THE ENVIRONMENT PROVIDES THE REFERENCE FRAME FOR SELF-MOTION PERCEPTION

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Abstract. The perception of self-motion is needed to successfully control body motion in the environment. This perception is originated by senses that register inertial body motions and senses that determine the environment in which the body moves. The perceived environment strongly influences self-motion perception. We argue that this occurs since the motion perceptual system searches for a reference frame in the environment, in order to place inertial body motion signals. We apply this idea to formulate a self-motion perception model. In this model, optimal estimators are applied to tune the inertial and environmental sensory signals and to model attention on specific motion frequency ranges. A quantitative model for perceived self-motion about the vertical axis is described, which is based on literature data.

Keywords: perception, visual, vestibular, visual-vestibular interaction, psychophysics, self-motion, perception models, optimal estimators

1. Introduction

There are different ways to achieve a displacement of the body in the environment. Whatever the means of motion (walking, horse ride, driving a car), a specific set of body actions is required to move. These actions range from moving our limbs as we walk, or the pushing of a button in an elevator, to handling the controls of an aircraft.

In order to successfully control body motion, the perception of the body motion state in the environment is needed: perceiving self-motion. Virtually every sense contributes to the perception of self-motion. Each sensory system has, however, its specific domain for registering motion stimulations. The visual system, for example, provides information on the position and velocity of the environment with respect to the eyes. Inertial sensory systems, like the vestibular system, register forces and accelerations on the body. The inertial systems are therefore insensitive to constant linear body velocities and to rotational velocities about the vertical axis in the horizontal plane [Guedry, 1974; Howard, 1982].

Psychophysical studies have shown that the perceived environment strongly influences the perception of self-motion. The visual environment in particular has a strong effect on perceived self-motion [Wong and Frost, 1978; Büttner and Henn, 1981]. However, it is still unclear how the central nervous system fuses body signals and environmental signals to give a perception of motion of the body in the environment.

We propose a self-motion perception model based on a search for a reference frame in which inertial body motion signals are placed. We argue that the perceptual system seeks for the reference frame in the environment. As a result, environmental motion influences self-motion perception. First, we will consider and discuss perceptual phenomena from psychophysical studies on self-motion. Then we will present a self-motion perception model and show the results of the model for motions about the vertical axis, the yaw motion. This yaw model is based on literature data.

2. Self-motion perception phenomena

Many experiments have been conducted to determine the influence of inertial body stimulation and environmental presentation on perceived self-motion and orientation. Some important results are stated below.

2.1. Inertial stimulation

From perception threshold experiments on roll and heave motions [Hoeman and Van der Vaart,
and yaw motions [Benson et al., 1989], the sensitivity of self-motion perception in the frequency domain was found similar to that of the primary vestibular afferents in the squirrel monkey [Fernández and Goldberg, 1971; 1976].

From experiments with exclusive inertial yaw motion, it was shown that subjects perceive accelerations quite accurately, but report a fainting motion sensation when the motion is at constant velocity [Parsons, 1970; Guedry, 1974]. The decay of motion sensation is, however, slightly less than the vestibular afferent dynamics suggest. Equivalent dynamics for inertial stimulation is found in cells of the vestibular nuclei in the brain stem [Waespe and Henn, 1977] and in reflexive eye movements [Raphan et al., 1979].

An attentional effect on motion perception thresholds was elegantly demonstrated by Hosman and Van der Vaart [1978]. They determined self-motion perception thresholds by slowly increasing the amplitude of a sinusoidal roll or vertical motion. The subject did not, however, know the motion type nor its frequency. When the subject detected the motion, the amplitude was slowly decreased and subjects had to report when the experienced motion had vanished. A substantial difference between the detection threshold and vanishing threshold was found, indicating an attentional effect.

2.2. Environmental presentation

A moving visual perceived environment [Wong and Frost, 1978; Büttner and Henn, 1981] as well as a moving somatosensory [Lackner and Dixio, 1984], auditory [Lackner, 1977], or even tactile or proprioceptive perceived environment [Brandt et al., 1977] can evoke a strong self-motion sensation. This (illusory) self-motion sensation is usually referred to as ‘vection’. In neurophysiological experiments on animals, cells in the vestibular nuclei have been found to be activated both during vection and during inertial stimulation of the whole body [Allum et al., 1976; Waespe and Henn, 1977].

