Neuronal mechanisms for detection of motion in the field of view

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Abstract

The visual system cannot rely only upon information from the retina to perceive object motion because identical retinal stimulations can be evoked by the movement of objects in the field of view as well as by the movements of retinal images self-evoked by eye movements. We clearly distinguish the two situations, perceiving object motion in the first case and stationarity in the second. The present work problem is to try to answer this question taking into account the neuronal mechanisms that are likely involved in the detection of motion.

Experimental data obtained in paralyzed animals showed that many neurones of the visual system are sensitive to the movement of visual stimuli, and several cells of the visual cortex are able to encode the speed of motion over large ranges of velocities (Orban, 1984; Riva Sansavero, Galletti, Maioi, & Squatrito, 1979). One could believe that all these neurones, being sensitive to various speeds of motion, are able to encode the movement occurring in the visual field, but this is clearly not the case. In physiological conditions, contrary to what happens in paralyzed animals, the animal moves the eyes, so the images of motionless objects move on the retina, exactly as the images of moving objects do. How can motion-sensitive neurones recognize the real movement of objects in the visual field?

In physiological conditions, the images of objects motionless in the visual field move on the retina even when the animal maintains a steady fixation, owing to eye micro-movements (drifts and flicks). As the velocity of these micro-movements is such as to activate many cells in paralyzed animals (drifts: <1° s⁻¹, flicks: ∼10° s⁻¹; see Carpenter, 1988), these cells will be activated by motionless objects as well as by objects moving slowly in the visual field during steady fixation; but, again, they will not able to discriminate between these two situations.

Fig. 1 shows the visual responses to stimuli moving at different speeds, and the velocity tuning curves, of cells recorded in the primary visual cortex of awake macaque monkey during steady fixation. The cell shown in Fig. 1 gave transient on-off responses to stationary stimuli and good responses to slow velocities of stimulus movement.

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1. Introduction

Visual perception of motion is clearly related to the movement of retinal images of objects present in our field of view. However, similar movements of retinal images can be evoked by eye movements, while the objects are still in the visual scene. How do we distinguish actual movements from the image movements self-induced by the movement of the eyes? The purpose of the present work is to try to answer this question taking into account the neuronal mechanisms that are likely involved in the detection of motion.

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Fig. 1. Visual responses and velocity tuning curves of motion-sensitive cells recorded in area V1 of awake monkey (modified from Battaglini, Galletti, & Fattori, 1993). (A) Responses of a V1 neurone to the optimal visual stimulus moved at different velocities (1–330° s⁻¹) across the receptive field. Responses are shown as peri-stimulus time histograms and raster displays of impulse sequences. (B) Responses to the same, stationary (ST), stimulus switched on and off on the receptive field. (C) Ongoing activity of the cell (SA) without any visual stimulation. (D) Bar histogram of the cell activity reported in A–C. The bars indicate the average of the highest peak frequencies shown over a 20 ms bin in five trials, expressed as percentage of the maximum peak frequency. (E) Normalized stimulus-response curves for two V1 neurones. Note that unit 10.009 is the same cell shown in A–D. Spontaneous activity was subtracted to visual responses. Vertical bars on empty circles indicate standard deviation for each estimate.

(from 1 to 20° s⁻¹); at speeds higher than 50° s⁻¹, the activity of the cell was not significantly modified by the visual stimulation. Fig. 1E shows the velocity tuning curve of this cell and that of another cell that was sensitive to high speeds of motion. Both cells were activated by moving objects, though they preferred different speeds of motion. According to their tuning curves, we could predict that they would be also activated by stationary objects when the eyes move, as the image of these objects sweeps across the cell’s receptive fields each time the eyes move. Cells preferring
high velocities would be activated by saccadic eye movements (velocities > 100° s\(^{-1}\)), and cells sensitive to slow speeds of motion by pursuit eye movement (1–50° s\(^{-1}\)), as well as by flicks and drifts during steady fixation. If this were the case, we would perceive a shift of the visual world each time we make a saccade, and we would perceive as in motion the motionless objects the image of which is moving on the retina owing to pursuit eye movements. As this is not the case, it means that the movement of the retinal image per se is not sufficient to evoke a sensation of movement of the object in the visual field. This sensation is evoked when the movement on the retina is due to a real motion of the object, and is not evoked when the retinal image movement is self-induced by the movement of the eyes.

