

Neurophysiology of the Interception Process in Primates

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## **Abstract**

*From hunting prey to catching a baseball, the process by which primates intercept moving targets is a fundamental, if complex, component of neural processing. Over the past 30 years, understanding of the interception process, in primates in general and humans in particular, has advanced significantly. Based on observations of interception behavior and recordings of the corresponding neural activity, several theories describing the involved processes have been generated and tested. This document presents a high-level summary of the physiology of the most relevant neural components of the interception process, an outline of the prevailing models used to describe this process, and a short discussion of recent experimental results used to confirm or reject those models.*

### **1.0.0 Introduction**

In order to coordinate the bodily movement involved in everyday tasks such as eating, avoiding or catching a moving object, or even moving through a static environment, prediction of motion and structure based on extrapolation from visual clues is necessary. To understand the processes involved, several models of primate interception have been fit to observed behavior, then experimental data collected mostly from single-neuron recording devices during the interception process were used to confirm or reject model hypothesis.

#### **1.1.0 Description of Terms**

Optical flow is the apparent motion due to changing image brightness on the retina, and is a useful representation of 3-dimensional motion and visual characteristics of the environment. Large-field optical flow refers to the motion of the global visual space, usually caused by self-movement through a stationary environment. Small-field optical flow refers to the motion of a small segment of the visual space, usually caused by a target in motion through a stationary environment. Tau is an estimate of time-to-contact between a moving target and a stationary observer or two moving targets. A retinal image is an optical projection of an external target onto the retinal space.

## 2.0.0 Relevant Neurophysiology

Over the past 30 years, increasing evidence has suggested that area 7a of the posterior parietal cortex and the motor cortex are the crucial components of visuomotor coordination. They share the involved processing load in a ratio defined by their firing rates during visual stimulus and motor tracking (Figure 1).

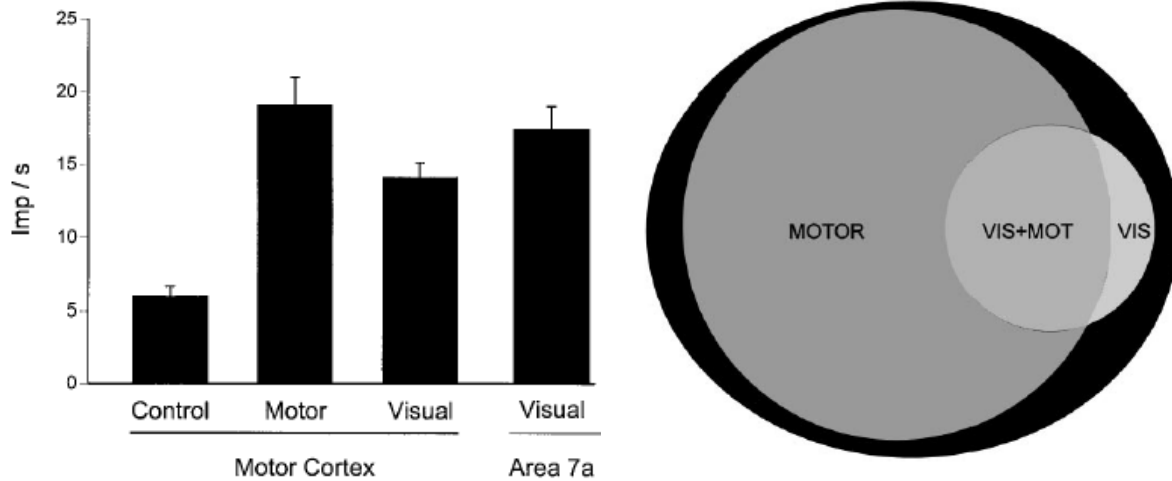


Figure 1: Percentage of cell activity for the indicated tasks (left) Venn diagram with proportionate areas (right) (Merchant, 2001)

## 2.1.0 Middle Superior Temporal

The Helmholtz theorem of kinematics suggests that optical flow can be represented as a sum of a translation within a small area, made up of four components: rotation (circular), expansion (radial), and two shear components (deformations). The middle superior temporal (MST), a cortical area which receives input from the middle temporal (MT) area in the pathway to the parietal cortex, is thought to contribute a higher-order motion analysis. To