Vection does not instantaneously occur but gradually builds up. From experiments on perceived yaw motion in a rotating striped drum, it was found that the time to full self-motion sensation depends on the visual acceleration applied [Melcher and Henn, 1981]. Furthermore, it was found that the layout of the environment is crucial for the generation of vection. When a ‘natural’ visual environment is at constant roll or pitch velocity around the subject, a complete head-over-heels motion sensation can be experienced [Howard and Childerson, 1994]. A perceived body tilt illusion occurs if a random dot pattern is used instead.

Perhaps introspectively, another phenomenon of environmental influence on self-motion perception can be illustrated. When a train on the opposite track starts to move, a passenger in the stationary train can perceive self-motion due to the relative visual motion in the peripheral visual field. When looking through the opposite window, where the waiting passengers walk on the platform, the perceived self-motion is recognised as an illusion and the self-motion sensation vanishes (almost?) instantaneously. This swift loss of self-motion sensation is not reported, however, from yaw experiments. The after effect of experienced self-motion persists longer when presenting a stationary environment which follows yaw velocity [Howard, 1982].

3. Phenomena discussed

3.1. Inertial stimulation

The entire inertial modality is often referred to as vestibular, suggesting that only the vestibular system is stimulated. Individual inertial senses are, however, hard to isolate. Other mechanoreceptors, such as somatosensory receptors, are stimulated as well in most experiments concerning vestibular psychophysics.

An enormous number of neuronal events takes place before the transduction of motion stimuli by the receptors leads to perceived self-motion. It is therefore striking that the magnitude of human self-motion perception from the perception threshold experiments [Hosman and Van der Vaart, 1978; Benson et al., 1989] resembles the squirrel monkey primary vestibular afferents so well.

From the similar dynamical behaviour for yaw motion of cells in the brainstem [Waespe and Henn, 1977], reflexive eye movements [Raphan et al., 1979], and self-motion perception [Parsons, 1970], it can be hypothesised that there is a signal in the brain that registers the motion of the body in the environment; a neuronal correlate for self-motion. This signal gives rise to reflexes of the body and evokes perceived self-motion. A time constant in these phenomena can be considered to be somewhat larger than the vestibular afferent time constant. This indicates a non-direct processing between vestibular afferent and registered self-motion. Raphan et al. [1979] state a storage of neuronal activity related to reflexive eye velocity which lengthens the decay of the vestibular afferent signal: ‘velocity storage’. 
3.2. Environmental presentation

Body motion with a certain magnitude in a specific direction through an inertially stable environment will result in an environmental motion of opposite magnitude and direction with respect to the body. If inertial body motion is absent, however, perceived self-motion appears to rely on environmental information. The reciprocity of body and environmental motion can therefore be considered to be represented in the brain. One way or the other, our perceptual system exploits this reciprocity [Wertheim, 1994].

From the experiments with rotating drums [Büttner and Henn, 1981; Melcher and Henn, 1981] it was shown that motion of the visual environment cannot account completely for self-motion sensation. Above certain acceleration amplitudes of the visual environment, the drum is perceived to move in the laboratory as well. From the animal neurophysiological experiments [Allum et al. 1976; Waespe and Henn, 1977], it can be argued that there actually is some kind of neuronal correlate in the brain for self-motion in the environment, located in the vestibular nuclei of the brainstem. This signal could be responsible for reflexes that stabilise the body and can be considered to evoke experienced self-motion.

4. The subjective reference frame

From the influence of the environment on perceived self-motion, we argue that the self-motion perceptual system seeks for a reference frame to place inertial self-motion signals. The body needs this inertial reference frame to define its self-motion and to generate reflexes to support the control of body motion in the environment.

We argue that this reference frame is constructed from the perceived environment. The environment only provides, however, a subjective estimation of the inertial reference frame. When this subjective reference frame does not coincide with the inertial reference frame, self-motion illusions, such as vection, can occur. It should be noted that a self-motion illusion only exists when regarding a reference frame that is different from the subjective reference frame, such as the inertial reference frame.

When our body moves, the perceived environment continuously updates the subjective reference frame. The quickly vanishing motion sensation in the train illusion shows that the update of the subjective reference frame can be very sudden: the frame is placed in the less ambiguous platform frame. The latencies of several seconds that are found in the drum experiments, on the other hand, suggest a slower update.

5. Model for self-motion perception

In our model for self-motion perception, we describe perceived body motion which is evoked by inertial stimulation of the body and by environmental presentation. The head is assumed to be fixed to the trunk. The trunk is assumed to be rigid. An inertial stimulation of the whole body consequently is applied to the head. We consider the environment to be perceived only visually.

