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A neural circuit model for prospective control of interceptive reaching

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Running Title: Prospective Control of Interceptive Reaching
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Abstract. Two prospective controllers of hand movements in catching – both based on required velocity control – were simulated. Under certain conditions, this required velocity control led to overshoots of the future interception point. These overshoots were absent in pertinent experiments. To remedy this shortcoming, the required velocity model was reformulated in terms of a neural network, the Vector Integration To Endpoint model, to create a Required Velocity Integration To Endpoint model. Addition of a parallel relative velocity channel, resulting in the Relative and Required Velocity Integration To Endpoint model, provided a better account for the experimentally observed kinematics than the existing, purely behavioral models. Simulations of reaching to intercept decelerating and accelerating objects in the presence of background motion were performed to make distinct predictions for future experiments.

Keywords: Interceptive reaching; Neural network; Model; Arm movement; Vector-integration-to-endpoint; Relative velocity; Perception-action cycle; Time-to-contact
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1. Introduction

For animals and humans to successfully interact with their environments, their actions must be guided by information. The visual guidance of interceptive actions is an excellent and much studied example in this regard. The manual interception of an object traveling on a passing trajectory requires matching the hand position with that of the object while it is within reach. Two types of strategies for the informational control of interceptive actions have been proposed in the literature, respectively called predictive (e.g., Lee, 1976; Tyldesley & Whiting, 1975; see also Tresilian, 1994; Regan, 1997) and prospective (e.g., Chapman, 1968; Lee & Young, 1985; Peper, Bootsma, Mestre, & Bakker, 1994; Bootsma, Fayt, Zaal, & Laurent, 1997, Montagne, Laurent, Durey, & Bootsma, 1999). Predictive strategies are based on information specifying a future event (e.g., the ‘when’ and ‘where’ of a forthcoming interception). In their purest form, such information is used for programming the entire hand movement prior to initiation (e.g., Tyldesley & Whiting, 1975). Prospective strategies are based on information specifying the actions, as they are currently required for a successful interception. By means of on-line control based on such information, the actor establishes a particular dynamic relationship with the environment, which leads to success if the relationship prevails (e.g., Chapman, 1968; Peper et al., 1994).

In general, predictive strategies without any on-line control form an uncertain means for controlling interceptive actions. The continuously changing environment may limit the accuracy of the predictions on which the programming of such actions is based, particularly when the time between prediction and interception is long. To remedy this shortcoming, it has been suggested that preprogrammed actions could be supplemented by on-line adjustments based on updated predictions (e.g., Tyldesley & Whiting, 1975). This possibility, however, has never been fully pursued in the literature, probably because in the analysis of kinematic data it is rather difficult to distinguish between repetitive updating of a motor program and genuine on-line control. Prospective strategies are dependent on such on-line control, leading to a continuous modification of the action as it unfolds in time. On-line control ensures a more robust perception-action coupling than predictive control, because the success of the former is not critically dependent on the accuracy of a single, instantaneous perception (Peper et al., 1994).

Any on-line control strategy suffers from the drawback that feedback can never be used instantaneously due to neural transmission times. Such delay times determine the accuracy of a closed-loop system, especially when the system quickly changes state. Short-term extrapolation of the available information may be used to compensate for feedback delays. Nevertheless, certain actions may be too short to allow for the use of feedback. Since feedback delays necessarily vary across effector and sensory systems and across age in growing animals, such short-term extrapolation has to be adaptive. Although the current study does not specifically address this problem, it will be revisited in the Discussion.

In predictive strategies, the current state of the actor-environment system specifies a future event, such as an object arriving at a particular point at a particular time. In this context, optical $\tau$ (Lee, 1976), the inverse of the relative rate of expansion, has received much attention in the literature as it specifies the first order time-to-contact ($TC_1$) of an object moving on a collision course with the observation point. Hence, optical $\tau$ could be used to time the initiation of an action with a certain movement time, provided that the discrepancy between the actual time-to-contact and $TC_1$ is not too large. Contrary to predictive strategies, prospective strategies are characterized by the fact that the evolving state of the actor-environment system specifies the currently required action.
The present study focuses on the prospective control of lateral hand movements in interceptive actions, with an explicit interest in its neural implementation. An advantage of the prospective controllers proposed in the recent literature is that they are formally explicit, which allows for numerical simulations of their behavior and direct comparisons of this behavior with available kinematic data (e.g., Tresilian, 1995). In the first part of this study, such simulations and comparisons are performed for two models for the control of lateral hand movements in catching that are both based on required velocity control, albeit in a different manner (i.e., Peper et al., 1994; Bootsma et al., 1997). To anticipate, it will be shown that both models suffer from a fundamental deficiency in accounting for the behavior they were designed to explain. To remedy this deficiency, a new prospective control model is derived by extending the Vector Integration To Endpoint, or VITE, model (Bullock & Grossberg, 1988a; 1988b; 1991). An advantage of this new model relative to the extant models is that it incorporates a neurophysiologically plausible instantiation of the control structures generating the motor outflow commands for the arm, thus providing additional handles for further modifications of the model. Simulations of the newly derived model show that such modifications are indeed required, resulting in a revised version of the model, which is capable of reproducing relevant empirically observed kinematic properties. Finally, from simulations of this new model specific predictions are derived for future experiments.

2. Required Velocity Control
2.1. The Peper et al. (1994) or RV Model

In the recent literature on interceptive actions, there has been a great deal of interest in the prospective control of interceptive actions (e.g., Bootsma, 1998; Bootsma et al., 1997; Montagne, Fraisse, Ripoll, & Laurent, 2000; Montagne et al., 1999; Regan, 1997). This interest was sparked in large part by the required velocity model proposed by Peper et al. (1994), which describes a simple yet effective way to control the instantaneous hand velocity in order to successfully intercept a moving object. Peper et al. proposed that hand movements are controlled on the basis of information about the currently required hand velocity $\dot{X}_{h_{req}}$ as specified, at any moment in time during the approach, by the ratio of the lateral distance between the hand position ($X_h$) and the object position ($X_o$) to the TC of the object with the axis of hand movement (see also Figure 1):

$$\dot{X}_{h_{req}} = \frac{X_o - X_h}{TC}$$

By continuously moving the hand at the currently required velocity, the lateral object-hand distance is reduced to zero in the remaining TC. Although Peper et al. used $\tau$ (one class of optical variables specifying TC) in their formulation, TC is used here to express the general nature of the $\dot{X}_{h_{req}}$ information. By itself, Equation 1 predicts a velocity jump at movement onset. Since in reality the hand velocity is initially zero and then increases smoothly, Peper et al. incorporated an activation function similar to that of the GO signal in the VITE model (see Bullock & Grossberg, 1988a):

$$\dot{X}_h = \Omega(t) \frac{X_o - X_h}{TC}$$

where

$$\Omega(t) = A \frac{\tau^*}{\phi^* + \delta t^*}$$

Insert Figure 1 about here
Here, $\dot{X}_h$ represents the current hand velocity and $\Omega(t)$ a time-dependent, faster-than-linear activation function with parameters $\phi$, $\delta$, and $n$ and the amplitude of activation $A$. In the following, this model will be referred to as the required velocity (RV) model.

Because the RV model posits a continuous control law, success does not critically depend on the moment of initiation. Whatever the initial and evolving conditions, Equation 1 specifies the currently required hand velocity. Furthermore, above a certain limit success does not depend on the magnitude of $A$, because the instantaneous multiplier of $(X_o - X_h)$ is $\Omega(t)/TC$ and the vanishing denominator ensures compensation for a slow start. Two further properties are noteworthy. First, the denominator in Equations 1 and 2 need not be the actual TC; any function that smoothly decreases to zero at contact could be used in principle. Therefore, a $TC_1$ variable as denominator in Equation 2, such as $\tau$ (see Peper et al., 1994), still leads to successful performance. Second, the ratio may call for arbitrarily large, and therefore unrealizable, hand velocities and accelerations near contact.