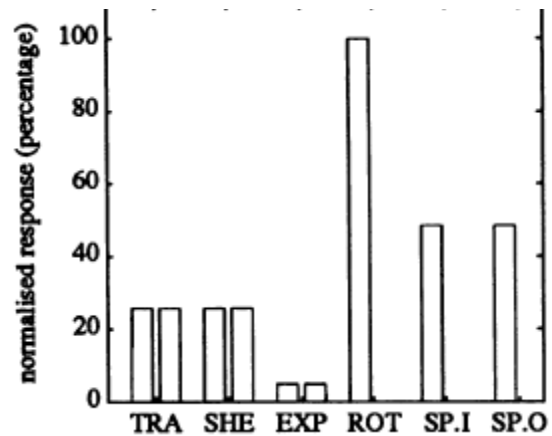


Figure 2: Normalize MST neuronal responses to pure translation (TRA), pure shear (SHE), pure expansion (EXP), pure rotation (ROT), contraction and expansion (SP.I), and pure expansion and rotation (SP.O) in the forward (left) and reverse (right) direction

understand the supposed third-order contribution of the MST to the transduction of rotation and expansion, sets of MST cells in monkeys have been recorded and correlated

to the four aforementioned elementary flow components (EFC) of optical flow. It was observed that nearly one-fourth of MST cells encoded for an EFC, and most only encode one specific EFC (Figure 1) (Orban, 1992).

The MST is divided into two regions. The lateroventral region of the MST (MSTl) contains neurons which respond most notably to the motion of small spots of light. Direct electrical stimulation of this region modifies pursuit eye movements, indicating that the MSTl is partially responsible for this tracking functionality (Komatsu 1989). Neurons of the dorsomedial region of the MST (MSTd) respond most notably to large-field motion, such as self-motion generated by the observer's movement through a stationary environment. These neurons have a large RF, covering more than a full quadrant of the contralateral visual field and extending even into the ipsilateral field (Duffy, 1991).

### **2.2.0 Posterior Parietal Cortex**

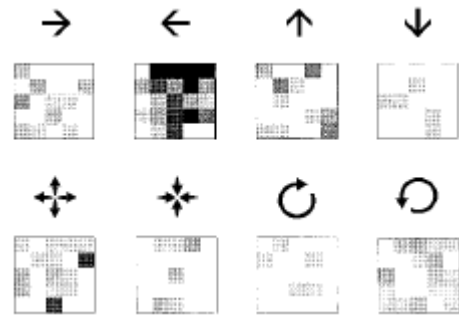
Area 7a of the posterior parietal cortex is responsible for a number of sensorimotor tasks, but perhaps its primary function is the response to visual moving stimuli.

#### **2.2.1 7a neurons**

Area 7a neurons of monkeys trained to perform psychophysical tasks requiring the detection of changes in variously structured optical flow fields have been recorded. The results indicate a dichotomy amongst area 7a neurons. Some are tuned directionally, as previously discussed; however, others are tuned to differentiate between classes of optic flow (planar rotation vs. radial motion). This characteristic has not been recorded in the MST or in the motor cortex, and may be unique to area 7a neurons. Thus, area 7a neurons have been characterized by higher-order optical analysis than the cortical areas MT or MST, and it is likely that this area is responsible for the three-dimensional reconstruction and spatial analysis of the observer's visual field (Siegel, 1997).

By visually stimulating monkeys with a eight different kinds of motion (right, left, upward, downward, expansion, contraction, clockwise, and counter-clockwise) on an liquid-crystal display (LCD) screen and recording the responses observed in both the

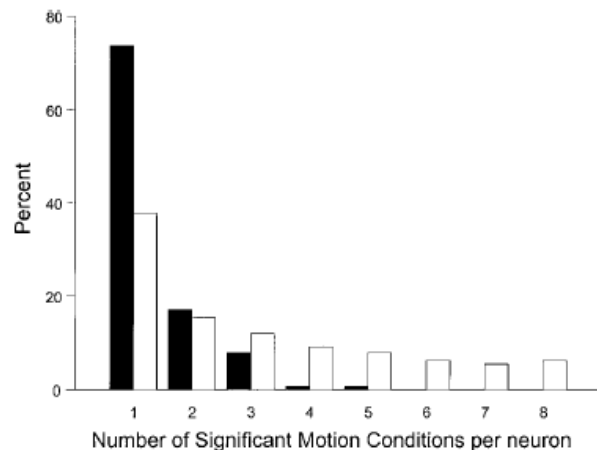
MST and the area 7a neurons, much of the area 7a functionality has been documented. Interestingly, the statistically significant area 7a cells responding to stimuli (63%) were three times greater than those of the motor cortex (21%). A majority of neurons in both cortical areas demonstrated a selective response to specific EFCs (Figure 3); however, the area 7a neurons demonstrated a visual receptive field (RF) structure that could be modulated by the stimulus type, while the motor cortex showed no such RF structure. (Merchant, 2001).