5.1. Motion variables

In the model, we have separated motion of the body (H) and motion of the environment (W).

The input of the inertial systems is body motion in the inertial reference frame. The visual input (V) is composed of a combination of two signals. First, motion of the environment can result in visual motion across the retina. This retinal motion will be referred to as retinal slip. We do, however, continuously fixate our eyes on locations in the environment. When being stationary in the environment and following a moving object, for example, the retinal slip will be non-zero, although the environment is perceived to be stationary. The retinal slip is assumed to be compensated by a registration of the eye motion in the socket. This registration is usually referred to as the efference copy [Von Hoist and Mittelstaedt, 1950]. The efference copy is the second input of the visual system.

To incorporate retinal slip ($R_s$) and efference copy ($EC$), eye motion in the socket ($E$) is included in the model.

5.2. Inertial and visual model inputs

The inertial sensory systems are sensitive to forces on, and accelerations of the body in the inertial reference frame.

The motion of the eyes is described by the gaze ($G$); the sum of eye and head motion in the inertial reference frame:

$$ G = E + H $$

(1)

When gaze and visual environmental motion are unequal, a flow of the visual environment across the retina will occur: retinal slip. This slip is defined as:

$$ R_s = W - G $$

(2)

The input of the visual system is the subtraction
of retinal slip and efference copy:

\[ V = R_x - EC \]  \hspace{1cm} (3)

5.3. Inertial and visual dynamics

The inertial dynamics (\( T_{\text{ine}} \)) are specific for the motion type, and are considered to resemble receptor physiology. For inertial yaw motion, there hardly is any other sensory system stimulated than the vestibular system. Consequently, the physiology found by Fernández and Goldberg [1971] can be applied for the inertial yaw dynamics. The visual dynamics (\( T_{\text{vis}} \)) is modelled as a time delay. The magnitude of this delay represents the slower perception of visual motion when compared to the processing of inertial motion [Hosman and Van der Vaart, 1988].

5.4. Neural filters

Neural filters are applied to transform inertial and visual afferent signals to an estimation of the stimulation that led to the signal. This transformation is considered as neuronal processing of the afferent signal in a motion estimate of the original stimulation. The visual and inertial neural filters are referred to as \( NF_{\text{vis}} \) and \( NF_{\text{ine}} \), respectively, the output of the filters are \( H' \) and \( V' \); the estimates of inertial and environmental motion.

To construct the original stimulation from an afferent signal, the sensory process that leads to the afferent signal has to be inverted. The inverse process therefore needs the characteristics of the sensory process. In the central nervous system a sensory signal will, however, always be corrupted by signals that do not correlate to the motion stimulation (noise). Consequently, no inverse process can be defined. In the neural filters, an optimal estimator (Kalman filter) is applied to handle the uncorrelated signals and achieve a (pseudo-)inverse process. Each neural filters contains an internal representation (\( IM \)) of the dynamics of the inertial and visual transformation of stimulus to afferent signal, and the intensities of the uncorrelated signals. Appendix A contains a more detailed description of the neural filters.

The neural filters are constructed in such a way that an attentional influence on the estimation can be modelled. This is achieved by shaping the input noise of the internal model to a specific frequency domain; see Appendix A.

5.5. Visual attraction

The heart of the model is the updating process by the subjective reference frame which is provided by the perceived environment. The visual environment is modelled to 'attract' the inertial motion estimate towards the subjective reference frame. This attraction mechanism is achieved by an interaction of the inertial and visual motion estimates, \( H' \) and \( V' \) respectively; see Figure 1.

\[ \begin{align*}
V' & \rightarrow \text{VA} \rightarrow M \\
H' & \rightarrow \end{align*} \]

Fig. 1. The visual attractor combines the inertial and visual motion estimates and generates the motion signal.

5.6. Self-motion signal

The motion signal \( M \) is supposed to give rise to perceived self-motion in the subjective reference frame. The motion signal also directs eye motion in the socket (\( E \)) through the oculomotor system (\( T_{\text{ems}} \)).

The complete model is depicted in Figure 2.

\[ \begin{align*}
& \text{EC} \rightarrow T_{\text{em}} \rightarrow \text{NF_{vis}} \rightarrow T_{\text{ine}} \rightarrow \text{NF_{ine}} \rightarrow M \\
& \text{G} \end{align*} \]

Fig. 2. The self-motion perception model.