2.2. The Bootsma et al. (1997) or RA Model

Bootsma et al. (1997) preferred not to use an activation function. (Montagne et al. (1999) stated it was judged inconsistent with the premises of the ecological approach.) They suggested to replace this activation function by an additional control loop in which a kinematic property of the flow (viz., required velocity) is used to specify a “kinetic” property of the movement or at least a property linked to the kinetics, that is, the acceleration of the hand. Accordingly, they suggested that the required velocity ($\dot{X}_{req}$, as specified in Equation 1) and actual hand velocity ($\dot{X}_h$) may be used to generate a specific hand acceleration ($\ddot{X}_h$) profile:

$$\ddot{X}_h = a\dot{X}_{req} - \beta\dot{X}_h$$

where $\alpha$ and $\beta$ are constants during a particular interceptive movement. Variations in these parameters may reflect variability between tasks and individuals. Equation 4 specifies that $\dot{X}_h$ is attracted to a value proportional to the required velocity. The rate of attraction depends on $\beta$ and the ratio $a/\beta$ represents the constant of proportionality. Given specific values of $\alpha$ and $\beta$, $\dot{X}_h$ reflects the hand acceleration that drives the hand velocity to a correct value for successful interception. Therefore, this model will be referred to as the required acceleration (RA) model.

Bootsma et al. (1997) suggested that a single control law is used for both movement initiation and execution. To this end, initiation was coupled to a critical value of the required velocity. As a consequence, the RA model predicts an acceleration jump at initiation. In their simulations, however, such a jump was not observed. Another puzzling aspect of their simulations was the fact that the simulated kinematics reflected successful interception, even though an uncompensated perceptuo-motor delay of 100 ms was incorporated.

3. Testing the Models

3.1. Data Constraints

In the following, a brief overview is presented of pertinent data from studies focusing on required velocity information, which will allow us to make relevant model-data comparisons later on.

In the experiment of Peper et al. (1994), the participants had to right-handedly catch balls that were swinging toward them and passing their heads on the right-hand side. Hand movements were restricted to a lateral axis (see Figure 1), and the ball trajectories intercepted this axis at one of two positions (the interception point, or IP). The angle at which the balls
approached these IPs was varied (five angles of approach for each IP). The observed arm trajectories had several systematic characteristics, which are summarized in Table 1. These characteristics implied that, even in case the balls passed the participant at exactly the same lateral distance (i.e., at the same IP), the ball’s trajectory toward this IP had systematic effects on the hand movements. Notably, the hand velocity reached the required velocity (i.e., Equation 1) some time before contact, circa 450 ms in the example presented by Peper et al. On average, the hand moved in a rightward direction at interception. Overshoots were seldom observed.

In a recent experimental study, Montagne et al. (1999) used an alternative version of the Peper et al. (1994) task. A ball approached along a straight trajectory with a constant velocity. Approach angle and initial hand position were manipulated. The goal of the experiment was to distinguish between the use of a predictive and a prospective strategy. With the hand placed initially at the interception point, a prospective (required velocity) strategy would predict movement direction reversals (MRs) for non-straight approaches, whereas a predictive strategy (using a perfect prediction of the object’s IP) would not. When the hand was initially positioned at the IP, MRs in the expected direction were indeed present in 40% of the trials with an outward approach and in 42% of the trials with an inward approach. However, MRs of unexpected direction were also present in 22% of the trials with an outward approach and in 11% of the trials with an inward approach. Left-to-right MRs were never present with the hand starting to the left of the IP, while right-to-left MRs never occurred with the hand starting to the right of the IP. For an initial hand position on the opposite side of the IP relative to the initial ball position, the incidence of MRs was 11% (left-to-right) and 4% (right-to-left). Straight approaches with the hand initially at the IP led to left-to-right and right-to-left MRs in 11% and 26% of the trials, respectively.

Exemplary kinematic data for one participant in this study are presented in our Figure 2. This figure clearly shows the MRs and the systematic kinematic variations over conditions. Even though this plot only presents the kinematics of one trial per condition for a single participant, it will be used here as a main reference for the simulations as it may be assumed to capture the main kinematic effects of the manipulation of interest. The difference between the currently required and the actual hand velocity approached zero circa 300 ms before contact in all conditions for the trials of a typical participant as shown in Figure 7 of Montagne et al. (1999), although detailed inspection of this figure suggests that in most trials the hand velocity was somewhat higher than the required velocity from that point onward.
Montagne et al. (2000) imply that maximal velocity was sometimes reached before, and sometimes after contact. This variation was not reflected in their Figure 3 (see our Figure 3), which shows the velocity profiles of one of the participants.

3.2. Methods

The models incorporating required velocity information are expressed as differential equations. The behavior of these differential equations was simulated and the resulting kinematics compared to the data discussed above. All simulations were run under MATLAB 5.2 on a standard PC. The simulations involved numerical integration with a fourth order adaptive step-size Runge Kutta method. The algorithm returned the system's state in steps of 0.001 s. Most parameter values were kept constant in all simulations: $\phi = 1$, $\delta = 0$ and $n = 1.4$. Other parameter variations are reported as appropriate.

3.3. Results

The primary aim of the present section was not to obtain a (close to) perfect quantitative match for the movement trajectories depicted in Figures 2 and 3, which are only exemplary, but rather to obtain a good qualitative match for the behavioral characteristics summarized above. Therefore, no further attempts were made to optimize specific individual parameter values.

3.3.1. Simulations of the Montagne et al. (1999) experiment

The most striking result of this study was the occurrence of MRs for non-straight approaches when the hand was initially positioned at the IP. Although these MRs did not occur in all trials, models for interceptive actions should be able to account for their presence (and absence). Our simulated kinematics were compared to the typical kinematics presented in Figure 2, which features MRs. In our simulations, initial hand position was set to 0.35 (IHP1), 0 (IHP2) or -0.25 (IHP3) m (i.e., corresponding to those used in the original experiment, cf. Figure 2). The object started to move (velocity: 2.8 m s$^{-1}$) at a linear distance of 4 m from the IP under one of three approach angles (-4°, 0° or 4°). For the RV model, $A$ was set to 1 or 3. For the RA model, the parameter values were set to those used by Bootsma et al. (1997) ($\alpha = 11$ or $\alpha = 17$, with $\beta = 5$). All plots have the same format as Figure 2, thus allowing a direct comparison with the data of Montagne et al. (1999). Only the most striking features of the simulated kinematics are reported in the text.

Because Montagne et al. (1999) did not present movement initiation times, this was an undefined variable that needed to be set to allow simulation. We decided to couple movement initiation to a critical value of $\dot{X}_{\text{req}}$ in these simulations. Since in conditions IHP2(±4°) $\dot{X}_{\text{req}}$ did not change after object onset$^2$, the critical value of $\dot{X}_{\text{req}}$ was chosen smaller than its initial value in these conditions (±0.195 m s$^{-1}$ for the Montagne et al. (1999)-task$^3$) to ensure initiation: a critical $\dot{X}_{\text{req}}$ value of 0.1 m s$^{-1}$ was used in all simulations of this task, implying that for conditions IHP2(±4°) initiation occurred immediately upon the object motion onset. This one feature does not fully match Montagne et al. (1999)'s Figure 3, which shows that initiation occurred about 450 ms before contact. This limitation on comparisons with Figure 2 does not affect the general conclusions stated below.
For the RV model (see Figure 4), MRs were indeed observed for conditions IHP2(±4°). In
addition, overshoots of the IP and subsequent MRs were present for conditions IHP1(4°) and
IHP3(-4°), that is, in those conditions in which the hand was not initially at the future IP and
the direction of the required hand movement was opposite to the lateral component of the
object’s approach trajectory. The occurrence of such overshoots is not in agreement with the
general features of the behavioral data. Like the MRs in conditions IHP2(4°) and IHP2(-4°),
these overshoots were larger for \( A = 3 \) than for \( A = 1 \). Another inconsistency with Figure 2
concerned the observation that for \( A = 3 \) the hand reached the IP some time before contact in
conditions IHP1(0°) and IHP3(0°). For the RA model (see Figure 5) the MRs and overshoots
discussed above were also present, with rather large amplitudes for both parameter settings
(see Figures 5A and 5B). Similar to Figure 4B, the hand reached the IP some time before
contact in conditions IHP1(0°) and IHP3(0°), after which it oscillated around the IP.