**Figure 3: Area 7a neuron with selective response for left-oriented motion (Merchant, 2001)**

### 2.3.0 Primary Motor Cortex

The functionality of the motor cortex is not limited to simple movement initiation and control; several high-order processes have been observed between the stimulus and the corresponding response (Alexander and Crutcher, 1990). Additionally, motor cortical neurons have been observed to respond to simple moving stimuli, so their contribution to interception cannot be dismissed (Port, 2001). Although their responses are simpler than those in area 7a, these neurons have the advantage of being more highly selective of visual stimuli, with over 75% responding only to one of the eight tested motion patterns (Figure 4).



**Figure 4: Selectivity of primary motor cortex neurons (black) and area 7a neurons (white) to eight motion patterns (Merchant, 2001)**

## 3.0.0 Response to Stimuli

### 3.1.0 Expansion

The first set of interception methods involves a stationary observer's perspective on an approaching target. The primary cue in this circumstance is the expansion of the image across a small section of the retinal area.

#### 3.1.1 Tau Model

In order to estimate the collision time with an oncoming object, primates use the ratio of the object's image size as it varies in time. This time-to-contact ratio, tau, is defined as the ratio of the size of the retinal image over the rate of expansion of the image. This is a first-order estimation, and as such, gives tau as an exact time-to-contact so long as the velocity of the object is constant (Lee 1976).

#### 3.1.2 Tau Threshold Model

For the case when closing velocity is not constant, as is most common in nature, it is supposed that a second-order prediction would be a more appropriate predictive system of time-to-contact. To test this theory, the diving gannet was observed. The gannet dives underwater to catch fish, and it streamlines its wings immediately before submersion to minimize risk of injury and improve dive depth at  $t_c$ . The recorded data included the total dive time  $t_d$  from various heights as well as the time of streamlining,  $t_c$  (Figure 5). The data shows that  $t_c$  increases with  $t_d$ , indicating that the bird does not actually perform a



Figure 6: Time sequence of the diving gannet

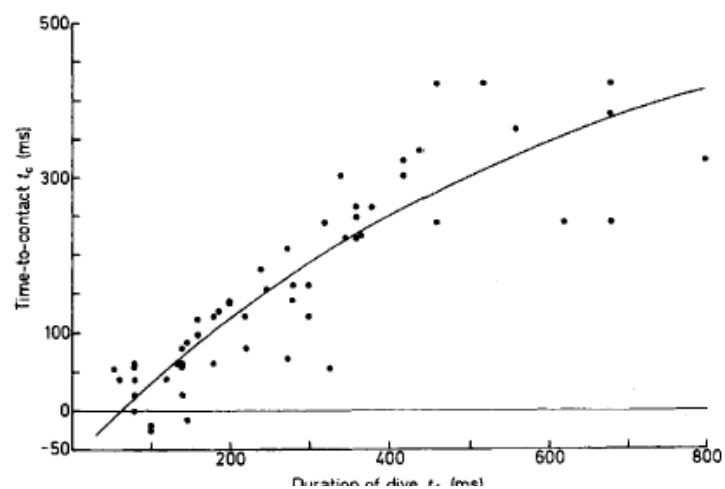
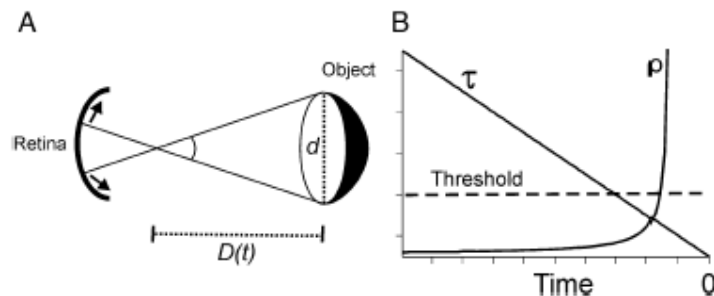