2. Perception of real motion

In order to give a proper evaluation of motion, the visual system takes into account the movement of the eyes besides that of retinal images. For instance, long-lasting afterimages, as well as phosphenes evoked by cortical stimulation, appear as motionless when they are viewed in complete darkness and the eyes are moved passively, but these afterimages appear to be moving when the eyes move actively, either for saccadic or slow pursuit movements (Brindley & Lewin, 1966; Grusser & Grusser-Cornelis, 1973; Mack & Bachant, 1969). It has also been reported that if the eyes are mechanically, pharmacologically or pathologically immobilized, the attempt to move them gives a sensation of movement of the objects present in the visual field (Brindley & Merton, 1960; Hamnond, Merton, & Sutton, 1956; Hughesings Jackson, 1932; Kornmuller, 1931; Mach, 1886; Von Helmholtz, 1909). In all these cases, there is a retinotopically “stable” neural stimulation associated with a perception of movement in the visual field that depends on performing an active ocular movement, or even on the intention to make it.

As we can perceive a movement of an object when its image is motionless on the retina, we also can perceive the absence of motion (stationarity) when the image of an object sweeps across the retina if the retinal-image sweeping is due to the movement of the eyes. It is a common experience that during the execution of saccadic eye movements, the stationary visual world is perceived as stable (motionless) in spite of the shift of its retinal images due to the eye movement. It has been suggested that this visual stability is due to a reduced sensitivity of the visual system during saccades (saccadic suppression; Bridgeman, Hendry, & Stark, 1975; Burr, Holt, Johnstone, & Ross, 1982; Volkmann, 1962, 1976). We know that this reduced sensitivity lasts some hundreds of milliseconds around the time of occurrence of the saccade, but which type of eye-motion signal is responsible for this loss of visual sensitivity is a matter of debate. Information about eye movements could result from retinal as well as extraretinal signals. A suitable retinal signal indicating the eye motion is the shift on the retina of images of the whole visual field occurring when the eyes move (Brooks & Impelman, 1981; Gibson, 1966; MacKay, 1970; Wallace, 1985). Suitable extraretinal signals are both the sensory one coming from eye muscle proprioreceptors (“inflow theory”, Sherrington, 1918; Skavenski, 1972) and a copy of the motor one sent to the eye muscles by the oculomotor centers (“outflow theory”, Sperry, 1950; Von Helmholtz, 1909; Von Holst, 1954). Which of these signals is used to allow the stability of visual perception is still an unsolved question, and is beyond the scope of this paper.

As the saccadic suppression is not a complete suppression of vision but a decrease of visual sensitivity, during the saccades at least weak and blurred visual images of the world ought to be perceived. This is not the case. In an elegant experiment, Judge, Wurtz and Richmond (1980) demonstrated that the blurring of visual perception during saccades is overcome by the masking effect of visual stimulation occurring soon before the saccade itself. Burr, Morrone and Ross (1994) have more recently suggested a second, not an alternative mechanism, that could explain the absence of motion perception during saccades. They found that saccadic suppression mainly affects the magnocellular section of the visual system, leaving the parvocellular one unaffected. As the cells of magnocellular system are sensitive to fast-moving stimuli (like the cell shown on the right in Fig. 1E), and would therefore be activated by the retinal shift of images of the visual world during saccades, the selective inhibition of these cells during saccades would prevent them from discharging, avoiding the sensation of visual world motion during the eye movement.

Cells sensitive to fast speeds of motion, but insensitive to high velocities of retinal images when motion is self-induced by saccadic eye movements, have been described in subcortical structures as PL and PI subdivisions of the monkey pulvinar (Robinson & Petersen, 1985) and superior colliculus in both monkey (Robinson & Wurtz, 1976) and cat (Strachilch & Hoffmann, 1970). Cells with similar behaviour were also found in cortical areas V1 and V2 (Fig. 2; Battaglini, Galletti, Aicardi, Squatrito, & Maoli, 1986), in area V4 (Fischer, Boch, & Bach, 1981), and in visual areas known to receive a strong magnocellular input as MT/V5 and MST (Thiele, Henning, Kubischik, & Hoffmann, 2002).

