Building blocks for time-to-contact estimation by the brain

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Abstract

The ability to estimate impending collisions is a vital requirement for any organism. Behavioral studies in several animal species have demonstrated sensitivity to time-to-contact. The proven capability to estimate time-to-contact in humans and animals must have its origin in brain processes that extract or compute correlates of time-to-contact from the visual input. Unfortunately, not many studies have looked specifically at neuronal sensitivity for time-to-contact. Specific investigations of this question in the primate brain (including humans) are still lacking. However, a great deal is known about the neuronal selectivity for the building blocks of time-to-contact mechanisms: visual motion, looming, binocular disparity, motion in depth, etc. This chapter presents a discussion of the properties of neurons that encode these cues and hopefully will be helpful for homing in on the biological foundations of time-to-contact.

Since we are able to precisely estimate time-to-contact, our brains must contain mechanisms that conduct the required sensory analysis. Candidates for neural time-to-contact mechanisms have been described in several animal species (Pigeon: (Frost and Sun, 2002), Locust: (Rind and Simmons, 1997; Gabbiani et al., 1999), Gerbil: (Shankar and Ellard, 2000)). The topic has not yet been specifically addressed, however, for the brains of higher mammals and especially primates. But a number of the sensory cues that are used to derive time-to-contact measurements

have been studied in great detail. These include visual motion, motion parallax, binocular disparity, looming and optic flow. After a brief overview of the motion analysis pathway of the primate brain I will review some of these studies and show how the building blocks for time-to-contact estimation are represented in the brain. The presentation will sometimes have to divert a bit towards the analysis of optic flow rather than time-to-collision, mainly because much more is known about the brain's representation of optic flow. As I believe the two task to have some commonalities at the basic level, however, I think it might be useful to consider them together.

The motion pathway

In the cerebral cortex, the processing of visual motion is attributed to a successive series of areas in the so–called dorsal stream pathway. The dorsal stream is specialized in the analysis of spatial relationships and the generation of spatially directed action. Within the dorsal stream, motion information proceeds from the primary visual cortex (V1) to the middle temporal area (MT, also called V5) and the medial superior temporal area (MST) and to several higher areas in the parietal cortex and the anterior part of the superior temporal sulcus.

Area V1 already contains cells that respond selectively to visual motion in a preferred direction. But area MT is the first cortical area that is dedicated specifically to the processing of motion. It contains a very high proportion of direction selective neurons and it has been linked to behavioral responses to motion stimuli in lesion and microstimulation studies. Typical MT neurons respond selectively to small moving stimuli with a preferred direction and a preferred speed of motion (Maunsell and Van Essen, 1983a). Area MT contains a topographic representation of the visual field, i.e. the receptive fields of neighboring MT cells correspond to neighboring locations of the visual field (Albright and Desimone, 1987). Receptive field sizes in MT vary with eccentricity and range from 1 to more than 10 degrees of visual angle in diameter (Albright and Desimone, 1987). The properties of MT neurons are well suited for establishing a cortical representation of motion in the visual field, solving computational problems in the estimation of visual motion such as the aperture problem (Movshon et al., 1985; Pack and Born, 2001).

Area MT projects heavily to area MST, a further specialized motion area in the superior temporal sulcus (Boussaoud et al., 1990). Like MT, MST contains a large proportion of motion selective neurons, but retinotopy in MST is much coarser than in MT and the receptive fields of MST neurons are much larger (Desimone and Ungerleider, 1986). Neurons in MST respond to motion patterns such as optical expansions or rotations (Tanaka and Saito, 1989; Duffy and Wurtz, 1991). The selective responses of MST neurons to motion patterns depends mainly on the spatial arrangement of motion vectors and on the size of the stimulated area. Other parameters such as shape and size of the individual motion elements, contrast, or speed gradients did not have much influence on neuronal responses (Tanaka and Saito, 1989; Geesaman and Andersen, 1996; Pekel et al., 1996). Area MST is believed to be involved in the analysis of optic flow and the control of self-motion (Duffy and Wurtz, 1991; Lappe et al., 1996). Area MT also projects to the ventral intraparietal area, or area VIP. Like cells in area MST, VIP cells respond to patterns of visual motion (Schaafsma and Duysens, 1996; Bremmer et al., 2000). However, they also respond to small objects moving toward the animal, especially when they are near to the head (Colby et al., 1993).