Figure 5: Time of streamlining ( $t_c$ ) vs. total dive time ( $t_d$ ), with best-fit curve

second-order estimate, but rather performs the streamlining action once tau, reaches a certain threshold  $\tau(t) = (t_d^2 - t^2)/2t$  (Figure 6). An exact calculation of time-to-contact would have generated a flat (zero slope)  $t_c \times t_d$  curve, because the gannet would always estimate time-to-contact perfectly, while an initial height-based estimate of time-to-contact would have generated a 45° line on a  $t_c \times t_d$  graph (Lee and Reddish, 1981).

### 3.2.0 Looming Target (Collision Course)

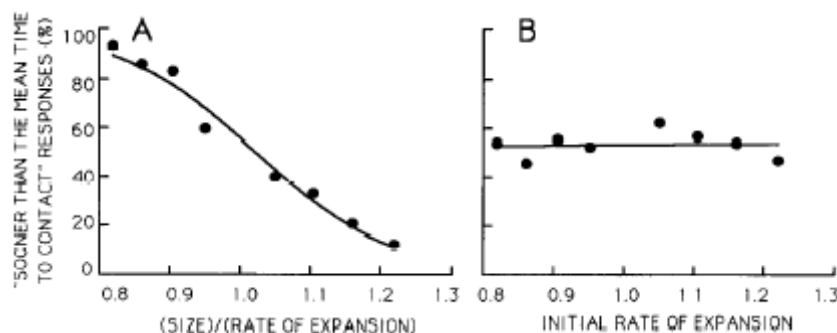
A retinal image increasing in size is interpreted as approaching the observer; thus, a looming image can be used to simulate this condition. In order to approximate tau, a conversion based on the size of the retinal image must first be made. This estimate is made in primates via a calculation of the function  $\rho$ , the absolute rate of expansion of the image (Figure 7).



**Figure 7: Transduction of changing image size ( $d$ ) into changing image distance ( $D(t)$ ) and time-to-contact ( $\tau$ ) via absolute expansion rate ( $\rho$ ) (Sun and Frost, 1998)**

### 3.2.1 Calculation of Expansion Rate

Using a series of looming stimuli in human subjects, the rate of expansion calculation has been characterized. Subjects were observed to ignore changes in both initial size and initial expansion rate of the target object when deciding on a value for tau, relying rather on a ratio between the two (Figure 8). This observation implies a neural method of calculating the angular rate of expansion of the image over the surface of the retina independent of the calculation of time-to-contact (Regan, 1993).



**Figure 8: Responses of subjects to the question, "Will the object collide sooner or later than the average trial" for various combinations of object size and rate of expansion (Regan, 1993)**

Similar studies of the locust have indicated that neurons that make up the lobula giant-movement detector (LGMD) respond to thresholds of speed and size of the approaching stimulus, and neurons in the descending contralateral movement detector (DCMD) respond to direct collision course scenarios. Although these responses involve low-level time-to-contact calculations and instinct-level reactions, the LGMD and DCMD are synaptically linked to respond to looming stimuli in a fashion consistent with primate behavior. Some evidence links the performance of these neurons to those of the MST as well as the PPC in primates (Orban 1992). MST neurons respond primarily to the focus of expansion; however, studies of the area 7a neurons in monkeys have demonstrated their ability to calculate tau from the results of this rate of expansion calculation (Duffy, 1995).

### 3.2.2 Calculation of Time-to-Contact

Once the absolute rate of expansion has been estimated, an extrapolation of the time-to-contact, tau, is formulated. To better understand this process, subjects were shown videos of approaching objects that went blank at a set time before the collision time. When asked to predict the time of impact, subjects consistently underestimated the time-to-collision, but when shown two coinciding approaching objects with collision times further than 150ms apart, subjects were able to distinguish the relative impact time with less than 10% error (Schiff, 1979). These experiments suggest that, although the tau threshold model is corroborated by the inability of subjects to determine time-to-contact without reaching the tau threshold, the model does not explain the accuracy with which primates estimate the future position of fast-moving targets relative to each other.

