurring image displacements (Kling and Riggs 1971; Kaufman 1974). In agreement with this hypothesis is the 'evaluating.Interfaces' hypothesis of MacKay (1973), according to which there is an internal representation of the field of view which, by taking account of eye/head movements and retinal image displacements, is stable despite the self-induced retinal image displacements due to eye/head movement. The neuronal network subserving this internal, objective map would continuously 'evaluate' if something changes its location in the visual environment. The elements of this network would change the internal map of the environment (the objective map) whenever their inputs change beyond a certain amount, otherwise the map would remain unchanged and the subject would perceive a stable visual environment in spite of possible movements of retinal images.

The hypothesis that the objective map would not change until the eye-motion input and/or the visual input change above a threshold value agrees very well with data obtained by several psychophysical experiments on human subjects. In experiments where the self-induced displacements of retinal images due to eye movement were altered by the experimenter, Yarbus (1967) demonstrated that when the amplitude of retinal image displacement was greater than that of eye movement a sensation of object movement was perceived by the subject. But Yarbus pointed out that if the difference between the two displacements was within 5°-15° the object was perceived as still, and it is worth noting that 5°-15° is just the normal range of eye micromovements during steady fixation. More recently, other authors reported that when their subjects were watching a luminous target in an otherwise dark field
and the output of the eye-movement recording system caused the target to move as long as the eye was in motion, the subjects perceived target motion only when the target shifts amounted to more than about 10–20% of the size of the eye’s movement (Mack 1970; Wippe and Wallach 1978).

Looking at the responses of visual cortical neurons to actual stimulus movements and to self-induced retinal image displacements, two different types of cells have been observed. Cells whose activity is about the same in the two situations, and real-motion cells, whose activity is greatly reduced (on average 64%) during self-induced movement of retinal images. The behaviour of the latter neurons supports our suggestion (Galletti et al. 1984, 1988) that real-motion cells may be neural elements of the network subserving the internal, objective map of the field of view proposed by MacKay (1973). According to this view, real-motion cells would change the internal map whenever their activity changes above a certain amount, otherwise the map would remain unchanged and the subject would perceive a stable visual environment. The internal map of the visual world, continuously updated by the activity of real-motion cells, would in turns be used by the visual system to properly interpret the plenty of sensory changes resulting from exploratory eye movements in a stable visual world.

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