Optical speed

Selectivity for the direction of visual motion is a well-documented feature of neurons in many areas of the brain. Direction selectivity is found as early as V1 and is the main feature of neural selectivity in areas MT, MST, and VIP. When tested with moving bars, gratings, or random dot fields of variable speed, most neurons in these areas also display selectivity for the speed of the stimulus. Typically, the speed tuning is independent of other tuning properties of the neuron. For instance, the speed tuning of an MT neuron is independent from its direction tuning (Rodman and Albright, 1987). MT responses have been modeled as the multiplication of a speed factor and a direction factor (e.g. Lappe et al. (1996)).

Whereas neurons in area V1 are influenced by the spatial frequency content of the stimulus and thus react to spatiotemporal frequency rather than visual speed, neurons in MT already display

true speed selectivity (Perrone and Thiele, 2001). The most prevalent type of speed selectivity in MT is band-pass tuning with optimal speeds ranging from 0.5-256 degrees per second (Maunsell and Van Essen, 1983a; Mikami et al., 1986; Lagae et al., 1993). Smaller proportions of cells have either low-pass or high-pass characteristics (Lagae et al., 1993). With tuned neurons, the representation of visual speed is not possible from the responses of individual neurons but requires some kind of population code (Lappe et al., 1996; Perrone and Thiele, 2001).

The global organization of the representation of visual motion in MT reflects a certain relation to optic flow patterns experienced during forward self-motion. Preferred speeds increase with eccentricity (Maunsell and Van Essen, 1983a) similar to the way optic flow speeds naturally do. Also, the number of direction sensitive neurons preferring motion away from the fovea is significantly higher than the number of neurons preferring motion towards the fovea (Albright, 1989).

Local differential motion and motion parallax

Differences in the motion of neighboring image elements can often be more informative than the visual motion of a single location itself (Nakayama and Loomis, 1974). On the one hand, local differential motion is important to segregate moving objects from the background. On the other hand, local differential motion provides local motion parallax information than can be useful to estimate distance and may indirectly contribute to the estimation of time-to-contact.

Many neurons in area MT are sensitive to local differential motion by virtue of the antagonistic center-surround organization of their receptive fields (Allman et al., 1985). The receptive field of a such a neuron can be described as composed of two parts. The *center* is an excitatory region in which the primary direction and speed selectivity of the neuron is established. Stimulation of the center is required to elicit a response from the neuron. The *surround* is a modulatory region of the receptive field. Stimulation of the surround increases or decreases the response to stimulation in the center, depending on the stimulation and selectivity of the surround (Born, 2000). Stimulation of the surround alone elicits no response.

The area covered by the surround is often many times larger than the area covered by the center (Allman et al., 1985; Raiguel et al., 1995). Despite that the name appears to suggest it, the surround must not lie concentrically around the center of a neurons receptive field. Rather, the surround is often asymmetric and its midpoint is displaced from the center of the receptive field (Raiguel et al., 1995). This suggests that the spatial organization of center and surround enables MT neurons to respond to differences in the motion of adjacent image locations.

A neuron's selectivity for local differential motion is shaped by the direction and speed tuning of the surround in comparison to the preferred velocity in the receptive field center. The direction preference of the antagonistic surround is usually opposite to the direction preference of the center and neurons with surround preferred direction orthogonal to the center preferred direction are rare (Born, 2000). The response rate of the neuron decreases if the surround is stimulated with the same motion as the center. The response might be enhanced, however, if center and surround are stimulated with motion in opposite directions.

The speed tuning properties of the surround can be used to distinguish three classes of neurons with antagonistic surround. In one type of neuron, stimulation of the surround with the same speed as the speed in the center leads to maximum suppression of activity (Allman et al., 1985). Both lower and higher speeds are less effective in suppressing the center response. These neurons therefore encode absolute speed differences. In other neurons, the speed influence is monotonic, either increasing or decreasing with increasing surround speed (Allman et al., 1985; Tanaka et al., 1986). Therefore, these neurons also encode the sign of the speed difference between center and surround. There is also an interaction between the speed preference and the spatial location of the surround (Xiao et al., 1998).