### 3.3.0 Predictive vs. Reactive

In order to test the tau threshold model as it applies to primates and, specifically, to humans, a method of recording interception times has been implemented. Human subjects were given a horizontally-moving cursor to use to intercept a diagonally-moving target (Figure 9). Interception was considered

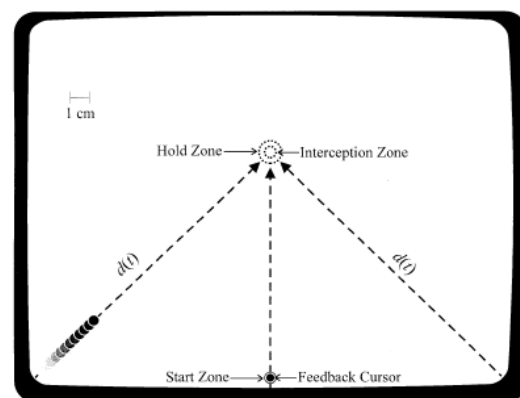


Figure 9: Diagram of the 2-D interception task

successful if the cursor arrived in the convergence zone within 100ms of the target. Different values for initial velocity, acceleration, and deceleration were used to correlate early and late arrivals to determine the method used for interception.

The two observed methods used for interception were predictive strategy, based on the tau-threshold model, and the reactive strategy, which is based on a distance-threshold model. Both models have been observed repeatedly, and each method tends to dominate according to circumstance; however, subjects also preferences for one strategy or the other, and the preferred strategy dominates in neutral circumstances.

### **3.3.1 Predictive**

The predictive strategy is based on the tau-threshold model, in which the observer uses the ratio of the size of the image vs. the absolute rate of expansion to calculate a time-to-contact. This strategy is statistically most accurate for constant target velocity; however, according to the data collected through the interception study, the predictive strategy was utilized most often during constant target acceleration. The calculated phase space (target displacement vs. velocity) for different constant acceleration values fits a large portion of the collected data, as do the calculated vs. recorded response times. However, this model does not represent behavioral observations accurately enough to be considered the default interception method in humans (Port, 1997).

### **3.3.2 Reactive**

The reactive strategy is so named because it requires that the image must move a certain minimum “threshold” distance across the retinal area before a response can be generated. The response time is modeled as the sum of two variables. The first is the time it takes for the target to move through the threshold distance, allowing the target velocity to be calculated by dividing that distance by the travel time. The second component of the response time is described as a processing delay time in the nervous system between the motion and the motor response (Van Donkelaar, 1992).

Interestingly enough, the reactive strategy is the method most commonly used in constant target velocity situations. In repeated constant-velocity experiments, previous velocity calculations are used to reduce the response time to the minimum processing

delay time, measured to be between 84ms and 214ms. However, in repeated, random, constant target velocity experiments, on-line corrections are necessary to make accurate interceptions based on previous velocity data. Although this model fits a large proportion of the recorded data in both phase space and response time, this model is not accurate enough to fully represent the human interception process (Figure 9 and Figure 10) (Port, 1997).

### 3.3.3 Dual-strategy

To most accurately model the 2-D interception response in human subjects, a compilation of both predictive and reactive models must be built. For constant velocity targets, the distance-threshold model is used, but for constant acceleration or constant deceleration target circumstance, the reactive model is employed. This model represents an accurate accounting of all of the recorded responses in the 2-D interception study (Figure 10 and Figure 11). One element of this model which has yet to be fully explained