3.3.2. Simulations of the Montagne et al. (2000) experiment
The same two models were simulated to generate predictions for the Montagne et al. (2000)
study, including the effects of varying the object’s initial TC on maximal velocity and
moment of maximal velocity (see Table 2 in Montagne et al., 2000, p. 67). In accordance
with the experimental settings, initial hand position was set to -0.65 m. The object moved
perpendicular to the hand movement axis (i.e., a 0° approach angle) at a constant velocity.
Initial TC of the object (a function of object velocity) was varied in the same manner as in the
experiment: values of 1, 1.25 and 1.6 s were used. Initial object distance was set to 4 m. The
average latencies reported by Montagne et al. (2000; i.e., 0.6, 0.81 and 1.103 s after object
motion onset) were used as inputs for the simulations. Note that these latencies were
averaged over the two initial object distances. To allow for comparison with Montagne et al.
(2000), simulated kinematics are presented in the same format as Figure 3. Parameter values
were varied to explore the models’ kinematic ranges, which are also discussed below.

Insert Figure 6 about here
Insert Table 2 about here

The velocity profiles resulting from the RV model varied from faster-than-linear (for low
values of \( A \)) to more or less bell-shaped (for high values of \( A \)). For very large \( A \)’s, the hand
reached the future IP before contact, after which the velocity fluctuated around zero. Since
for the RV model \( A \) was the only parameter that was varied, the kinematic range of the model
was rather small. This is illustrated by the fact that in order to obtain a velocity peak that is
not followed by too precipitous a velocity drop just before contact, \( A \) had to be small, which
also caused the peak velocity to be rather high and to occur rather late (see Table 2). The
simulation in Figure 6A used a compromise value of \( A \) that produced a reasonably realistic
time and magnitude of the maximal velocity. However, this choice also led to a much faster
drop of hand velocity just before contact than the one depicted in Figure 3.

For the RA model, velocity profiles ranged from continuously increasing (for low values
of \( \alpha \) and \( \beta \)) to part of a bell shape (for high values of \( \alpha \) and \( \beta \)). For large differences between
\( \alpha \) and \( \beta \), overshoots of the future IP occurred. Better fits were obtained if \( \alpha \) and \( \beta \) were
adjusted according to the initial TC of the object (while keeping the ratio \( \alpha / \beta \) constant, larger
values of \( \alpha \) and \( \beta \) led to better results for smaller initial TCs and vice versa). Although the
“acceleration jump” caused a mismatch between the velocity profiles and Figure 3 in the
initial part of the trajectory (see Figure 6B), the times and magnitudes of maximal velocity
were close to the experimental values reported by Montagne et al. (2000, see our Table 2).
Nevertheless, for a large range of $\alpha$'s and $\beta$'s, $X_h$ deviated from $X_o$ at interception to a larger extent than the RV model (e.g., 0.03 m for TC$_{im} = 1.00$ in Figure 6B).

3.4. Adequacy of the RV and RA models

In simulating the results of Montagne et al. (1999), both models demonstrated clear MRs in conditions IHP2($\pm 4^\circ$), as observed in a considerable portion of the behavioral data. The amplitudes of the MRs were more realistic for the RV model. In addition, our results indicate that for the RV model these amplitudes tend to vanish for smaller values of $A$. However, for very small values of $A$, $X_h$ is not geared strongly enough to $X_{req}$, resulting in unsuccessful interceptive performance. This holds even stronger for the RA model; the MR amplitudes tend to vanish for $\beta > \alpha$, but then performance only comes close to success if $\alpha$ is very high ($X_h$ is attracted very strongly to a value several times larger than $X_{req}$). Thus, both models show problems in dealing with the frequently observed absence of MRs in conditions IHP2($\pm 4^\circ$).

Systematic overshoots and subsequent MRs for conditions IHP1($4^\circ$) and IHP3($-4^\circ$) were observed for both models. However, such overshoots only occurred in 4 and 11% of the Montagne et al. (1999) data, respectively. Neither model could account for the kinematics of condition IHP3($-4^\circ$), in which the hand arrived at the IP before contact and remained there (see Figure 3). In spite of their shared shortcoming in reproducing conditions IHP1($4^\circ$) and IHP3($-4^\circ$), the kinematics obtained for the RV model were in better agreement with Figure 2 than those obtained for the RA model. Neither model could accurately produce the velocity profiles of the Montagne et al. (2000) study (i.e., Figure 3), although in this case the RA model led to the better match. However, this required parameter variations over conditions.

Especially the inability of both models to reproduce the kinematics of conditions IHP1($4^\circ$) and IHP3($-4^\circ$) of the Montagne et al. (1999) study constitutes a major drawback of the extant models. Simulations of Equation 2 for the Montagne et al. (1999) task, with $X_h$ equaling $\dot{X}_{req}$ (i.e., $\Omega(t) = 1$), revealed that overshoots in conditions IHP1($4^\circ$) and IHP3($-4^\circ$) are an intrinsic property of required velocity control (see Figure 7). This is caused by the fact that within a certain period, $X_h$ is attracted to $X_o$. Obviously, an adequate model should produce no overshoots in these conditions, while maintaining a good match with the kinematics observed in the other conditions. In the following, such a model will be derived.

4. Towards a New Model

Our simulations revealed that neither the RV model nor the RA model could produce a good match of Figure 2 for a single parameter set. This implies that, regardless of the way in which $\dot{X}_h$ is geared towards $\dot{X}_{req}$ (i.e., either by means of an activation function, or by means of acceleration control, according to Equation 4), required velocity control as specified by Equation 1 is in itself not sufficient to account for the behavioral results considered. On the other hand, the MRs present in conditions IHP2($\pm 4^\circ$) were accounted for reasonably well (especially by the RV model). As such, the core of both models, that is, Equation 1, may still serve as a useful starting point for further modeling. Prior to such modeling, two essential considerations will be discussed.

The RV and RA models describe kinematics at a behavioral level. Mathematical extension of such behavioral models runs the risk of becoming more and more abstract, without allowing for or facilitating adequate informational or biological interpretations of
their functioning. Such interpretations may be more straightforward in a neural network approach. Furthermore, such an approach takes neural dynamics into account, which may be important in unraveling the precise control structure of interceptive actions. These considerations led us to adopt a neural network approach for further modeling efforts. An interesting observation in this regard is that the mathematical formulation of the RV model is very similar to that of the Vector Integration To Endpoint (VITE) model (cf. Bullock & Grossberg, 1988a, 1988b, 1991), as was already recognized by Peper et al. (1994). The VITE model is a neural network model that was proposed for the control of hand positioning in point-to-point movements and incorporates neurophysiologically plausible control structures for generating the motor outflow commands for the arm. In view of these properties, the VITE architecture was chosen as a starting point for our further model developments. In the next sections, this model will be discussed, together with the extensions that were made to have the model produce motor outflow commands corresponding to realistic kinematics.

In developing the new model, we refrained from the use of acceleration control for two reasons. First, the extension of the original RV model did not result in improved performance (viz. our simulations of the RA model). Second, most neurophysiological evidence contradicts exclusive or predominant acceleration control: cell firing in voluntary cortical control areas correlates strongly with limb position and limb velocity, while force correlations are largely restricted to a subset of the cortico-spinal projection neurons in the posterior part of area 4 (e.g., Georgopoulos, Kalaska, Caminiti, & Massey, 1982; Kalaska, Cohen, Hyde, & Prud'homme, 1989; Kalaska, Cohen, Prud’homme, & Hyde, 1990; Lacquaniti, Guigon, Bianchi, Ferraina, & Caminiti, 1995). Furthermore, stretch reflexes generating compensatory muscle commands during movement are guided by signals whose principle components reflect stretch amplitude and stretch rate (e.g., Matthews, 1972). Based on these considerations an activation function was used to gear $X_{11}$ towards $X_{\text{req}}$, which is already present in the original VITE model.

