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A dynamical neural network for hitting an approaching object

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Abstract. Besides making contact with an approaching ball at the proper place and time, hitting requires control of the effector velocity at contact. A dynamical neural network for the planning of hitting movements was derived in order to account for both these requirements. The model in question implements continuous required velocity control by extending the Vector Integration To Endpoint model while providing explicit control of effector velocity at interception. It was shown that the planned movement trajectories generated by the model agreed qualitatively with the kinematics of hitting movements as observed in two recent experiments. Outstanding features of this comparison concerned the timing and amplitude of the empirical backswing movements, which were largely consistent with the predictions from the model. Several theoretical implications as well as the informational basis and possible neural underpinnings of the model were discussed.

1 Introduction

Skilled actors perform high-speed hitting tasks with a remarkable degree of accuracy: for a successful hit, the object must be intercepted within a small spatial region of the workspace within a narrow time window. The spatial accuracy in hitting is about 3–5 cm (McLeod 1987; Regan 1992), while the temporal accuracy is about 3–7 ms (Bootsma and Van Wieringen 1990; Regan 1992). Clearly, such high accuracy demands push the human action system to its limits: for instance, in baseball batting a success rate of 40% is already extremely high.¹ Besides the high accuracy demands, this success rate critically depends on the batter's ability to control the direction and velocity of the object after interception, so as to prevent the field

team from getting the ball to first base before the batter arrives there. The remarkable performance levels that are achieved even in the presence of these (and other) constraints have inspired a wealth of studies on the control of interceptive actions.

In the literature on interceptive actions, two types of control strategies have been proposed: *predictive* and *prospective*. Predictive strategies (e.g., McLeod 1987; Tyldesley and Whiting 1975) posit that the actor predicts the time and location of interception and then selects an appropriate action, which is executed in a feedforward manner and adjusted by feedback when sufficient time is available. Prospective strategies (e.g., Chapman 1968; Peper et al. 1994), in contrast, posit that the actor does not need to estimate the time and location of interception before initiating an action. Rather, by continuously controlling certain aspects of the movement (e.g., effector velocity) on the basis of specific information, both the time and place of interception follow from the invoked continuous control. Predictive strategies have been proposed predominantly in the context of hitting, which is not surprising considering that in hitting there is generally very little time available for on-line adjustments, possibly ruling out prospective control as a viable option altogether. Movement times for hitting are generally on the order of 100–300 ms (e.g., Bootsma and Van Wieringen 1990; Smeets and Brenner 1995; Tresilian and Lonergan 2002), such that the visuomotor delay, typically estimated to be on the order of 100–200 ms (e.g., Bootsma and Van Wieringen 1990; Brenner et al. 1998; Lee et al. 1983; McLeod 1987; Savelsbergh et al. 1991; Van der Kamp 1999), covers a relatively large portion of the movement. Hence, it is reasonable to assume that the possibilities for feedback-based adjustments during hitting are limited at best.

The distinction between predictive and prospective control, however, becomes less clear-cut if one recognizes that internal models can be used to integrate the available (sensory inflow and motor outflow) information to predict the consequences of the motor commands sent to a limb and the time course of the sensory inflow signals (using “forward” models). In this manner, the position and velocity of object and effector can be estimated with

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¹ Success rate is defined here in terms of the rules of baseball, that is, the percentage of at-bats on which the batter gets safely to first base or beyond after having hit the ball into the field.

negligible delays or even predicted in advance, thus allowing feedback control for fast movements (e.g., Desmurget and Grafton 2000; Miall and Wolpert 1996).