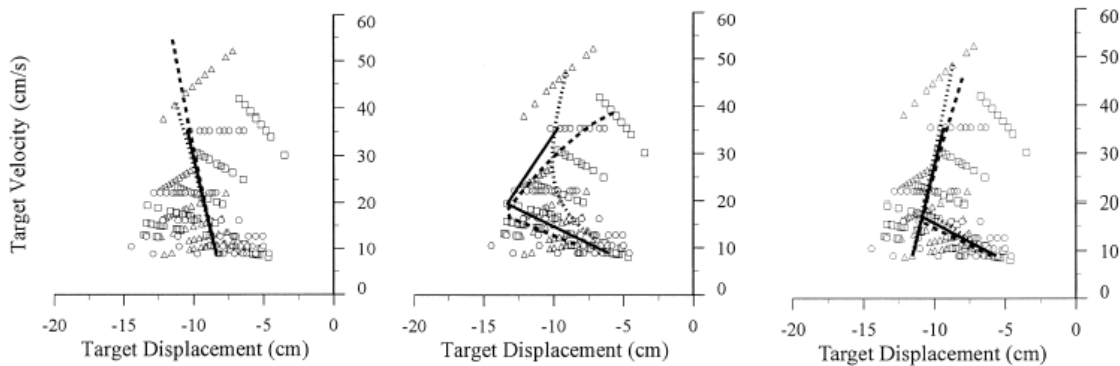


Figure 11: Phase space model of target velocity vs. displacement for tau-threshold (left), distance-threshold (center), and dual strategy (right). Lines are model predictions for constant acceleration (dotted), constant deceleration (dashed), and constant velocity (solid). (Port 1997)

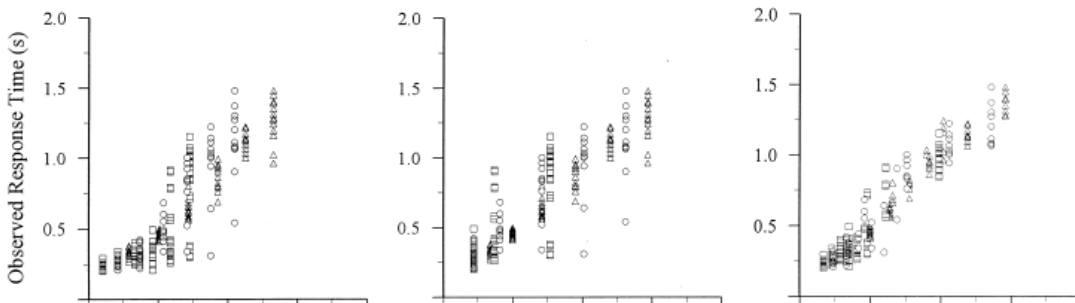


Figure 10: Predicted vs. actual response times for tau-threshold (left), distance-threshold (center), and dual strategy (right). Lines are model predictions for constant acceleration (dotted), constant deceleration (dashed), and constant velocity (solid). (Port 1997)

the nature and method involved in the on-line corrections made during the interception process.

### 3.4.0 Tau-coupled Hypothesis

During the study to determine the use of threshold models described in the previous section, it was observed that, for fast-moving targets, subjects moved their hands with symmetrical, bell-shaped velocity/time curves. However, for slow-moving targets, subjects maintained near-equal tau values between the target and the interception point and between their hand and the interception point. In order to further examine this tau-coupling hypothesis, neurons in the primary motor cortex (M1) of rhesus monkeys were monitored during the same interception task in response to real and apparent motion. Also, M1 neurons were studied during no-go tasks, when the subject did not display an interceptive response to the target stimuli (Merchant, 2003).

#### 3.4.1 Real vs. Apparent Motion

In an effort to most accurately recreate the interception process, the difference in subject responses to real and apparent moving targets has been studied. Subjects were to attempt interception of a circularly moving target at a specific point in its rotation. The real motion target smoothly moved through its orbit, while the apparent motion target could only exist at discrete points in the circle (Figure 12).

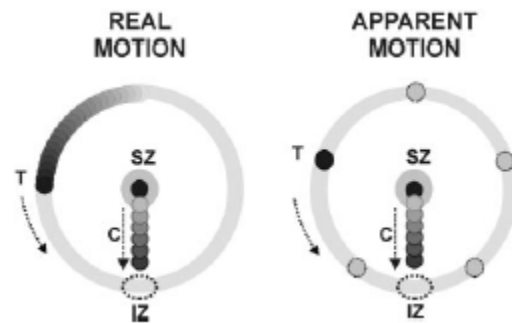


Figure 12: Test environment for real vs. apparent motion experiment

Subjects showed a linear interception error with respect to target angular velocity, but it was much more pronounced in the apparent motion examples (Figure 13). This showed that, although apparent motion targets can be intercepted using similar if not