Cells of the parvocellular system, supposed not to be inhibited during saccades, are insensitive to fast-moving stimuli (see the tuning curve of the cell shown on the left in Fig. 1E), and therefore are not activated by visual stimulations evoked by saccades. This type of cell would be activated by stationary or slow-moving images during saccades, but both events are virtually absent in physiological conditions. According to this view, if we stimulate the retina with a stable image during a saccade, we would perceive the object represented by that image thanks to the activity evoked in the non-inhibited cells. This prediction can be easily verified. When looking out from a window of a train in motion, the sleepers of the track line at our side are clearly seen each time we make a saccade in the direction opposite...
to that of the train. The perception of sleepers is vivid and, oddly, they are perceived as absolutely still. The stillness of sleepers contrasts with the instability of their retinal images during saccade. In fact, sleeper images move on the retina during saccade as the speed of saccade cannot always exactly match that of the train. Retinal images move at speeds that are likely in the range of activation of cells of the parvocellular system (from less than 1◦ to some tens of degrees per second), and this evokes a sensation of stillness of sleepers.

If this view is correct, it means that the sensation of motion or stationarity of an object in the visual field depends on the type of cells activated by visual stimuli rather than the type of retinal stimulation. According to this view, we would perceive the motion of an object when the image of the object activates a particular set of cells (likely, the cells receiving a magnocellular input), whereas perception of stationarity would depend on the activation of another set of cells (likely, the cells receiving a parvocellular input). Both types of cells would be active during steady fixations and not active during saccades, the first because inhibited and the second because not activated by fast visual stimulations. The activities of both types of cells during steady fixation would mask the absence of specific activation of these same cells during the few tens of milliseconds of the saccade duration, resulting in a stability of the visual perception.

3. Correct evaluation of motion during tracking eye movement

During steady fixation, as an object moves in the visual field its image moves on the retina and we soon perceive the object as in motion. During visual tracking of a moving object, conversely, the image of the followed object is quite still on the retina while the images of motionless visual world around the moving object are in motion. Despite this, everyone clearly perceives the object as in motion and the visual world as motionless.

The stability of perception of the visual world during pursuit cannot be explained with a selective inhibition of motion-sensitive cells during eye movements, as suggested for the saccadic eye movements, because pursuit lasts for seconds, and during this time we correctly perceive any movement occurring in the visual field. But if motion-sensitive elements are not inhibited, they should be activated by the motion of retinal images self-induced by pursuit, and this fact contrasts with the stability of visual perception we have during pursuit. Which are the neural mechanisms that support the visual stability and proper evaluation of motion during tracking eye movement?

Many laboratories in the last two decades addressed this question, looking for cells (real-motion cells) able to recognize whether a movement of a retinal image is the consequence of an actual movement that occurs in the visual field, or is self-induced by an ocular movement while the object is motionless in the visual field. Typically, the experimental paradigm used to look for these cells uses one of two conditions. In the first, the animal is required to fixate a stationary target while an optimal visual stimulus sweeps across the receptive field of the cell evoking a neural response. In the second, the animal is asked to pursue the target moving in the opposite direction with respect to the stimulus in the previous condition, while the visual stimulus is maintained still. The visual stimulation is the same in the two conditions (same relative movement between retinal image and receptive field). Consequently, the neural responses ought to be the same.

Real-motion cells show good responses when the visual stimulus really moves in the visual field, and weak responses or no response at all when the eye moves the image of the stationary stimulus on the retina (Fig. 3). Such cells were found in the cortical areas V1 (Bridgeman, 1973; Galletti, Squartrito, Battaglini, & Maioli, 1984), V2 (Galletti, Battaglini, & Aicardi, 1988), V3A (Galletti, Battaglini, & Fattori, 1990), MT/V5 (see Figs. 2C and 4A of Erickson & Thier, 1991), MST (Erickson & Thier, 1991) and 7a (Sakata, Shihutan, Kawano, & Harrington, 1985).

In areas V1, V2, V3A and MT/V5, the eye movement weakened the visual response to less than half of its value during steady fixation, but the visual response seldom disappeared during eye movement. In areas MST and 7a in most cases eye movements completely suppressed the visual response. Some real-motion cells of the occipital
Fig. 3. Real-motion cells of areas V1, V2 and V3A, sensitive to slow-moving stimuli (modified from Battaglini et al., 1993; Galletti et al., 1988, 1993). For each area, the responses of a real-motion cell to receptive-field stimulation during steady fixation (stimulus movement), visual tracking (eye movement) and tracking eye movement without visual stimulation (control) are reported. Other details are same as in Figs. 1 and 2. Scales: neural activity, three spikes/division; eye position, 2° per division.
visual areas were able to discriminate between real and self-induced motion also in darkness, but the presence of a visual background further decreased their visual response during an eye movement, and in some cases the response completely disappeared when pursuit was performed against a textured background (Galletti et al., 1990). Thus, it seems that several types of inputs modulate the visual response of real-motion cells: (i) an extraretinal eye-motion input, responsible for the real-motion effect observed in darkness, that likely acts directly on the visual input as the activity of real-motion cells was not affected in control trials (see Fig. 3); (ii) a retinal eye-motion input, evoked by the retinal slip of the visual world; and possibly (iii) a vestibular input, which would be well suited to account for head movement. Each of these inputs might weaken the visual response during eye/head movement with a mutual, synergic action, up to a complete inhibition of the response of real-motion cells in circumstances (lighted environment, structured visual background) that are frequently present in everyday life.