The center-surround architecture of MT receptive fields generates a variety of selectivities for local differential motion. These selectivities may be used for visual tasks like foreground-background segregation, optic flow analysis, or three-dimensional shape recognition (as theoretical analysis has shown (Nakayama and Loomis, 1974; Buracas and Albright, 1996; Royden, 1997; Beintema et al., 2001)) and could also be useful for estimation of time-to-contact.

Optic flow and looming

Theories of time-to-contact often involve the analysis of motion patterns, especially looming. Selectivity to motion patterns is first found in parietal areas beyond area MT (Lagae et al., 1994). Early studies occasionally identified neurons in the superior temporal sulcus that responded to rotations in depth or to optical expansions (Bruce et al., 1981; Saito et al., 1986; Sakata et al., 1986). Later, systematic investigation of the response properties of neuron in area MST revealed selectivity to unidirectional motion, rotation, expansion, and contraction patterns (Tanaka and Saito, 1989; Duffy and Wurtz, 1991). The selectivity of these neurons clearly relies on the spatial arrangement of motion vectors. Shape, size, number, or contrast of the individual motion elements did not have much influence on the response (Tanaka and Saito, 1989; Duffy and Wurtz, 1991; Geesaman and Andersen, 1996; Pekel et al., 1996). The same is true for the size change of individual motion elements that normally accompanies approaching motion. MST neurons respond to optical expansion patterns in which the size change is removed in the same way as when the patterns contain size change (Pekel et al., 1996).

Although some MST neurons are selective for only one particular pattern of the set of expansion, contraction, rotation and uniform motion, the majority of MST neurons responds to several of these stimuli (Duffy and Wurtz, 1991). Many neurons respond similarly to unidirectional motion in a preferred direction, rotation in one of the two principle directions (clockwise, counterclockwise), and either expansion or contraction. Other cells respond to unidirectional motion and to either rotation or expansion/contraction. These two response types form the majority of cells. Very few neurons respond to rotation and expansion/contraction but lack direction selectivity. The smallest group is formed neurons that responded to only one type of motion pattern.

At first sight, these response properties seem to open up the possibility that neurons in MST perform a decomposition of the visual motion field into a set of basic invariants. Mathematically, any motion vector field can be locally approximated by a set of four differential invariants: divergence (related to expansion/contraction), curl (related to rotation), and two components

of deformation (Koenderink and van Doorn, 1976). A closer look, however, shows that the properties of MST cells are incompatible with such a mathematical decomposition. To extract divergence in a mathematical sense a cell would have to respond with equal activity to pure expansion and to a stimulus where the same expansion is superimposed by another motion component, for instance rotation. This is not true for MST cells (Graziano et al., 1994; Orban et al., 1992). Instead, some MST cells even prefer vectorial combinations of rotation and expansion/contraction over the two individual patterns and display a selectivity for spiral motion (Graziano et al., 1994). Secondly, mathematical decomposition predicts selectivity for deformation, since a full local description requires deformation in addition to divergence and curl (Koenderink and van Doorn, 1976). Cells responding exclusively to deformation are rare in MST (Lagae et al., 1994). Thirdly, decomposition is a *local* linearization of the flow field (Koenderink and van Doorn, 1976) and valid only within a small neighborhood of any point in the field. Because the receptive fields in MST are quite large they are less likely to signal local properties. Altogether, MST does not appear to form a set of channels selective for expansion, contraction and rotation, but rather a continuum of selectivities in which single neurons respond to several different motion patterns.

Area MST is believed to contribute to the analysis of optic flow for the control of self-motion and in particular to the computation of heading. (Duffy and Wurtz, 1991; Lappe and Rauschecker, 1993) A number of computational models have shown how the response properties of MST neurons can be linked to optic flow based heading estimation (overview in Lappe (2000)). These models share the assumption that area MT serves as a representation of the optic flow field while area MST performs computations on this representation that generate selectivity for the heading inherent in the flow field. In the output stage, area MST forms a computational map of heading directions. This map could be represented either implicitly by the population, or explicitly by dedicated neurons that individually encode specific headings.