6. Model for yaw motion

Results from experiments on neurophysiology, eye movements and perception of body motion are well documented for yaw motion. For this motion type, the model is described quantitatively and is based on literature data.

In the yaw model, the visual dynamics (\( T_{\text{vis}} \)) is modelled as a time delay of 150 ms, see Appendix B. This time delay incorporates both the delay of the retinal slip and the efference copy. The inertial dynamics (\( T_{\text{ine}} \)) relates input acceleration and afferent output and is modelled as the dynamics found by Fernández and Goldberg [1971]. This dynamics resembles an overdamped torsion pendulum with an additional lead component; see Appendix B.

The visual attractor compares estimated environmental yaw velocity and estimated inertial yaw
velocity. The difference between these estimates is first-order low-pass filtered. The filtered difference and the inertial estimate are added and generate the motion signal $M$.

The oculomotor dynamics, generating compensatory horizontal eye movements from the motion signal ($M$), is considered to be unity. This contrasts to, for example, roll motions where compensatory eye movement can only reach a small torsion angle.

When the gains of both the efference copy and the retinal slip are taken unity and both signals have a same time delay in the central nervous system, the signals are synchronised, the visual input can be described by:

$$V = W - G + EC = W - (E + H) + M = W - (M + H) + M = W - H$$ (4)

With these assumptions, the feedback loops of the efference copy and the retinal slip are avoided. Then, the model only has $W$ and $(W - H)$ as the inputs. $W - H$ is the yaw motion of the visual environment with respect to the head. The yaw model is depicted in Figure 3.

The settings in the neural filters are chosen for the specific stimulus condition tested. These settings are demonstrated for both the inertial and the visual neural filter.

### 7.1. Inertial neural filter

The inertial neural filter provides the estimate of inertial stimulation of the body. Therefore, it contains the inertial sensory dynamics. The afferent signal is provided by $T_{in}e$, see Figure 3. A Bode plot of the inertial sensory dynamics [Fernández and Goldberg, 1971] is depicted in Figure 4. It should be noted that the input is a sinusoidal inertial angular velocity and the output is afferent firing rate.

![Fig. 4. Bode plot of the inertial sensory dynamics for yaw, according to Fernández and Goldberg [1971].](image)

The neural filter is applied to estimate the angular velocity in the frequency range of interest. This range is set by the shaping filter (see Appendix A). The effect of the filter on the afferent signal for a frequency range of 0.1 to 10 rad/s is demonstrated in Figure 5.

![Fig. 5. Bode plot of the cascade of the inertial dynamics and its neural filter for a frequency range of 0.1-10 rad/s.](image)

When comparing Figures 4 and 5, it can be seen that the transfer function of the cascaded systems is close to unity in the frequency range selected by the shaping filter, resulting in a unity gain and zero phase.

### 7.2. Visual neural filter

The dynamics of the cascaded visual dynamics and its neural filter is depicted in Figure 6. The selected frequency range is 0-0.1 rad/s.

The improvement of the visual transfer function
is small. Due to large phase lags in the visual dynamics, a higher frequency range selected results in an insignificant improvement of phase lag while the gain drops far below unity.

8. Model results

The results of the model for self-motion perception are shown for three conditions. First, the results for an inertial yaw motion with a visible environment are presented: a rotation in the light (RL). Secondly, the results are shown for an inertial yaw motion without visual information: a rotation in the dark (RD). Finally, the results for a yaw motion with only visual input are shown. The latter type of stimulation is referred to as circular vection (CV).

8.1. Rotation in the light

In Figure 7 can be seen that the model correctly duplicates the sensation of yaw motion in a visual environment. The time constant of the visual attractor, $\tau_{va}$, is chosen 1 s. The effect of the visual attractor reduces as $\tau_{va}$ increases. When increasing the time constant, perceived angular velocity sticks to the gain that is provided by the inertial estimate. The gain of the velocity estimate during rotation in the light can be improved by selecting a smaller value for $\tau_{va}$. Ultimately, the gain converges to unity when $\tau_{va}$ is set to zero. The perceived self-motion will then be reciprocal to the motion of the visual environment. Independent of the time constant of the visual attractor, however, the response converges to the body velocity, as defined by the visual environment as the subjective reference frame.