4. Cortical stream for real motion detection

An increasing percentage of cells in areas V1, V2 and V3A responds better to externally-induced retinal image slip than to image slip self-induced by the eye movement (10, 15 and 41%, respectively; Battaglini et al., 1986; Galletti et al., 1984, 1988, 1990). Many cells in area MT/V5 (Erickson & Thier, 1991; Thiele et al., 2002), and the great majority in areas MST and 7a (Erickson & Thier, 1991; Sakata et al., 1985; Thiele et al., 2002), show the real-motion behaviour. The higher percentage of real-motion cells in high-order cortical visual areas is likely due to the fact that these areas receive stronger retinal as well as extraretinal eye-motion inputs. In fact, though it has been recently found that even cells in V1 can be modulated by large stimuli outside the classical receptive field (Cavanaugh, Bair, & Movshon, 2002), it is well known that this interaction is stronger in high-order visual areas (Allman, Miezin, & Mac, 1995), as it is well known that the high-order visual areas receive strong extraretinal eye-motion inputs through the extrageniculo-striate system (via superior colliculus and pulvinar).

Other cortical areas, not previously tested with the real-motion paradigm, could contain real-motion cells. In order to look for them, we have applied the real-motion paradigm to visual cells recorded in the medial parieto-occipital cortex of the awake macaque. This region of the brain contains two visual areas, V6 and V6A, recently defined on functional basis (Galletti, Fattori, Gamberini, & Kutz, 1999; Galletti, Fattori, Kutz, & Gamberini, 1999). V6 is a retinotopically-organized visual area that receives directly from V1 (Galletti et al., 2001); V6A, a non-retinotopically organized visuomotor area receiving visual input from V6 (Galletti et al., 2001; Shipp, Blanton, & Zeki, 1998). The results obtained with the real-motion paradigm show that area V6 contains many real-motion cells, whereas none of the cells tested in V6A showed the real-motion behaviour.

The presence of real-motion cells in area V6 is not surprising, as V6 is target of the magnocellular input. It has been recently demonstrated that V6 receives a strong magnocellular input from the layer IVB cells of area V1 (Galletti et al., 2001), which in turn are known to receive directly from the cells of the magnocellular layers of the lateral geniculate nucleus.

Fig. 4 shows the cortical areas containing real-motion cells, and their interconnectivity according to data from
Fig. 5. Cortical network involved in real-motion detection. Left: Medial and dorsal views of macaque brain showing the functional parcellation of the posterior part of the macaque brain. Parieto-occipital (POs), medial parieto-occipital (POM), inferior occipital (IOs), occipito-temporal (OTs), intraparietal (IPs), lunate (Ls) and superior temporal (STs) sulci are open to show the occipital and posterior parietal areas hidden in the depth of these sulci (modified from Colby, Gattass, Olson, & Gross, 1988). Sulci opened are shown in light grey, and as thickened lines on the brain silhouettes in the middle part of the figure. Dashed lines are the borders between different cortical areas according to (Desimone & Ungerleider, 1986; Galletti et al., 1999; Gattass & Gross, 1981; Gattass, Sonía, & Gross, 1988; Matelli et al., 1998; Pandya & Seltzer, 1982). Right: Occipito-parietal network processing real-motion. Connections are according to (Boussaoud et al., 1990; Galletti et al., 2001; Luppino, Calzavara, Rozzi, & Matelli, 2001; Matelli et al., 1998; Shipp et al., 1998; Tanne-Gariepy, Rouiller, & Boussaoud, 2002).
literature. Note that apart from V1 and V2, that are known to distribute visual information to both dorsal and ventral visual streams, all other cortical areas belong to the dorsal visual stream. It is known that the dorsal visual stream projects visual information to the premotor areas of the frontal cortex, to be used to visually guide actions (Caminiti, Ferraina, & Johnson, 1996; Galletti et al., 2003; Galletti, Kutz, Gamberini, Breveglieri, & Fattori, 2003; Matelli, Govoni, Galletti, Kutz, & Luppono, 1998; Rizzolatti, Fogassi, & Gallese, 1997; Shipp et al., 1998). Visual information follows two main routes to reach the frontal cortex, one through the visual areas of the superior parietal lobule (dorso-medial visual stream) and one through the inferior parietal lobule (dorso-lateral visual stream). According to the schema presented in Fig. 5, information on real movement reaches the frontal cortex only through the dorso-lateral visual stream, as area V6a, which receives from V6 and is strongly connected to premotor cortex, is devoid of real-motion cells.