4.1. The VITE Model

The VITE model (Bullock & Grossberg, 1988a, 1988b, 1991, see Figure 8) is an internal circuit that generates on-line planned movement trajectories with or without perceptual input. It is best thought of as a central pattern generator that can be guided by perceptual information. Firing characteristics of different cell populations, of the type used to compute population vectors (e.g., Georgopoulos et al., 1982; Lacquaniti et al., 1995), are incorporated in the model. These vectors represent the target position (the Target Position Vector, TPV, $X_\theta$ in the sections above), the current hand position (the Present Position Vector, PPV, $X_h$ in the sections above) and the hand-target distance (the Difference Vector, DV). The PPV is continuously updated by integrating the DV over time. This integration is gated by an internally generated GO-signal, which increases during the movement time with a faster-than-linear or sigmoidal shape (Bullock & Grossberg, 1988a). As a discrete movement generator, the model is specified by:

\[
\dot{V} = \gamma(-V + T - P) \tag{5}
\]
\[
\dot{P} = G[V]^+ \tag{6}
\]
\[
G = G_0 g(t) \tag{7}
\]

Here, $T$, $P$, $V$ and $G$ represent TPV, PPV, DV and the GO-signal, respectively. $\gamma$ is an integration rate scalar and $G_0$ a scalar of the invariant $g(t)$. The movement vector $V$ tracks the difference $T - P$ at rate $\gamma$ and $P$ changes at rate $G[V]^+$. The symbol $[\arg]^+$ means max(0, arg),
which stops the integration when $V$ equals zero. $\dot{P}$ represents the Desired Velocity Vector (DVV). Signal $g(t)$ can be generated by a two-cell (i.e., $g'$ and $g$) cascade, to result in a faster-than-linear or sigmoidal shape, depending on the parameter setting. Such a cascade can be specified mathematically by:

\begin{align*}
    g' &= -Bg + (C - g') \\ 
    g &= -Bg + g'(C - g)
\end{align*}  

$V$ starts updating as soon as the object is presented (i.e., priming), whereas the movement $P$ only starts updating at initiation (i.e., when the GO signal is turned on). The VITE model can account for many kinematic features of fast reaching movements involving stationary objects and has a firm and extensive neurobiological grounding (e.g., Bullock & Grossberg, 1988a, 1988b, 1991; Bullock, Cisek, & Grossberg, 1998; Cisek, Bullock, & Grossberg, 1998; see also below). Although $G_0$ allows for the control of movement time to a fixed object (i.e., a stationary object), the VITE model as defined by Equations 5-9 does not explain how to intercept a moving object within a given time (Beek & Bootsma, 1991, see also Peper et al., 1994).

4.2. The RVITE Model

As a first step in appropriating the VITE model for interceptive actions, it was reformulated to incorporate required velocity control, resulting in a model that was mathematically (and thus behaviorally) very similar to the RV model. The model thus could be called the Required Velocity Integration To Endpoint model (RVITE). Two formulations were considered: (i) gating the GO signal with $TC_1$ and (ii) gating the TPV and PPV inputs to the DV with $TC_1$. These possibilities are mathematically nearly equivalent and are not mutually exclusive (see also below). It was decided to start out with formulation (i), because it preserves the conceptual clarity and "factorization" of the original VITE model and it coheres with earlier proposals as to how to incorporate a temporal signal into the VITE model (Beek & Bootsma, 1991). Mathematically, the RVITE model is expressed by changing Equation 7 to:

\begin{equation}
    G = \frac{G_0 g(t)}{TC}
\end{equation}

To allow for a change in movement direction during a movement the rectification of $V$ ($V_1$ in Equation 11, in anticipation of the model extension presented below) was removed:

\begin{equation}
    \dot{P} = GV_1
\end{equation}

In the original VITE model, movement time scales inversely with $G_0$. $G_0$ therefore was also made responsive to $TC$ at the moment of initiation, by letting:

\begin{equation}
    G_0 = \frac{\lambda}{TC_{int}}
\end{equation}

where $\lambda$ is a constant and $TC_{int}$ is the object's TC at initiation. (Variations of $\lambda$ thus allow for voluntary control of movement velocity). The system described by Equations 7-12 integrates $(T-P)$ to zero within the remaining $TC$.

The RVITE model is consistent with earlier model constructs that assume that movements towards static and moving objects result from the same underlying dynamics (e.g., Schöner, 1990; Zaal, Bootsma, & Van Wieringen, 1999). Additionally, it allows the hand to arrive at a static object with a non-zero velocity, lending it greater flexibility than the original VITE model (cf. Bullock & Grossberg, 1988a, 1988b, 1991). Compared to the RV model, the RVITE model entails a more specific and elaborate neural instantiation of possibly relevant control loops. Therefore, in our opinion it provides a more appropriate architecture for implementing additional modeling steps aimed at accommodating the intrinsic drawbacks of
required velocity control that were revealed by our simulations. The next section is dedicated to the formulation of such an improved model construct.

4.3. The RRVITE Model

The kinematics in condition IHP3(-4') of Figure 2 appears to suggest the use of a prediction: the hand reached the IP before contact and remained there. (Putatively, the system 'knew' that no further movement was required.) This argument is strengthened by the fact that MRs were not observed by Montagne et al. (1999) in a considerable part of the trials for conditions IHP2(±4'). Furthermore, Jacobs and Michaels (2001) interpreted their data in a task similar to the Peper et al. (1994) task in favor of the on-line use of predictive information. Contrary to what is commonly assumed, the use of a prediction does not necessarily imply the use of a "contact point" predictive strategy, with a programmed movement, as will be shown below.

Required velocity control neglects essential features of the actual hand movement and object motion, namely their (lateral) velocities. When hand and object move towards each other, \( \bar{X}_{h-o} \) does not account for the fact that both hand movement and object motion reduce the relative position error: the instantaneous need for hand movement is, therefore, overestimated. Similarly, when hand and object move away from each other, \( \bar{X}_{h-o} \) underestimates the instantaneous need for hand movement. Information about the difference between hand and object velocity (i.e., relative velocity information) can help overcome these 'errors' and the current results may suggest that such information is not ignored in the control of interceptive actions.

The RRVITE model was adapted by adding an input to the DVV in the form of a parallel information pathway: the Relative Velocity Vector (RVV). For unitary consistency the RVV must be gated by a temporal signal (i.e., TC) before projecting to the DVV. The resulting Relative and Required Velocity Integration To Endpoint model (RRVITE) is schematically presented in Figure 9. Mathematically, this extension is made by adding Equation 13 and changing Equation 11 to Equation 14:

\[
\dot{V}_2 = \rho (-V_2 + \dot{T} - \dot{P}) \quad (13)
\]
\[
\dot{P} = G(\psi V_1 + \chi TC V_2) \quad (14)
\]

where \( V_2 \) is the output of the RVV stage, which is attracted to the difference between object velocity (\( \dot{T} \)) and the hand velocity (\( \dot{P} \)) at rate \( \rho \). \( \psi \) and \( \chi TC \) scale the \( G \) gating on \( V_1 \) and \( V_2 \), respectively.

The RVV input exerts a compensatory effect on the DVV. When object and hand move towards each other, \( V_1 \) and \( V_2 \) tend to have an opposite sign and thus \( V_2 \) slows the hand down, compared to the RVITE model. When object and hand move in the same direction, \( V_1 \) and \( V_2 \) tend to have the same sign and thus \( V_2 \) speeds up the hand.

As stated above, the RVITE model was evaluated in two forms, with a TC\(^{-1}\) gating either on the GO signal or on the DV inputs. The second form, not used above, would eliminate the need for a temporal gating of the RVV input to the DVV. Both inputs to the DVV would in fact be velocity signals. The next section will clarify that the available neurophysiological data does not allow for a definite choice between these two forms, which are not mutually exclusive. The reasons why we chose the first form were provided earlier.

4.3.1. Neurophysiological Evidence for the RRVITE Model
Too little is known about the brain areas responsible for interceptive reaching to allow a definitive association between nodes/connections in any proposed model and those in the primate brain. However, it is possible to piece together a compelling correspondence for some parts of the RRVITE model and a provisional correspondence for others. In prior papers introducing VITE-based models, several aspects of the neurobiological substrate have been treated quite extensively. Those aspects will be briefly reprised before treating the novel aspects of the RRVITE model.