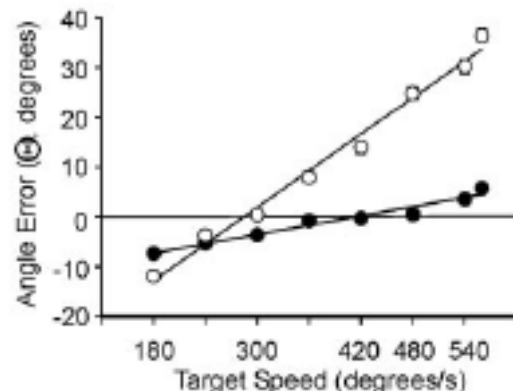


Figure 13: Interception error vs target speed in human subjects

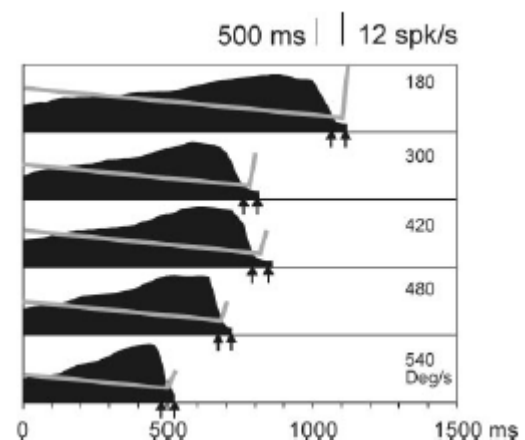
identical processes, the performance is greatly degraded, and motion studies should simulate real motion as accurately as possible (Port, 1996). The data collected fit results calculated by the tau-threshold to a first-order estimate in the apparent motion case, but did not correlate well with the tau-threshold or tau-coupled hypothesis in the real motion case, even for slow moving targets. Rather, the critical variable seemed to be the angular position of the target in real motion circumstances (Merchant, 2003).

### 3.4.2 Interception vs. No-Go Tasks (Merchant, 2004)

Three major findings resulted from a comparison of interception and no-go behaviors in rhesus monkeys. First, the recording of M1 activity showed modulation during both tasks as a function of target motion characteristics (velocity profile, acceleration, etc.), suggesting that relevant visual motion information used for directing interception is passed to the motor cortex.

Second, using a multiple regression model, the modulation of neuronal activity in the motor cortex was shown to correlate with a first-order

tau estimate of time-to-contact, suggesting that the M1 region is responsible for processing the gap closure time and coupling that time with tau (Figure 14). Finally, analysis of the spike density functions classified the neurons into two groups. The first group followed the motion of the hand during interception with respect to time, while the second group held information regarding target velocity as calculated by a series of sub-movements characteristic of the reactive strategy. This suggests a high volume and rate of intercommunication between target descriptor neurons and motion control neurons in the motor cortex (Merchant, 2004).



**Figure 14: SDF of response of motor cortical neuron (black), target time-to-contact (grey) during interception at 5 different target speeds. Arrows indicate beginning and end of subject interception movement.**

## 4.0.0 Conclusion

A convincing quantity of evidence has confirmed the tau-threshold model for target interception in simple target circumstances like impending collision or constant-

velocity interception. The studies of locusts and gannets have described the classical definition of tau, a ratio of image size to rate of image expansion (Lee, 1981). In order to better understand the higher-order time-to-contact calculations necessary for the completion of more complicated interception tasks, the activity of motor cortex neurons in rhesus monkeys has been documented during several interception tasks. The results of these studies have led to an enhanced theory of tau-coupling which requires the taus between any two objects to be kept in proportion during interception (Merchant, 2001). This theory allows for the observed ability for subjects to compensate for gap-closure rate changes. Based on tau-ramps recorded in neurons in the motor cortex and in area 7a of the posterior parietal cortex, it is apparent that even if the area 7a neurons contribute to the reconstruction of motion, the motor cortex is primarily responsible for synchronizing the interception movement (Port, 1997). The physiological and experimental evidence indicates that the most defining variable in the interception strategy is the context defined by the target (velocity and acceleration profile, accuracy requirements, and learned subject preferences). As such, the evolved strategies are as varied and complex as the visual circumstances encountered in everyday tasks. As several of the most popular strategies have been documented, the remaining research tasks surround the definition of the strategy selection criteria and the precise physiology of each strategy implementation.

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