It might be that other cortical visual areas of the dorso-medial stream not yet tested with the real-motion paradigm (as areas MIP and VIP) do contain real-motion cells. Area VIP in particular seems to be a good candidate, as it contains many cells sensitive to the direction of movement (Colby, Duhamel, & Goldberg, 1993), like areas MT/V5, MST and V6 (Desimone & Ungerleider, 1986; Galletti, Fattori, Battaglini, Shipp, & Zeki, 1996; Mannsell & Van Essen, 1983; Zeki, 1974), and is strongly connected with them (Boussaoud, Ungerleider, & Desimone, 1990; Galletti et al., 2001). However, recent experiments have demonstrated that a large majority of VIP neurones show significant differences in directional tuning for passive and active visual motion, but the response amplitudes to passive and active visual motion are not significantly different (Gabel, Misslisch, Gielen, & Duysens, 2002). The fact that several cells show opposite preferred directions for passive and active motion leaves open the possibility that VIP cells are able to discriminate between these two situations.

5. An internal map of visual world for motion detection

The real-motion cells are able to distinguish whether a movement of a retinal image is due to a real movement in the visual field or is self-induced by a movement of the eyes. These cells allow one to recognize the actual movement of an object across a structured or non-patterned visual background, as well as in complete darkness. They could act as ‘sensors’ of real movement in a neural network that subserve an internal, objective map of the visual field. Such an internal representation of the field of view could allow one to properly interpret real motion as well as the plethora of sensory changes resulting from exploratory eye movements in a stable visual world.

The existence of an internal representation of the visual world, stable despite eye/head movements, was suggested by many authors in the past. MacKay (1973) advanced the hypothesis that a neural representation of this world would continuously ‘evaluate’ whether something changes its location (i.e. moves) in the visual environment. We suggest that the real-motion cells are responsible for this evaluation process. According to this view, the internal map of the visual world would change whenever the activity of real-motion cells changes above a certain amount, otherwise the map would remain unchanged, and the subject would perceive a stable visual environment.

The hypothesis that the internal map of the visual world would not change until the eye-motion input and/or the visual input changes above a threshold value agrees with data obtained by several authors in psychophysical experiments. Yarbus (1967), for instance, demonstrated that when the amplitude of retinal image displacement was altered by the experimenter so that it was greater than that of eye movement, a sensation of object movement was perceived by the subject. As Yarbus pointed out, if the difference in retinal displacement was within 5–15′, the object was perceived as still; note that 5–15′ is just the normal range for the micromovements of the eyes during steady fixation. Along the same line of evidence, other authors reported that when their subjects were watching a luminous target against a darkened background, and the output of eye-movement recording system caused the target to move when the eyes moved, the subjects perceived target motion only when the shift of the target was 10–20′ larger than that of gaze (Mack, 1970; Whipple & Wallach, 1978).

The right part of Fig. 5 shows the cortical areas and pathways that could be part of the network subserving the internal map of the visual world involved in detection of motion. According to this view, it has been demonstrated that cortical regions that could include the human homologues of areas containing real-motion cells in monkey: (i) evoke the perception of object motion when electrically stimulated (Lee, Hong, Seo, Tae, & Hong, 2000; Richer, Martinez, Cohen, & Stuhilaira, 1991); (ii) are activated in normal subjects during vision of moving stimuli (DuPont, Orban, De Bruyn, Verbruggen, & Mortelmans, 1994; Kleinshmidt et al., 2002; Sunaert, Van Hecke, Marchal, & Orban, 1999; Watson et al., 1993); and (iii) are damaged in patients severely impaired in detection of movement in the visual field (Zihl et al., 1983). These patients describe the perceptual experience of looking at a moving object as if the object remains stationary but appears at different successive positions. In other words, they realize that objects moving in the visual world change in position but are unable to detect the occurrence of this movement.