Regardless of the exact control strategy used in hitting, the actor always requires information to ensure successful performance. For hitting (and interceptive actions in general), the main focus has been on the optical information used for timing the movement. The prevailing experimental strategy in this regard has been to provide various trajectories of to-be-intercepted objects and to examine which informational variable(s) best explain the variations in movement initiation (with initiation being assumed to occur when a threshold value of this informational variable is reached, e.g., Caljouw et al. 2004b; Michaels et al. 2001). Although much work has been devoted to uncovering the informational basis of the control of timing in interceptive actions, no consensus exists about which informational variable(s) is (are) used (see Beek et al. 2003; Caljouw et al. 2004a for reviews). However, there is converging evidence suggesting that the expansion pattern generated by an approaching ball plays a crucial role in this regard (Caljouw et al. 2004b; Michaels et al. 2001).

Markedly fewer research efforts have been devoted to identifying the spatial information used to adequately position the effector in hitting. This might be related to the fact that no singular behavioral aspect can be readily identified to direct the search for the spatial informational variables used in interceptive actions (as opposed to the timing of specific events in the search for temporal information). It is evident that object motion is taken into account in hitting: for laterally moving objects participants generally aim ahead of the current object position (e.g., Brenner and Smeets 1996; Brouwer et al. 2002; Smeets and Brenner 1995). However, these data did not allow teasing apart whether participants continuously predicted the location of the future interception point (IP) or just extrapolated object motion over a certain time window.

For both hitting and catching, behavioral models have been proposed that stipulate how (optical) information constrains movement or plays into a continuous perception-action dynamic (Bootsma et al. 1997; Lee 1998; Peper et al. 1994; Smeets and Brenner 1995; Tresilian 1994). Thus far, however, the control of object motion after interception (which is crucial in most hitting tasks) has remained largely unaddressed. To examine this aspect of hitting, the goal of the present study is to explicitly model the control of effector velocity at interception (X_{ip}). The modeling approach adopted, however, is rather different from that underlying the behavioral models just mentioned. These behavioral models focus on the relation between optical information and movement without addressing how the identified relation between the two results from the interplay of the various (i.e., sensory, neural, and musculoskeletal) subsystems involved. Yet, modeling these subsystems and their relations may allow for unraveling the behavioral dynamics in terms of its informational, neural, and musculoskeletal constituents (cf. Beek et al. 2003). In this approach, modeling is dependent on the availability of

structural knowledge but can also guide the search for this knowledge.

The present study specifically focuses on the neural subsystem: a dynamical neural network is proposed for the control of effector velocity at interception in hitting, which builds on earlier neural network models for the control of reaching movements (Bullock and Grossberg 1988, 1991) and interceptive arm movements (Dessing et al. 2002). To evaluate the model's ability to account for hitting, the planned kinematics generated by the model is compared qualitatively to the kinematics observed in two recent experiments on hitting (Caljouw et al. 2004b, c). In making this comparison, we assumed that the planned (i.e., simulated) movement trajectories are reflected in systematic, essential features of experimentally observed kinematics (cf. Bullock and Grossberg 1988).

2 The model

Successfully hitting an object requires that the end-effector (e.g., hand or hand-held implement) and the object (nearly) simultaneously occupy (nearly) the same position in the workspace of the effector, while the effector velocity should be within the desired limits. In many hitting tasks, the effector velocity vector is strictly constrained at interception in order to control the velocity and direction of the object after contact. In this section, a dynamical neural network model is presented for the planning of hand trajectories in hitting an approaching object. The model, which is an extension of the Required Velocity Integration To Endpoint (RVITE) model presented by Dessing et al. (2002), provides an account for the control of both the spatiotemporal aspects of the interception (i.e., being at the right place at the right time) and $\dot{X}_{ip}$.