Consistent with model predictions, MST neurons have been found to exhibit selectivity for heading and the location of the focus of expansion in a flow field stimulus (Lappe et al., 1996). In

these experiments, a monkey was presented with large–field (90 by 90 deg) computer generated optic flow stimuli simulating approaching (expansion) and receding (contraction) self–motion with respect to a random cloud of dots in three-dimensional space. The stimuli displayed realistic flow fields in which dots accelerated with eccentricity, grew larger in size as they approached the animal, and moved with motion parallax according to their distance in depth. To determine the dependence of neuronal responses on the singular point in the optic flow, different stimuli depicted self–motion in different directions. Neural responses in MST varied smoothly with the position of the singular point. They often showed a sigmoidal response profile that saturated as the focus of expansion moved into the visual periphery. These experimental findings could be recreated in computer simulations of neurons from the heading model in which the focus of expansion is recovered from the population response. Similarly, the location of the focus of expansion could be retrieved from a population analysis of the neuronal activities in MST with a precision close to that obtained in human psychophysical studies of heading estimation.

One of the main problems in heading estimation from optic flow is the combination of translational and rotational self-motion components and the disturbance of the retinal flow field by eye movements. Superimposed visual rotation because of eye movement can drastically change the appearance of the optic flow field on the retina and thus complicate the task of its analysis (overview in Lappe et al. (1999)). Neurons in MST appear to be able to cope with the problem of eye movements and represent heading also during eye pursuit, at least at the population level (Bradley et al., 1996; Page and Duffy, 1999; Krekelberg et al., 2001). Combinations of translational and rotational self–motion components also occur during movement on a curved path. MST neurons faithfully encode momentary heading even when it changes because of a curve in the path (Paolini et al., 2000; Krekelberg et al., 2001).

How can MST's selectivity to optic flow be related to the analysis of time-to-contact? On the one hand, several factors argue against an involvement of MST in time-to-contact estimation. MST neurons generally respond best to very large motion fields, ideally several tens of degrees in diameter. MST neurons respond not only to optical expansions but also to optical rotation,

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uniform motion fields, or spiraling motion. These patterns are not directly linked to time-to-contact mechanisms. On the other hand, MST neurons can also be driven by small stimuli, albeit to a lesser degree. The computational mechanisms for heading detection could in principle also be used to compute the direction of approach of a moving object, at least if the image area that is analyzed is restricted to the size of the object. The capability to deal with combinations of translation and rotation might be useful in estimating the approach of a rotating object such as a flying ball. If MST provides the machinery to perform a complex analysis patterns of of image motion that result from translational and rotational movements, this machinery might be put to use for both self–motion and object–motion tasks.

A point that is more directly related to time-to-collision analysis is MST's ability to extract the speed of an optical expansion. Early work on MST had focused mainly on pattern selectivity. Speed effects were disregarded or, after cursory inspection of the data, declared non-existent. Later studies have specifically addressed the influence of speed on the responses to expansion and rotation patterns (Orban et al., 1995; Duffy and Wurtz, 1997). Like MT, MST contains neurons with band-pass, low.pass, or high-pass speed characteristics. Duffy and Wurtz (1997) also described neurons that respond well to low and to high speeds but less to intermediate speeds. The preferred speeds of band-pass neurons in MST are typically higher than in MT, however, and the speed selectivity curves are shallower. Typical speed tuning curves appear quite linear over a large range up to the preferred speed. The response drops quickly for speeds that exceed the preferred speed. Speed or rate of expansion might be retrieved from these responses by a population code. In addition to selectivity for the average speed of a motion pattern, MST neurons also display selectivity for the speed gradient within the pattern (Duffy and Wurtz, 1997). Such selectivity might be useful to encode properties of the three-dimensional structure of the environment.

Binocular disparity and motion in depth

Neural selectivity for binocular disparity is a common feature of many areas in the visual motion pathway (overview in Poggio (1995)). For instance, the response to visual motion in many neurons of area MT is modulated by the disparity of the stimulus (Maunsell and Van Essen, 1983b). Most disparity selective MT neurons prefer disparities near zero, but some also prefer stimuli placed nearer or farther than the horopter (Maunsell and Van Essen, 1983b; Bradley et al., 1995; DeAngelis et al., 1998). MT appears to be involved in the perception of depth from disparity (DeAngelis et al., 1998; Bradley et al., 1998). It is therefore conceivable that the disparity of a stimulus can be retrieved from a population code of MT responses to be used in time-to-collision judgments as well. However, the disparity selectivity of MT neurons may also be used to enhance the representation of the visual motion field, particularly in relation to self–motion (Lappe, 1996).