Bullock et al. (1998) proposed an extended VITE model that also encompassed proprioception-based load compensations. This model corresponded to a cerebro-cortical circuit comprising the primary motor cortex (area 4) and the posterior parietal cortex (anterior and posterior area 5, and area 7). Its main extension comprised the separation of the Present Position Vector into a Perceived Position Vector (PePV) in parietal area 5 and an Outflow Position Vector (OPV) in area 4, which reciprocally excite each other. The DV is computed in area 5 from a comparison of the TPV, probably in area 7, with the PePV. It may be activated, or primed, prior to its overt performance. In the absence of vision the PePV can be derived by subtracting spindle-based feedback of position error, which is routed to area 5 via area 2, from an efference copy of the OPV from area 4. The DV projects to the DVV in area 4. The voluntarily scaleable GO signal, generated by the basal ganglia and motor thalamus, gates the DV input to the DVV in area 4. By virtue of the scaled gating signal, the phasic cell activity of the DVV serves as a volition-sensitive velocity command, which activates lower centers including gamma-dynamic motoneurons. The DVV command is also integrated by a tonic cell population in area 4, whose activity serves as an OPV to lower centers, including alpha and gamma-static motoneurons.

As the movement evolves, the DV activity in area 5 is driven toward baseline. This leads to termination of excitatory input to the DVV, and thus to termination of the movement itself. The reciprocal connection between the PePV and OPV cells enables the OPV to track any movement imposed by external forces and also helps to keep spindles loaded and to avoid instabilities that would otherwise be associated with lags due to finite signal conduction rates and loads.

A key assumption of the VITE model is that a pathway traversing the basal ganglia and associated parts of the “motor” thalamus corresponds to the VITE model’s GO signal pathway, and is responsible both for movement gating and continuous modulation of movement rate. The initial proposal of this correspondence (Bullock & Grossberg, 1988b) was based on the stimulation and lesion studies of Horak and Anderson (1984a,b), which showed that manipulations in arm-related parts of the pallidum affected reaching movement rate without affecting spatial aspects of movement. A similar role of the basal ganglia output has now been demonstrated for both voluntary locomotion (including gait transitions; Skinner & Garcia-Rill, 1990) and voluntary saccadic eye movements (Hikosaka, Takikawa, & Kawagoe, 2000). Moreover, this interpretation coheres with the fact that basal ganglia diseases result in a continuum of motor syndromes ranging from the hyperkinetic (e.g., hemiballism due to lesions of the subthalamic nucleus) to the hypokinetic (e.g., the bradykinesia and akinesia of Parkinson’s Disease). Indeed, Contreras-Vidal, Poluha, Teulings, and Stelmach (1997) showed that a combination of a basal ganglia circuit model and the VITEWRITE (Bullock, Grossberg, & Mannes, 1993) model of handwriting production could explain micrographia in Parkinson’s disease.

In a paper that extended the VITE model to explain the planning, performance, and detailed kinematics of viapoint movements, Bullock, Bongers, Lankhorst, and Beck (1999) proposed that TC information was used to control switching between primed movements. They noted the following neurobiological bases for interactions between TC and the putative GO signal pathway in the basal ganglia. The existence of a TC detecting stage is consistent
Prospective Control of Interceptive Reaching

with neurophysiological data originally presented by Wang and Frost (1992) and since supplemented by additional studies (e.g., Sun & Frost, 1998). Pigeons viewed a computer screen, on which an approaching 'soccer ball' was projected. Whenever the ball approached the pigeon's eye along a collision course, cells in the dorsal posterior part of the nucleus rotundus abruptly increased their firing activity at a certain time before predicted collision, independent of ball velocity or distance. Moreover, a tight relation between the activity of the rotundal looming-sensitive cells and EMG activity of the large pectoralis flight muscle was observed (Wang & Frost, 1992).

These results indicate one key brain pathway for processing TC information. The nucleus rotundus is a thalamic nucleus that receives a strong visual projection from the optic tectum (OT), which in primates is called the superior colliculus (SC). In birds, it is part of a pathway called the tecto-rotundal-ecostriatal pathway, which parallels the colliculo-pulvinar-extrastriate cortical pathway in mammals (Frost, Wylie, & Wang, 1990; Pettigrew & Konishi, 1976). In each group, a relatively direct complete circuit is formed by a return projection from visual cortex to the OT/SC. This descending projection is complemented by disinhibitory frontal projections to OT/SC mediated by the basal ganglia (including the striatum and the substantia nigra). In amphibians that lack significant cerebro-cortical visual centers, there is a tecto-thalamo-striatal pathway returning to modulate tectal activity. Moreover, the striato-tectal component of this circuit is present in less or more elaborated forms in amphibians and all land vertebrates (Butler & Hodos, 1996; Marin, Smeets, & Gonzales, 1998). It has been shown in the frog that if the thalamic stage is surgically destroyed, then the frog’s optic tectum is disinhibited and the frog thereafter readily attacks large, looming stimuli as if they were prey.

That the TC pathway traverses the basal ganglia (including striatum and pallidum/substantia nigra in primates) provides one basis for TC-GO signal interactions in the RRVITE model (see Figure 9). However, it has long been known that signals from the pulvinar also reach the parietal cortex, which in the VITE theory is responsible for computing target position, hand position, and the difference vector between the two. Evidence suggests that the parietal cortex computes such variables both for the oculomotor system and for the arm motor system. In the case of the oculomotor system, Lynch and colleagues (Lynch, 1987; Tian & Lynch, 1996) have established the existence of parallel parieto-frontal circuits for control of saccadic and smooth pursuit eye movements. Interestingly, these circuits can be viewed as affording comparisons in both the position and velocity domains, since the saccadic system can be regarded as a position servo and the smooth pursuit system as a velocity servo. It seems likely that there is a similar parieto-frontal parallelism for controlling forelimb trajectories. Psychophysical studies have demonstrated cross-links between the oculomotor and forelimb control systems, e.g., humans can generate smooth pursuit eye movements that accurately track their own cyclic hand movements in the absence of vision (cf. Lazzari, Vercher, & Buizza, 1997, and references therein).

In this context, it is very suggestive that the two areas of parietal cortex (5 and 7) believed to correspond to elements of the core VITE model are also areas that have been most strongly linked to both the pulvinar and the basal ganglia. In a recent pathway tracing study in the cat, Pare and Smith (1996) reported observations that we have summarized in the form of Figure 10. It shows a pathway from the midbrain roof (SC and pretectum) to the lateral posterior and pulvinar nuclei of the thalamus (LP-PUL). The LP-PUL, which also receives inputs from the Medial Superior Temporal (MST) area and the Floor of the Superior Temporal (FST) area (both cortical visual motion processing areas) and object recognition areas TE and TEO (anterior and posterior part of the inferotemporal cortex, respectively), projects both to parietal areas 5 and 7 and to striatal areas receiving strong projections from areas 5 and 7. Finally, it also shows that the latter cortico-striatal projection sends strong collaterals back to
the LP-PUL complex. Given what is known about the TC signal carried by the midbrain-PUL projection, and about arm-control computations in areas 5 and 7, the circuit in Figure 10 appears to be a very promising candidate as neurobiological substrate for the control loops proposed in the RRVITE model.

Insert Figure 10 about here

Above it was mentioned that the LP-PUL receives a projection from both the pretectum and the SC. Masino and Grobstein (1989) showed that, at least in early land vertebrates, namely frogs, the pretectum has a binocular-based spherical coordinate representation (elevation angle, azimuth angle, radial distance) of object locations relative to the head. Data suggest that a spherical coordinate system can also be found in area 5 of the primate parietal cortex (Lacquaniti et al., 1995). For these reasons, the original version of the DIRECT model (Bullock, Grossberg, & Guenther, 1993), which incorporated VITE principles but added a learned inverse differential kinematic transform between spatial and motor coordinates, employed such an ego-centric spherical coordinate representation of space as basis for reaching movements made with or without a tool. A neural network for computing spherical coordinates of targets from binocular signals was presented in Guenther, Bullock, Greve, and Grossberg (1993).