The RVITE model resulted from implementing the required velocity model proposed by Peper et al. (1994) in the Vector Integration To Endpoint (VITE) model of Bullock and Grossberg (1988, 1991, see Fig. 1, back lines), a dynamical neural network model for voluntary planning of goal-directed arm movements. The VITE model operates to reduce a difference vector (DV), coding the difference between a present (hand) position vector (PPV) and a target position vector (TPV), to zero. This DV is multiplied by a voluntarily scalable, time-varying GO signal to determine the desired velocity vector (DVV), which is inte-

Fig. 1. The RVITE model operates to eliminate the difference vector (DV) within the remaining time-to-contact (TC). The target position vector (TPV) codes the present (*lateral*) ball position ($X_{ball}(t)$); the DV codes the difference between this TPV and the present position vector (PPV) and is scaled by a TC^{-1} -dependent GO signal to determine the desired velocity vector (DVV). Integration of the DVV ensures the continuous updating of the PPV, even in the absence of PPV-related perceptual information

grated continuously to update the PPV. Thus, the overall DVV is determined by movement amplitude but is also under voluntary control by means of the GO signal.

The VITE model cannot account for the control of interceptive actions since it does not control the temporal aspects of the movement on the basis of perceptual information (Beek and Bootsma 1991). Following the required velocity model (Peper et al. 1994), the RVITE model accounts for such control by incorporating a TC^{-1} scaling of the GO signal (TC = time-to-contact), which assures that the PPV reaches the TPV exactly when the TC reaches zero (see Fig. 1, gray lines; see Dessing et al. 2002 for an elaborate discussion). The RVITE model is formalized by the following equations:

$$\dot{V} = \gamma (-V + T - P), \quad (1)$$

$$\dot{P} = \left(\frac{G_0 g_2}{TC} \right) V. \quad (2)$$

Here, V , P , and T are the DV, PPV, TPV, respectively, γ is the integration rate of the DV population, and TC is the remaining time-to-contact of the target. G_0 scales the amplitude of the GO signal, which is defined by a two-cell cascade (g_1 and g_2 , with parameters A and B):

$$\dot{g}_1 = -A(g_1 + (B - g_1)), \quad (3)$$

$$\dot{g}_2 = -A(g_2 + g_1(B - g_2)). \quad (4)$$

An important aspect of the VITE model is the feedback loop from the PPV to the DVV; since this is an internal feedback loop, the VITE model operates in a feedforward manner (which implies that, in principle, no feedback about the actual hand position is required). This allows an online generation of motor outflow commands even for fast reaching movements (in fact, for this feedback loop the PPV can be considered an internal model of hand position). In this respect, the RVITE model is different from the model proposed by Peper et al. (1994), where the required velocity was a perceptual variable used for prospective control. Due to its feedforward nature the RVITE model is less hampered by perceptuomotor delays, which is particularly interesting in the context of hitting (cf. Introduction). Moreover, because the proposed TC^{-1} scaling of the GO signal (which implies continuous availability of TC information) is taken to correspond to a relatively fast visuomotor pathway to the globus pallidus (the proposed site for the GO signal generation; see Bullock and Grossberg 1991) the RVITE model allows for a fast online modulation of the DVV on the basis of perceptual information.

Dessing et al. (2002) showed that the RVITE model accounts for successful interceptions (i.e., being at the right place at the right time), but the model could not account for some specific kinematic features of catching movements. To improve the account of the catching kinematics, the RVITE model was extended with a parallel relative velocity channel, resulting in the Relative and Required Velocity Integration To Endpoint (RRVITE) model. With respect to the control of hitting, however, it should be noted that, although the RRVITE model can account for planned velocity profiles that have a peak close to contact (as is typically the case in hitting), $\dot{X}_{ip}$ is a secondary, rather than a controlled, aspect of movement planning. To account for the explicit control of $\dot{X}_{ip}$,

the present study presents an alternative extension of the RVITE model.