Disparity selectivity is also found in area MST, but there neurons dominate that prefer disparities different from zero (Roy and Wurtz, 1992; Takemura et al., 2001). A population code can retrieve stimulus disparity from MST responses and suggests a link to the control of vergence eye movements (Takemura et al., 2001). The disparity selectivity of MST neurons together with their selectivity for optic flow patterns also appears well–suited for the analysis of self–motion (Roy and Wurtz, 1992; Lappe and Grigo, 1999).

With respect to the measurement of time-to-contact, disparity selectivity is mainly interesting as a contribution to mechanisms that estimate motion in depth. While early work has suggested that the combination of motion and disparity selectivity could lead to selectivity to motion in depth (Zeki, 1974) a later study found no evidence for genuine motion in depth selectivity in MT (Maunsell and Van Essen, 1983b). Rather it appears that MT neurons possess selectivity for a certain preferred range of fixed disparities such that their response is determined by the two-dimensional visual motion present within this disparity range (Bradley et al., 1995; Lappe, 1996). However, selectivity for binocular motion in depth has been described in studies of the lateral suprasylvian cortex of the cat, which may contain homologues of primate cortical

areas MT or MST (Sherk and Fowler, 2000). Akase et al. (1998) investigated the responses of neurons in the posteromedial lateral suprasylvian cortex (area PMLS) to object motion in three dimensions. Their stimulus was a small cube presented by a computer graphics setup in which motion, disparity, looming, texture, and shading cues could be included in or removed from the stimulus. A substantial proportion of the PMLS cells they studied preferred movement towards or away from the animal over lateral motion. Testing with stimuli in which depth cues were partially eliminated revealed that the selectivity to approaching or receding motion depended mostly on binocular disparity and looming and less on texture and shading cues. Removal of disparity cues affected selectivity in ninety percent of the cells and removal of size change (looming) in forty percent. Interestingly, the response rates of cells selective to approaching movements usually increased during the approach of the object and were maximal when the object was nearest to the animal. Although Akase et al. did not discuss this observation in relation to time-to-contact, one might expect that this type of response behavior could serve as a basic mechanism for time-to-contact analysis.

Somewhat similar behavior has been described, albeit briefly, in the ventral intraparietal area (area VIP) of the rhesus monkey. Area VIP is part of the motion pathway and receives input from area MT and area MST. Several properties of neurons in area VIP suggest that area VIP is especially concerned with the representation of motion in the space near to the animal (Bremmer et al., 1997): In addition to being selective to visual motion patterns (Colby et al., 1993; Schaafsma and Duysens, 1996; Bremmer et al., 2000) VIP neurons also often possess somatosensory responses to tactile stimulation on the head (Colby et al., 1993). VIP neurons are also selective for the distance of a visual stimulus and often prefer near or ultra-near ($<$5cm) stimuli (Colby et al., 1993). VIP neurons are disparity sensitive and the number of near-selective neurons is larger than the number of far-selective neurons (Bremmer et al., 1999). Some neurons in VIP are selective for stimuli moving in depth towards the animal. Colby et al. (1993) reported that the critical variable for these neurons is the projected point of impact of the object on the body. The impact point that elicits the strongest response is associated with the tactile receptive

field of the neuron. The response of the neuron is independent of the trajectory along which the object is approaching the point of impact as long as the point of impact remains the same. This type of response behavior seems to suggest a connection to time-to-collision estimation, although little is known yet about the temporal response properties of these neurons.

Conclusion

It is obvious from the above that our current knowledge of the neural mechanisms of time-to-contact estimation is only cursory and comes from only a few occasional observations. This is surprising when one considers that the basic suggestion of using τ as a simple optical variable for powerful behavioral control is more than 25 years old. But as theories of time-to-contact have become more variable in recent years and the necessity to use many different optical cues has become clear, the knowledge we have about the encoding of general visual cues to motion and depth may become more valuable for research on time-to-contact. With the neural representations of optical velocity, motion parallax, looming, disparity, and motion-in-depth the building blocks for a variety of time-to-contact mechanisms are there. The question that still remains is how these encodings are used and combined to form appropriate representations for time-to-contact judgments.

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