4.3.2. Simulations of the RRVITE model

To test the RRVITE model, it was simulated for the same experiments as the RV and RA models, using the same methods and procedures as explained in the preceding. Most parameter values were fixed in the simulations: \( r = 150; \lambda = 3.5; B = 1; C = 6; \psi = 0.28 \) and \( \chi = 0.22 \). In order to obtain a good match for the kinematics shown in Figures 2 and 3, a different \( \rho \) was used for the two experiments. However, these values were kept constant over all conditions within each simulated experiment.

Figure 11 shows the simulated kinematics of the RRVITE model for the Montagne et al. (1999) task. With appropriate parameter settings \( (\rho=0.8) \), the RRVITE model (Equations 5, 8-10 and 12-14) led to a good match of the kinematics shown in Figure 2. The RRV effectively prevented the overshoots from occurring in conditions IHP1(4”) and IHP3(-4”), while preserving a good performance for the other conditions. The RRVITE model can also account for the absence of MRs in conditions IHP2(±4”), as observed in a considerable part of the trials by Montagne et al. (1999). By increasing \( \chi \) (e.g., to 0.5), the PPV can be made to oscillate around the IP, with a small amplitude of oscillation (<3 cm). An important difference with the RV and RA model is that interceptive success was not affected by this parameter change in the RRVITE model.

Insert Figure 11 about here

Although the RRVITE model was developed mainly on the basis of the Montagne et al. (1999) data, the RRVITE model was also simulated for the Montagne et al. (2000) study. By only varying \( \rho \) relative to the simulations discussed above (i.e., \( \rho = 12 \)) the RRVITE model could accurately match the behavioral data in Figure 3 (see Figure 12). The RRVITE model performed much better than both the RV and RA model. The range of peak velocities over conditions was slightly larger than reported by Montagne et al. (2000), but qualitatively all systematic effects were present (compare Table 2 with Table 3).

Insert Figure 12 about here

Insert Table 3 about here
The simulations of this task, in which object velocity and \( T_{C_{\text{ini}}}} \) varied substantially and randomly across trials, used a considerably higher value of \( \rho \) than the simulations of the Montagne et al. (1999) task, in which object velocity and \( T_{C_{\text{ini}}}} \) were constant across trials. The variation of \( \rho \), which controls relative velocity integration rate, may thus reflect subjects' greater need for vigilant attention to object and relative velocity information in order to meet more stringent and less predictable temporal constraints. Judging from the movement times and velocity profiles provided by Montagne et al. (2000), the participants initiated their movements quite late after object onset (0.6-1.103 s) and intercepted the object's trajectory with a high hand velocity. Consequently, the temporal constraints were stringent, and the performance more akin to hitting than to catching a moving object.

4.3.3. New experimental predictions

So far, this study has presented comparisons of simulated kinematics with kinematics reported in the literature. To derive experimentally testable predictions of the RRVITE model, simulations were run for a new task. The addition of the RVV in RRVITE implies that manipulating the relative velocity between hand and object will alter the kinematics. In this section, two ways of manipulating this relative velocity are simulated. One way is object acceleration or deceleration. As a result, the RVV changes as a function of hand and object movement, rather than solely as a function of hand movement, as occurs for constant velocities. Another way may be to introduce background motion in order to manipulate perceived object velocity without manipulating the perceived position (Smeets & Brenner, 1995). This manipulation is interesting in the context of the RRVITE model and its proposed substrate in Figure 10. For example, based on observations on cells in areas MST (e.g., Komatsu & Wurtz, 1998) and adjacent area MT (e.g., Born & Tootel, 1992), Pack, Grossberg, and Mingolla (2001) have modeled MST as a substrate for combining information about background motion, retinal motion, and eye motion to specify object motion.

In our simulations, object movement (under constant acceleration or deceleration) toward the axis of hand movement, along a straight 4 m trajectory, took 1.5 s. Accelerating objects started and decelerating objects ended with a zero velocity, meaning an acceleration of ±3.56 m s\(^{-2}\). Only an approach angle of -4° was used\(^5\). Initial hand position relative to the IP was set to 0.5, 0 and -0.25. To focus on the kinematics and to reduce initiation time variability, initiation was dictated by an onset cue, occurring at, or 0.75 s after, object motion onset. Background velocity was set to ±0.5 m s\(^{-1}\). The effect of background motion on object velocity perception (but not on position perception) was simulated by adding a constant to \( \dot{\chi} \) in Equation 13. This constant had a magnitude of -0.5 times background velocity, consistent with the negative superimposed effect of background motion on the perceived lateral object velocity (at a magnitude of around 0.5-0.75 times background velocity) observed by Smeets & Brenner (1995). In the simulations \( \rho \) was set to 3 for decelerating and 8 for accelerating objects. This choice was based on our interpretation of the variations of \( \rho \); movement times were larger than in the Montagne et al. (2000) task and rapid integration of the RVV was judged to be more important for accelerating objects than for decelerating objects. Furthermore, all values were similar to those used in the previous simulations of the RRVITE model. \( T_{C_{1}} \) was used for \( T_{C} \) in Equations 10, 12 and 14. To visualize the effect of the RVV, kinematics from the RVITE model (i.e., setting \( \chi \) to zero) are also reported.

Insert Figure 13 about here

As can be appreciated from Figure 13, a much earlier inward hand movement occurs towards decelerating (left column) than towards accelerating (right column) objects. This
pattern mimics the lateral object motion. MRs that occur if the hand is initially located at the IP are larger for movements towards accelerating objects. For both approach types, the RVV generally slows down the hand (compare dash-dotted and solid lines in Figure 13), such that it does not reach the IP before contact. Note that this effect is the reverse of that observed in our simulations of the Montagne et al. (1999) task (i.e., when the object approaches at a constant velocity).

The most striking prediction from the simulations of the RRVITE model is the occurrence of MRs in IHP2 conditions wherein the initial direction is opposite to that of background motion (Figure 13E and F). The reversed direction of these MRs is a direct consequence of the effect of background motion on the RVV, as can be appreciated from the comparison with the RVITE model’s behavior. These effects of background motion are similar for decelerating and accelerating objects. Simulated kinematics with objects moving at a constant velocity (not reported here) were somewhere ‘between’ the kinematics for decelerating and accelerating approaches. Thus, manipulation of background motion may provide an interesting way of examining the potential use of relative velocity information in the coordination of interceptive task. If indeed the predicted effects of perceived velocity can be induced by means of such manipulations, this may be interpreted as support for the presently proposed model (i.e., RRVITE). Note, however, that the absence of such effects would not necessarily falsify the model, as it remains to be established whether the coordination process itself is indeed susceptible to illusory percepts (cf. Smeets & Brenner, 1995).

5. Discussion

Two strategies for interceptive actions were simulated in order to evaluate their effectiveness in reproducing empirically observed movement kinematics. Both models, the RV model and the RA model, are prospective control structures based on required velocity information. Although in some cases the simulated kinematics showed a reasonable match with experimental data, several persistent mismatches were identified. With regard to the results of Montagne et al. (1999), these mismatches included overshoots of the future IP when the hand had to move in a direction opposite to the lateral component of the object’s approach trajectory (i.e., in conditions IHP1(4°) and IHP3(-4°)). Such overshoots were absent in more than 90% of trials. The models also failed to account for the hand arriving early at the IP and subsequently staying there, as was observed for condition IHP3(-4°) by Montagne et al. (1999). In addition, neither model could accurately match the kinematic patterns observed by Montagne et al. (2000).

These shortcomings underscored the need for additional model developments. Three considerations led to our choice in this respect. First, despite the imperfections of the simulation results, the information proposed by Peper et al. (1994), that is, Equation 1, led to a reasonable match in many conditions. Second, the acceleration control proposed by Bootsma et al. (1997) did not improve the simulation results and is inconsistent with a large body of neurophysiological findings. Third, a neural network approach may provide us with better possibilities for informational and biological interpretations of the model construct. Thus, the RV model was implemented in the form of an adapted VITE model. In this model, the informational signals that jointly determine the currently required velocity are integrated by the VITE network, hence the name Required Velocity Integration To Endpoint model.