8.2. Rotation in the dark

Model parameter settings for rotation in the dark are different from the settings needed for model simulations in the light. The noise-signal ratio of the visual system in the neural filter (see Appendix A) has to be set much higher because of the lacking input of the retinal receptors in the dark. Secondly, because of lacking visual information, the visual dominance is much weaker. As a consequence, $\tau_{va}$ is taken larger. In the simulation, $\tau_{va}$ is 80 s.

Figure 8 shows the decreasing yaw sensation when accelerations are absent. This decrease is slower than the decrease of the afferent output of the inertial receptors.

8.3. Circular vection

The responses to exclusive visual stimulation are solely dependent on the parameters of the visual system (time delay and visual neural filter settings). The most important parameter is the strength of the environmental updating, which is expressed in the time constant of the visual attractor.

Figure 9 shows that the model mimics the influence of environmental motion on perceived self-motion. The sensitivity of the model responses...
9. Discussion

9.1. Model outline and performance

In the literature, different models have been suggested to account for the interaction of visual and inertial signals [Robinson, 1977; Raphan et al., 1979; Zacharias and Young, 1981; Borah et al., 1988]. Those approaches concentrated on the notion that motion of the visual environment unquestioningly drives the self-motion signal; both to evoke compensatory eye movement and to perceive self-motion. Our proposal that the perceptual system pursues a reference frame in the environment for perceived self-motion is of a greater generality. As we showed for the perception of yaw motions, this concept appears to form an excellent basis for describing self-motion phenomena.

The optimal estimation method in a model for human spatial orientation was first applied by Borah, Young and Curry [1988]. The purpose of the Kalman filter in their model is, however, different from our purpose. They applied the filter to describe self-motion perception from visual-vestibular interaction. We have applied optimal estimators in the visual and inertial neural filters to tune the afferent signal from a single sensory modality. The filters straighten the magnitude and improve the phase of the afferent output.

With the shaping filter in the internal model of the neural filter, the bandwidth of the expected stimulus frequency range can be selected. One of the consequences is that a longer persisting self-motion sensation in the dark can be achieved, usually referred to as ‘velocity storage’ [Raphan et al., 1979]. In our model, this storage is not explicitly modelled. It is the result of an ‘attempt’ of the neural filter to estimate body velocity in the low frequency domain of inertial velocities.

Long latencies in the build up of vection emerge from rotating drum experiments. We have modelled this by selecting a visual attractor time constant of about 5 seconds. It should be noted, however, that a ‘natural’ environment lacks in the drum experiments. We think that the visual attraction can be described by a much smaller time constant of about 1 s, or even less, when a natural visual environment is applied [Howard and Childerson, 1994].

9.2. Model extension

As a good approximation, only the semicircular canals are stimulated when applying an inertial yaw motion about the gravitational vector. The dynamics of this stimulus transduction can therefore be described by the well documented vestibular physiology. When extending the model to more motion types, the question emerges whether or not a single (dominant) sensory system can be taken as the generator of afferent signals.

A reference frame that is in uniform linear motion with respect to the earth inertial frame, is inertial by itself. Therefore, we think that the reference frame updating by the visual attractor has similar dynamics for linear motions as it has for pure yaw motions. The updating dynamics could, however, be different for motions in which the orientation with respect to the gravity vertical changes.

The extension of the model for a non-rigid body will result in an extended definition of the efference copy. The efference copy has to be taken as a combination of eye motion in the socket and head motion on the trunk.

Attentional effects on perceived self-motion can be described when applying the concept of a shaping filter in the internal model. This enables future modelling of an ‘active observer’ in this model.

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10. REFERENCES


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### A. Mathematical outline of neural filters

The neural filters represent low-level signal processing. They transform afferent output in an optimal estimate of sensory stimulations under a priori assumptions about:

1. the sensory system dynamics
2. the expected stimulus spectrum
3. the noise in each sensory measurement

These assumptions are referred to as the internal model. If the internal model satisfies the following conditions:

1. linear system representations
2. Gaussian white processes
3. stationary

the neural filter can be modelled as an optimal linear estimator or the well-known steady state...
Kalman filter. Below, the complete set of equations are summarised to calculate a neural filter.