One way to incorporate control of $\dot{X}_{ip}$ into the RVITE model is by placing the TPV at the end of the swing (i.e., beyond, rather than at, the IP) such that the end-effector has a nonzero velocity when it travels through the IP and hits the object. This possibility, however, does not seem very realistic because the interception would be more or less accidental and would not result from the specific goal to hit the object with minimal spatiotemporal variability at the IP. Another possibility is to combine position and velocity servos, ensuring that when $TC = 0$, both the position and velocity of the effector reach a desired value. The RVITE model already provides the corresponding TC -modulated position servo. In a similar fashion, the velocity servo may be suggested to depend on an explicit comparison between the desired effector velocity at interception ($\dot{X}_{ipdes}$) and the actual hand velocity ($\dot{X}_h$), scaled by TC^{-1} , thus providing a required acceleration ($\ddot{X}_{hreq}$):

$$\ddot{X}_{hreq} = \frac{\dot{X}_{ipdes} - \dot{X}_h}{TC}. \quad (5)$$

To integrate such a velocity servo in the RVITE model, one has to assume explicit acceleration-based control. However, given the weak neurophysiological support for acceleration-related coding in movement-related cortical areas (e.g., Ashe and Georgopoulos 1994; Kelso et al. 1998, an alternative option was pursued. Figure 2 illustrates the rationale for the extension, which entails a direct influence of $\dot{X}_{ipdes}$ on the DVV. In principle, at any given moment during an object's approach, the required velocity ($\dot{X}_{hreq}$) equals the average velocity needed to travel the remaining distance to the target in the remaining time. If $\dot{X}_{ipdes}$ exceeds this average velocity, $\dot{X}_h$ has to be lower

Fig. 2. Rationale for RVITE extension. At any moment, the required hand velocity ($\dot{X}_{hreq}(t')$) indicates the required *average* velocity for the remaining time window (*dash-dotted horizontal line*). To reach a higher (*lower*) velocity at interception ($\dot{X}_{ipdes}$), the hand velocity ($\dot{X}_h$) should be lower (*higher*) than $\dot{X}_{hreq}(t')$ at least during part of the remaining time. The assumption of a future hand movement with a constant acceleration (*solid line*) yields $\dot{X}_h(t') = \dot{X}_{hreq}(t') - (\dot{X}_{ipdes} - \dot{X}_{hreq}(t'))$; another assumed future hand movement that yields an average hand velocity equal to $\dot{X}_{hreq}(t')$ is shown by the *dashed line* and yields $\dot{X}_h(t') = \dot{X}_{hreq}(t') - \dot{X}_{ipdes}$.

than $\dot{X}_{\text{hreq}}$ at least for some period prior to interception in anticipation of the higher $\dot{X}_h$ at interception. This principle was implemented in the RVITE model by adding an interception velocity vector (IVV), inhibiting the DVV by a magnitude related to $\dot{X}_{\text{ipdes}}$.

The new hit-RVITE model is formalized by replacing (2) with

$$\dot{P} = \frac{G}{TC} (V - I). \quad (6)$$

Here, $G = G_0 g_2$ and I is the IVV, which may be defined as $TC \cdot (\dot{X}_{\text{ipdes}} - \dot{X}_{\text{hreq}})$ (Fig. 2, solid line) or $TC \cdot \dot{X}_{\text{ipdes}}$ (Fig. 2, dashed line), where the TC multiplication is added for unitary consistency. The latter option is more straightforward and will be used in the remainder of this article, although all conclusions hold for both versions. As is explained in the Appendix, the proposed hit-RVITE model effectively involves integrated TC^{-1} -regulated position and velocity servos, ensuring that P and $\dot{P}$ reach their desired values when $TC = 0$. Equation (12) of the Appendix shows that the set point for the velocity servo equals $(G / (G - 1)) \dot{X}_{\text{ipdes}}$, which suggests that a mapping of the IVV (depending on $(G - 1) / G$) is required to ensure that the velocity servo is attracted to the appropriate value. For successful performance it is sufficient that this mapping depends on G at interception. We therefore used a GO signal (i.e., replacing (4)) that reached a known value (G_0 in this case) at interception, using the required velocity principle:

$$I = \left(\frac{G_0 - 1}{G_0} \right) \cdot TC \cdot \dot{X}_{\text{ipdes}}, \quad (7)$$

$$\dot{g}_2 = \frac{g_1(1 - g_2)}{TC} \quad (8)$$

It should be noted that this (convenient but arbitrary) choice of the GO signal is not critical for model performance: most qualitative effects are also present when it is implemented as a scalar (although this yields an unrealistic velocity jump at initiation).