Required velocity control is only concerned with reducing the hand-object distance within the remaining TC, regardless of how this is accomplished. To improve the control of the hand velocity vector an extension of the RVITE model was proposed. A relative velocity vector was added in a parallel pathway, operating to compensate for deficiencies of required velocity control. Consequently, the resulting Relative and Required Velocity Integration To
Endpoint model efficiently cancels the position error within the available time, while largely avoiding movements that are superfluous given the ongoing object and hand motions.

Simulations showed that the RRVITE model successfully avoided the unwanted overshoots while reproducing the kinematics of Figures 2 and 3 rather well. To account for the task differences only $\rho$ needed to be varied between simulations of the Montagne et al. (1999) and Montagne et al. (2000) tasks. In RRVITE, relative velocity information can thus be used to control hand velocity at interception: for the Montagne et al. (2000) task a low $\rho$ with other parameters constant resulted in a lower contact velocity (i.e., a more bell-shaped velocity profile than the one depicted in Figure 12). In this regard, the difference between typical catching (e.g., Alderson, Sully, & Sully, 1974; see also Servos & Goodale, 1998) or reach-and-grasping velocity profiles (Mason & Carnahan, 1999; Zaal et al., 1999) and hitting velocity profiles (e.g., Bootsma & Van Wieringen, 1990; Smeets & Brenner, 1995) seems relevant. Despite the fact that sufficient time was available (see note 6), the participants in the Montagne et al. (2000) study may have preferred executing the experimental task more like hitting than catching, which would explain the late initiations and the near maximal contact velocities. The fact that the participants did not have to grasp the object may also have influenced the execution (see Marteniuk MacKenzie, Jeannerod, Athenes, & Dugas, 1987). Perhaps as a consequence of this, different magnitudes of $\rho$ had to be used for the simulations of the two tasks.

In sum, the simulations reported in the present study clearly indicated that the RRVITE model is better equipped to account for the behavioral data. Below, some conceptual remarks are made about this model as well as some potential problems related to it.

5.1. The use of relative velocity information in RRVITE

The RVV was added to the RVITE model to account for specific features of human data. We focused on possibly relevant neural control circuits, and not so much on the exact informational input used by these circuits. Jacobs and Michaels (2001) considered several candidate optical variables (replacing the term $X_0$ in Equation 1) in their simulations of a slightly altered version of the RA model to account for catching data in a task like the one used by Peper et al. (1994). On the basis of their empirical data, they concluded that subjects most likely were continuously using information approximating place-of-contact. However, among other things, such a variable cannot account for the occurrence of MRs in the Montagne et al.’s (1999) conditions HHP2±4°, which were actually taken as evidence for the use of lateral object position information. Thus, for now, it remains to be seen whether the actual lateral object position as such or some prediction of a future position should be taken as TPV. The new tasks simulated allow for testing the RRVITE model’s specific predictions. Other manipulations, such as using curved trajectories, might provide further hints about the informational basis of the TPV.

Adding the RRV to the prospective RVITE does not jeopardize interceptive success since the hand movements are controlled continuously. The RVV makes actions more efficient, without affecting interceptive performance. In an abstract sense, this result is similar to Guenther and Barreca’s (1997) demonstration that a supplementary efficiency term endows the DIRECT neural network model (which is an adaptive, motor-redundant enhancement of VITE; Bullock et al., 1993) with on-line avoidance of extreme or uncomfortable postures without threatening the accuracy of movement direction control.

The informational components in the dual path in the RRVITE model are reminiscent of common models of how position and velocity errors detected by muscle stretch receptors (whose set points are controlled by static and dynamic gamma motoneurons) help the limb track descending commands without overshoots (Bullock & Grossberg, 1992; Contreras-Vidal, Bullock, & Grossberg, 1997; Feldman, 1986; Gielen & Houk, 1987). They are also
reminiscent of the human oculomotor system (Lynch, 1987; Tian & Lynch, 1996), in which a tracking episode results from both saccadic eye movements, guided by position error (i.e., retinal eccentricity of the object), and smooth pursuit eye movements, guided by velocity error (i.e., retinal slip velocity of the object). Figure 10 depicts known connections from LP-PUL to the parietal cortex, which, together with known connections from LP-PUL to the basal ganglia, may serve as neurobiological substrate for connections proposed in the RRVITE model. Due to the lack of specific studies on the brain structures involved in interceptive control the link between this figure and the RRVITE model is somewhat tentative, but we believe the circuit represents a good candidate. Future behavioral, neurophysiological, and modeling studies will provide additional insights into this matter.

5.2. Perceptuo-motor delays

In the (R)RVITE model, $\dot{P}$ represents the desired hand velocity. The emphasis on such internal, neurophysiologically interpretable variables has allowed the VITE model to be given a full neurobiological interpretation in recent extensions (Bullock et al., 1998; Cisek et al. 1998). On the other hand, the use of planned kinematics has fundamental implications for the neural control of movement. In getting from planned kinematics to the actually observed behavior the central nervous system must take many constraints into account, such as the presence of neural delays and other delaying aspects of the neuro-musculo-skeletal system.

For internal planning models to be successful when incorporating a perceptuo-motor delay, a compensation for its effects is required. By definition, a perceptuo-motor delay involves neural transmission times in the sensory as well as the motor system. For interceptive actions, an uncompensated delay implies that the object will have already moved once the hand reaches the object's (former) location (e.g., Brenner & Smeets, 1996). Even for static objects acquired by negative feedback controllers, an uncompensated delay readily produces a ringing instability (i.e., oscillations) around the endpoint, because at the time that the error is perceived to be zero, the motor command channel has a residual (excess) command that remains to be executed. Thus, perceptual and motor delays act as major constraint on the control of interceptive actions. This constraint is larger for faster movements.

Compensations for perceptuo-motor delays typically involve extrapolation of the available information about object motion and end effector movements. Because different types of actions may involve different neural pathways, and because musculo-skeletal dynamics are effector and state dependent, the net perceptuo-motor delay must not be considered to be a constant (see also Michaels, Zeinstra, & Oudejans, 2000; Van der Kamp, 1999). Additionally, for on-line control such a prediction is most important in the terminal phase of the movement before contact, when too little time is available for new incoming information to further affect the kinematics. The extrapolation must thus be adaptive and interact with information about the current state of the end-effector.

It has been argued that the effects of perceptuo-motor delays and musculo-skeletal dynamics may be overcome by learned compensation through the cerebellum (e.g., Bullock, Fiala, & Grossberg, 1994; Contreras-Vidal et al. 1997; Kettner et al., 1997; Spoelstra, Schweighofer, & Arbib, 2000). In this context it has been argued that for explosive movements the scope of internal kinematic planning may be limited, because the compensations would make up for the entire planning signal (Van Soest & Bobbert, 1998). Although the word 'compensation' may suggest that the musculo-skeletal dynamics has only a negative impact on performance, some aspects of musculo-skeletal dynamics may greatly facilitate stabilizing the system, especially during the execution of fast movements (Van Soest & Beek, 1996; Van Soest, Bobbert, & Van Ingen Schenau, 1994). For interceptive actions, such aspects can be expected to have distinctive effects on the coupling between
information and the muscle activation patterns sent out by the neural control circuits. Van Soest and Beek (1996) warned in this regard that care should be taken in attributing systematic kinematic patterns in certain (interceptive) tasks to variations in the informational input, because musculo-skeletal dynamics most certainly also influence the details of these kinematic patterns (see also Beek, Peper, Daffertshofer, Van Soest, & Meijer, 1998). In future work, it will therefore be essential to combine the identified RRVITE architecture with an appropriate model of the musculo-skeletal dynamics.