The transfer functions of the sensors are formulated in state-space:

\[
\begin{align*}
\dot{x}_1 &= A_1 x_1 + B_1 u_1 \\
y_1 &= C_1 x_1 + D_1 u_1 + v
\end{align*}
\]  
(5)


The state-space notation of the shaping filter:

\[
\begin{align*}
\dot{x}_2 &= A_2 x_2 + E_2 w \\
y_2 &= C_2 x_2
\end{align*}
\]  
(6)

If \( \dot{u}_1 = y_2 \), then the shaping filter and the sensor are connected in series:

\[
\begin{bmatrix}
\dot{x}_2 \\
\dot{x}_1
\end{bmatrix} =
\begin{bmatrix}
A_2 & 0 \\
B_1 C_2 & A_1
\end{bmatrix}
\begin{bmatrix}
\dot{x}_2 \\
\dot{x}_1
\end{bmatrix} +
\begin{bmatrix}
E_2 \\
0
\end{bmatrix} w
\]  
(7)

or:

\[
\begin{align*}
\dot{x} &= A x + E w \\
y &= C x
\end{align*}
\]  
(8)

The steady state covariance of the state is the solution of the Lyapunov equation:

\[
\Phi_{xx,s} = A \Phi_{xx,s} + \Phi_{xx,s} A^T + Q E E^T
\]  
(9)

Where \( Q \) is the system noise power spectral density.

The steady state covariance of the observation is:

\[
\Phi_{yy,s} = C \Phi_{xx,s} C^T
\]  
(10)

The observation noise power spectral density is defined as a fraction of the covariance of the observation:

\[
R(i, j) = \left\{ \begin{array}{ll}
0 & \text{if } i \neq j \\
\rho(i) \Phi_{yy,s}(i, j) & \text{otherwise}
\end{array} \right.
\]  
(11)

The steady state error covariance of the Kalman filter is the solution of the Ricatti matrix equation:

\[
\dot{\Sigma}_s = A \Sigma_s + \Sigma_s A^T + Q E E^T - \Sigma_s C^T R^{-1} C \Sigma_s
\]  
(12)

The steady state Kalman filter gain matrix:

\[
G_{kf} = \Sigma_s C^T R^{-1}
\]  
(13)

The differential equation for the optimal observer is formulated as follows:

\[
\dot{\hat{x}} = A \hat{x} + G_{kf} (\hat{y}_1 - C \hat{x})
\]  
(14)

or

\[
\dot{\hat{x}} = A_{kf} \hat{x} + G_{kf} \hat{y}_1
\]  
(15)

where

\[
A_{kf} = A - G_{kf} C
\]  
(16)

An observation equation can be defined by only measuring the sensory stimulation, \( \dot{u}_1 \):

\[
\begin{align*}
\dot{y}_{kf} &= \dot{u}_1 = \begin{bmatrix} C_2 & 0 \end{bmatrix} \begin{bmatrix} \dot{x}_2 \\
\dot{x}_1
\end{bmatrix}
\end{align*}
\]  
(17)

or:

\[
\begin{align*}
\dot{u}_1 &= C_{kf} \hat{x} \\
\dot{y}_{kf} &= \begin{bmatrix} C_2 & 0 \end{bmatrix} \begin{bmatrix} \hat{x}_2 \\
\hat{x}_1
\end{bmatrix}
\end{align*}
\]  
(19)

The state-space relating the afferent signal, \( \dot{y}_1 \), and the estimated sensory stimulation, \( \hat{u}_1 \), is summarised as:

\[
\begin{align*}
\dot{x} &= A_{kf} x + G_{kf} \dot{y}_1 \\
\dot{u}_1 &= C_{kf} \hat{x}
\end{align*}
\]  
(20)

B. Transfer functions of the sensory systems

The transfer function of the visual system in Laplace domain is modelled as a time delay. The time delay is approximated by a Padé filter to maintain model linearity. The Padé filter is complemented with a low-pass filter to account for physiological constraints on receptor transduction:

\[
H_{vis}(s) = \frac{1}{1 + \tau_v s + \frac{\tau_d s}{2}}
\]  
(22)

where \( \tau_v \) is the time constant of the low-pass filter, and \( \tau_d \) is the effective time delay of the visual system. The following values are implemented in the yaw model:

\[
\begin{align*}
\tau_v &= 0.1 s \\
\tau_d &= 0.15 s
\end{align*}
\]  
(23)

The transfer function of the whole body inertial motion sensors is according to Hosman and Van der Vaart [1978]. Relating input angular velocity and sensory afferent output, this function is described as:

\[
H_{ins}(s) = \frac{s(1 + 0.11 s)}{(1 + 5.5 s)(1 + 0.005 s)}
\]  
(25)

To transform input angular acceleration to input angular velocity, in which the visual output is defined, the numerator must be multiplied by \( s \).