At this juncture, it is interesting to consider a property of the hit-RVITE model that is not directly apparent from its formal introduction in the previous paragraphs. It arises when the effector is initially positioned at the future IP, with $\dot{X}_{\text{ipdes}} \neq 0$. In this case, a “conflict” occurs between the spatiotemporal requirements and the control of $\dot{X}_{\text{ip}}$: being at the right place at the right time requires no movement, which, however, would imply that the effector velocity cannot reach its desired value. The solution emerging from the model is a backswing movement: the planned trajectory initially deviates from the IP, to subsequently reverse direction and reach the IP at the correct time. This backswing occurs because the DVV is initially equal to $-(G/TC) \cdot I$ (since the DV is initially zero; see (6)) and ends when V exceeds I , after which both the velocity and position converge to their desired values at interception.

Before turning to more detailed model-data comparisons, the basic model performance is illustrated by simulations of a hitting task with a particular $\dot{X}_{\text{ipdes}}$. These simulations, like those reported later, were run in Matlab 6.5 (The MathWorks, Inc., Natick, MA, USA) by

Fig. 3. Illustrative simulated kinematics (PPV and DVV) of the hit-RVITE model given variations in G_0 . The hand started 1 m from the IP, and $\dot{X}_{\text{ipdes}}$ was set to 5 m s^{-1} . For the higher G_0 s a small backswing is evident (see text for further details)

numerically integrating (1), (3), (6), (7), and (8) using a fifth-order, variable step size Runge–Kutta ODE solver. The PPV arbitrarily started at -1 , the TPV was located at 0 , the IVV was set to 5 , and the simulated movements started 0.3 s before interception. The only free parameter in the model, G_0 , was varied to illustrate its effect on the effector velocity profile. Figure 3 shows the simulated planned kinematics (i.e., PPV and DVV). For $G_0 \leq 1$, $\dot{X}_{\text{ip}}$ cannot be controlled because the velocity servo is unstable (see Appendix); for higher values of G_0 both the position and velocity at interception are successfully controlled.

For larger values of G_0 , small backswings emerged from the model (cf. Fig. 3); contrary to the situation where the hand starts at the IP, these backswings are not required for success. They are, however, important in view of the to-be-reported model-data comparisons, because such small backswings delay the initiation of the forward movement and, thus, the moment of initiation (T_{ini}) as determined using a standard (relative) velocity threshold for movement in the direction of the IP only. For the profiles depicted in Fig. 3, such a threshold would result in a large variation in T_{ini} for the different values of G_0 , which does not correspond to the T_{ini} 's at the planning level (which was always 0.3 s in these simulations). Thus, for adequate comparison of our simulation results with empirical data, it was important to determine T_{ini} in the behavioral data with an algorithm that allowed for detecting small initial backswing movements. To this end, the data sets of interest (Caljouw et al. 2004b, c) were reanalyzed accordingly.

3 Model-data comparison

3.1 Data constraints

To evaluate the model's performance, its output was compared to the kinematic data obtained by Caljouw et al. (2004b, c). In the experiments in question, the participants

had to hit white balls (diameter 0.075 m) that approached their head at a straight angle from 1.90 m away, moving at one of three constant velocities (i.e., 1.0, 1.5, or 2.0 m s⁻¹) at 1.35 m above the ground. In their right hand (moving 0.30 m below eye level), they held a 0.30-m-long rod pointing upward that was constrained to move in a lateral direction along a horizontal bar; a square Perspex block was attached to the distal tip. Participants were instructed to hit the ball with this block onto one of two target areas presented on the ground whose centers were located at 0.55 and 1.05 m from the IP, respectively (the goal distances). The hand was initially positioned approximately 0.30 m to the right of (Caljouw et al. 2004b) or at the IP (Caljouw et al. 2004c), which was defined as the crossing between the hand and ball movement axes. Note that in the latter condition considerable backswings were expected to occur, which were also investigated by Caljouw et al. (2004c).