5.3. Conclusion

The present study elaborated on the relevance of required velocity information in the control of interceptive actions by demonstrating that independent information about relative velocities can markedly improve the effectiveness of extant model constructs in reproducing the relevant kinematic properties of such actions. Moreover, given that the elaboration in question was based on the VITE model for trajectory formation in discrete aiming movements, a generalization of the adopted approach was achieved for the control of discrete movements to both stationary and moving objects. Furthermore, Ulloa and Bullock (2001) have recently applied VITE principles to model the temporal coordination of reaching and grasping. The model robustly achieved opening and closing of the grip “aperture” within the movement time of reaching, even though there was no pre-planning of component movement times. Thus, a more comprehensive model of the complete action of catching is beginning to emerge within this modeling tradition.
References


Footnotes

1 In their formulation of Equation (1) \( X_0 \) (here \( X_0 \)) and \( X_h \) were switched. This cannot be correct, as the required velocity would then always specify a movement away from the ball.

2 For \( \dot{X}_o \) being constant, \((X_o - X_h)\) and TC in Equation 1 change with the same rate before initiation, resulting in \( \dot{X}_{hreq} \) remaining constant.

3 Initial \((X_o - X_h) = \pm 4\sin(4^\circ)\) and initial object TC = 4/2.8. Thus, initially \( \dot{X}_{hreq} = \pm 2.8\sin(4^\circ) = \pm 0.195\).

4 The mathematical formulation of Equation 2 and Equations 5, 10 and 11 is very similar. For a high value of \( \gamma \), \( \lambda \) and \( A \) can be chosen such that the behavior of both models is almost identical.

5 The manipulation of background motion was symmetric (i.e., in both directions), such that the manipulation of initial hand position has nearly the same effect as the manipulation of approach angle.
Tables

Table 1
The General Trends in the Effects Observed by Peper et al. (1994) for the Moments of Movement Initiation ($T_{ini}$) and of Maximal Hand Velocity ($T_{v_{max}}$) and the Magnitudes of Maximal Hand Velocity ($V_{max}$) and of Hand Velocity at Interception ($V_{int}$).

<table>
<thead>
<tr>
<th>Approach Angle</th>
<th>Outward</th>
<th>Inward</th>
</tr>
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<tbody>
<tr>
<td>$T_{ini}$*</td>
<td>Earlier</td>
<td>Later</td>
</tr>
<tr>
<td>$T_{v_{max}}$</td>
<td>Later</td>
<td>Earlier</td>
</tr>
<tr>
<td>$V_{max}$*</td>
<td>Smaller</td>
<td>Larger</td>
</tr>
<tr>
<td>$V_{int}$*</td>
<td>Larger</td>
<td>Smaller</td>
</tr>
</tbody>
</table>

*p<.1.  **p<.01.

Table 2
The Maximal Velocities (MV) and the Moments of Maximal Velocity (MMV), relative to initiation, for the Montagne et al. (2000) Data and for the Simulations of the RV and RA Models, Corresponding to Figure 6.

<table>
<thead>
<tr>
<th>TC$_{ini}$ (s)</th>
<th>M. (2000)</th>
<th>RV</th>
<th>RA</th>
</tr>
</thead>
<tbody>
<tr>
<td>MV (m s$^{-1}$)</td>
<td>1.00 2.48</td>
<td>3.63</td>
<td>2.41</td>
</tr>
<tr>
<td>1.25</td>
<td>2.29 3.11</td>
<td>2.24</td>
<td></td>
</tr>
<tr>
<td>1.60</td>
<td>2.09 2.63</td>
<td>2.10</td>
<td></td>
</tr>
<tr>
<td>MMV (s)</td>
<td>1.00 0.360</td>
<td>0.356</td>
<td>0.331</td>
</tr>
<tr>
<td>1.25</td>
<td>0.403 0.372</td>
<td>0.380</td>
<td></td>
</tr>
<tr>
<td>1.60</td>
<td>0.422 0.395</td>
<td>0.468</td>
<td></td>
</tr>
</tbody>
</table>

Note. TC$_{ini}$ = initial time-to-contact of the object; M. (2000) = Montagne et al. (2000).

Table 3
The Maximal Velocities (MV) and the Moments of Maximal Velocity (MMV), relative to initiation, for the Simulations of the RRVITE model, Corresponding to Figure 12.

<table>
<thead>
<tr>
<th>TC$_{ini}$ (s)</th>
<th>MV (m s$^{-1}$)</th>
<th>MMV (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.00</td>
<td>2.58</td>
<td>0.351</td>
</tr>
<tr>
<td>1.25</td>
<td>2.32</td>
<td>0.395</td>
</tr>
<tr>
<td>1.60</td>
<td>2.03</td>
<td>0.455</td>
</tr>
</tbody>
</table>
Figures

**Figure 1.** One condition of the task for which Peper et al. (1994) proposed the required velocity model. IP represents the interception point of the moving object with the plane of hand movement. See text for details.

**Figure 2.** Data from the Montagne et al. (1999) experiment: hand position plotted as a function of normalized movement time. IHP1-3 represent the different initial hand positions. These were 0.35 to the left of, at (i.e., 0 m) or 0.25 m to the right of the future IP. Ball approach angles are indicated in the figure. Approach angles of 0° were perpendicular to the movement axis, -4° refers to approaches from the left, 4° refers to approaches from the right. Adapted with permission from Montagne et al. (1999)’s Figure 6.
Figure 3. Data from the Montagne et al. (2000) experiment: hand velocity ($\dot{X}_h$) is plotted as a function of time from object appearance. The magnitude and timing of maximal hand velocity was clearly affected by the object's initial TC (1.00, 1.25, 1.60 s). Initial object distance did not significantly influence the velocity profile. Reprinted with permission from Montagne et al. (2000)'s Figure 3.

Figure 4. Simulated kinematics of the RV model under the conditions of Montagne et al. (1999). Plotting convention as in Figure 2. A: Activation parameter $A=1$; B: $A=3$. 
Figure 5. Simulated kinematics of the RA model under the conditions of Montagne et al. (1999). Plotting convention as in Figure 2. A: $\alpha=11$, $\beta=5$; B: $\alpha=17$, $\beta=5$. 
Figure 6. Simulated kinematics of the RV and RA models for the Montagne et al. (2000) task. A: RV model, with $A=5$. B: RA model; $\alpha \beta$ was kept constant across conditions: $\alpha_{1.00}=9.333$, $\beta_{1.00}=7$; $\alpha_{1.25}=8$, $\beta_{1.25}=6$; $\alpha_{1.60}=6$, $\beta_{1.60}=4.5$.

Figure 7. Simulated kinematics of Equation 2 with $\Omega(t)=1$, meaning that $\dot{X}_h$ equals $\dot{X}_{kreg}$ from initiation to contact. Overshoots of the future IP are present for conditions IHP1(4°) and IHP3(-4°).
Figure 8. The VITE circuit. DV is the difference between TPV and PPV. It is scaled by GO at the DVV stage and integrated at the PPV stage, which outputs the desired position. \( T(t) \) is the lateral ball position at each instant.

Figure 9. The RRVITE circuit. DV and RRV are gated by the same GO signal at the DVV stage. The \( TC^-1(t) \) signal projects to the GO signal and to the DVV input from the RVV. \( T(t) \) and \( T'(t) \) respectively are the lateral ball position and velocity at each instant.
Figure 10. Connections as reported by Pare and Smith (1996), taken as a hypothetical basis for the TC pathways assumed in the RRVITE circuit model shown in Figure 9. Not shown here, but demonstrated in other studies reviewed in Bullock et al. (1998), are strong reciprocal anatomical links between areas 4 and 5 and a pathway from the striatum to area 4 that traverses the pallidum and ventral thalamus. See text for further details.

Figure 11. Simulated kinematics for the RRVITE model for the Montagne et al. (1999) task, with $\psi = 0.28$, $\chi = 0.22$ and $\rho = 0.8$.

Figure 12. Simulated kinematics for the RRVITE model for the Montagne et al. (2000) task, with $\psi = 0.28$, $\chi = 0.22$ and $\rho = 12$. 
Figure 13. Simulated kinematics for the RVITE model (dotted lines) and the RRVITE model (solid lines) with object deceleration (A, C and E) and acceleration (B, D and F) and with background motion in negative (i.e., downward in the figure) direction (A and B), without background motion (C and D) and with background motion in positive (i.e., upward in the figure) direction (E and F). See text for further details.