Recently, a very selective impairment in motion detection has been described after bilateral lesions of the extrastriate cortex in human (Haarmeier, Their, & Repnow, 1997). The patient suffered from false perception of motion, due to his inability to take into account eye movements when judging whether a retinal slip was self-induced or due to an actual movement. He interpreted any retinal image motion
as object motion, even when it resulted from his pursuit eye movements. No other visual functions, even in the motion domain, revealed any relevant disturbance. In particular, his perception of visual motion during steady fixation did not reveal any deficiency. The same was true for his perception of ego-motion. Magnetic resonance imaging revealed that the lesion involved the parieto-occipital cortex, affecting parts of dorsal areas 18, 19 and the cortex in and around the intraparietal sulcus. We suggest that this lesion included areas with high percentage of real-motion cells, e.g. the human homologues of monkey areas V3A, V6, MT/V5, MST and 7a (see Fig. 5). Strong support for this view comes from the fact that V3A, V6, MT/V5, MST, are located within the limits of Brodmann’s areas 18 and 19, and area 7a is the monkey homologues of human area 39 that surrounds the intraparietal sulcus, that is they are the same areas damaged in the patients suffering from false perception of motion.

A particular perceptual problem is raised by the retinal stimulations evoked by tracking eye movement carried out to follow an object moving across a stationary background. During the pursuit, we actually perceive the motion of images of the motionless visual world around the moving object, but we interpret them as due to the eye motion, and not due to the motion of the visual world. The visual world far from the moving object we are pursuing, on the contrary, is clearly perceived as motionless despite the fact that images of that world are moving on the retina as those around the moving object. In other words, the same retinal slip evokes two different percepts depending on the retinal location of the slip. In terms of neural correlates, this means that: (i) the visual system is able to distinguish between actual and self-induced retinal slip wherever it happens on the retina; and (ii) the neural mechanisms involved in this process are likely different for central and peripheral representations of the visual field.

Supporting this view is the fact that patients who are unable to detect movement in the visual field are still able to perceive movements at slow speeds in the central part of the visual field (Zihl et al., 1983). Further support comes from neurophysiological data from monkeys. Area MT/V5 represents mainly the central part of the visual field (Gattass & Gross, 1983) while area V6 mainly represents the peripheral part of it (Galletti et al., 1999). We advance the hypothesis that MT/V5, together with the neighboring areas MST and 7a, is particularly involved in interpreting signals evoked from the central retina during pursuits of moving objects, while V6 would be involved in detection of actual movement in the whole visual field. This view is in line with data from the literature as, in addition to real-motion cells, areas MT/V5, MST and 7a contain retinal eye-motion signals (cells responding to pursuit eye movement, also in darkness, Newsome, Wurtz, & Komatsu, 1988; Sakata et al., 1985). Area V6, on the contrary, does not contain cells activated by pursuit eye movements in darkness (Galleti, Battaglini, & Fattori, 1991), but contains real-motion cells as well as cells activated by the movement of large visual stimuli and cells modulated by pursuit movements in light (Galletti, unpublished observations).

6. Conclusions

Cells able to distinguish real from self-induced motion (real-motion cells) are distributed in several cortical areas in the brain. This cortical network, that seems to exist also in the human brain, could be responsible for the proper evaluation of motion and the stability of visual perception despite eye movements.

Real-motion cells are distributed in areas of the dorsal visual stream that are strongly influenced by the magnocellular input. Among these areas, V3A and V6 are likely involved in the fast form and motion analyses needed for visual guidance of action (see Galletti et al., 2001, 2003). The real-motion cells of these areas could signal actual movements in the field of view, and these signals could be used to orient the animal’s attention towards moving objects, to parry a blow, to grasp the moving objects or simply to update their spatial location.

The other visual areas of the dorsal visual stream, MT/V5, MST and 7a, are known to be involved in the control of pursuit eye movements as well as in the analysis of visual signals evoked by tracking eye movements (Allman et al., 1995; Komatsu & Wurtz, 1988; Newsome et al., 1988; Sakata et al., 1985). The real-motion cells of these areas could interpret retinal and extraretinal signals evoked by eye-tracking of moving objects, in order to give a proper evaluation of motion during pursuit.

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1726


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