As indicated above, we reanalyzed the data of Caljouw et al. 2004b, c to extract model-relevant kinematic variables. Our definition of the dependent variables slightly differed from that used by Caljouw et al. 2004b, c and is therefore presented here. First, the velocity profile was checked for the presence of a (small) backswing: if the second to last velocity peak exceeded -2% of the peak velocity, it was deemed part of a backswing.² In this way, small backswings were identified in 94 of the 599 analyzed trials of Caljouw et al. 2004b (with three participants showing backswings in less than 5% of their trials, five participants in 10–20%, and one participant in 68% of the trials). If a backswing was present, T_{ini} was defined as the moment the lateral hand velocity exceeded 2% of the maximal (negative) velocity reached during the backward movement; otherwise, T_{ini} was defined as the moment the lateral hand velocity exceeded 2% of the peak velocity reached during the forward movement. The moment of initiation of the front swing (T_{FS-ini}) was defined as the moment at which the forward velocity exceeded 2% of the peak front swing velocity, that is, T_{FS-ini} equaled T_{ini} for trials in which no backswing movement was detected. Both these temporal variables were defined relative to the moment of contact, which was defined as the moment in time at which the lateral distance between ball and effector became smaller than 0.0375 m (the ball's radius). In addition, $\dot{X}_{ip}$ was determined and the amplitude of the backswing (A_{BS}) was defined as the difference between the rightmost hand position and the hand position at initiation.

T_{ini} , T_{FS-ini} , $\dot{X}_{ip}$, and A_{BS} were subjected to a 2 (goal distance) $\times$ 3 (ball velocity) repeated measures (RM) ANOVA for both experiments. Paired-sample t -tests were used for post hoc analyses. Effects were considered significant if $p < 0.05$, both for the RM ANOVA and the post hoc analyses, but tendencies toward significance ($p < 0.1$) are also reported. The average values of the dependent variables, which served as reference for the model simulations, are presented in Figs. 4 and 5. The statistical results are presented in Sect. 3.3 and Table 1.

² Visual inspection of the velocity profiles confirmed that this algorithm successfully identified the small backswings as part of the movement in cases where the hand started to the right of the IP.

Fig. 4. Average moments of front swing initiation (T_{FS-ini}), impact velocities ($\dot{X}_{ip}$), and backswing amplitudes (A_{BS}) as a function of ball velocity (V_{ball}) and goal distance (white bars: near goal; black bars: far goal) for the experiment with the hand initially located at 0.30 m to the right of the IP. The left and right columns show the values extracted from Caljouw et al.'s (2004b) data and from simulations of the hit-RVITE model, respectively

Fig. 5. Average moments of front swing initiation (T_{FS-ini}), impact velocities ($\dot{X}_{ip}$) and backswing amplitudes (A_{BS}) as a function of ball velocity (V_{ball}) and goal distance (white bars: near goal; black bars: far goal) for the experiment with the hand initially located at the IP. The left and right columns show the values extracted from Caljouw et al.'s (2004c) data and from simulations of the hit-RVITE model, respectively

3.2 Model simulations

Two sets of simulations were performed to examine the correspondence between the hit-RVITE model and the empirical data of Caljouw et al. 2004b, c. The first set concerned the performance averaged over participants, using T_{FS-ini} , $\dot{X}_{ip}$, and A_{BS} . Note that model-data comparison for T_{ini} was impossible since the model accounts for

Table 1. Means and standard deviations of the moment of initiation (T_{ini} in s before contact) based on reanalysis of Caljouw et al.'s (2004b, c) data for all six conditions (2 goal distances $\times$ 3 ball velocities)

Ball velocity (m s^{-1})	Caljouw et al. (2004b)		Caljouw et al. (2004c)	
	Near	Far	Near	Far
1.0	0.403 (0.044)	0.373 (0.137)	0.726 (0.195)	0.708 (0.148)
1.5	0.379 (0.049)	0.364 (0.114)	0.656 (0.165)	0.645 (0.145)
2.0	0.385 (0.052)	0.326 (0.093)	0.552 (0.105)	0.555 (0.081)

the generation of the planned trajectory *after initiation*. Consequently, T_{ini} was dictated in these simulations using the average T_{ini} s calculated from the data of Caljouw et al. 2004b, c (i.e., averaged over participants; see Table 1). $\dot{X}_{\text{ipdes}}$ was set to the participants' average $\dot{X}_{\text{ip}}$ for each condition (i.e., each combination of ball velocity and goal distance).

The second set of simulations was performed to specifically compare the PPV and DVV profiles with the kinematic (position and velocity) profiles of four individual participants as obtained for the two different experiments (two participants per experiment). In these simulations, T_{ini} and $\dot{X}_{\text{ipdes}}$ were set to each participant's average T_{ini} and $\dot{X}_{\text{ip}}$ as obtained for each condition. TC in (6) and (7) was taken to be the actual time remaining before contact, and T in (1) was set at -0.0375 (the rightmost edge of the ball at $\text{TC} = 0$). The simulations were stopped 5 ms before contact (which corresponds to one sample in the experimental data) to eliminate the rapid changes in the DVV that occurred immediately before contact due to the vanishing TC term. For both sets of simulations, G_0 was varied slightly between tasks but was held constant over the different participants (hand starting to the right of the IP: $G_0 = 1.8$; hand starting at the IP: $G_0 = 2.2$); the other parameters were fixed ($\gamma = 100$; $A = 6$; $B = 3$).

3.3 Results

For the experiment in which the hand was initially positioned 0.30 m to the right of the IP (Caljouw et al. 2004b), the average T_{ini} s are presented in Table 1 and the average $T_{\text{FS-ini}}$, $\dot{X}_{\text{ip}}$, and A_{BS} are presented in the left panels of Fig. 4. The RM ANOVA for T_{ini} showed no significant effects, whereas $T_{\text{FS-ini}}$ occurred significantly later for the far than for the near goal ($F(1, 8) = 106.87$; $p < 0.001$). Together these results imply that a small backswing occurred predominantly when the ball had to be hit towards the far goal, thereby significantly delaying the initiation of the front swing. However, this was not reflected in the A_{BS} , which was not significantly influenced by any of the independent variables. The small backswings occurred more often for the far (in 72 out of 303 trials) than for the near goal (in 22 out of 296 trials), a difference that was consistent in the six participants that showed small backswings in more than 10% of the trials. Examination of the average T_{ini} s suggested that the absence of an effect of goal distance on T_{ini} was largely due to interindividual differences. Specifically, the three participants that showed

backswings in less than 5% of the trials initiated earlier for the near than for the far goal, whereas two of the other participants initiated distinctly later for the near than for the far goal, and four showed only a very small difference. Thus, the absence of an effect of goal distance on T_{ini} must be considered in view of these interindividual differences. In accordance with the task requirements, $\dot{X}_{\text{ip}}$ was significantly higher for the far goal than for the near goal ($F(1, 8) = 194.61$; $p < 0.001$). Moreover, there was a significant goal distance $\times$ ball velocity interaction ($F(2, 16) = 5.65$; $p < 0.05$). Post hoc analyses revealed that for the far goal $\dot{X}_{\text{ip}}$ was significantly higher for a ball velocity of 1.0 m s^{-1} than for a ball velocity of 1.5 m s^{-1} and tended to be higher than for a ball velocity of 2.0 m s^{-1} ($p = 0.08$), while for the near goal only the latter difference tended towards significance, albeit in the opposite direction ($p = 0.08$).

The average T_{ini} s for the experiment in which the hand was initially at the IP (i.e., Caljouw et al. 2004c) are presented in Table 1, and the average $T_{\text{FS-ini}}$, $\dot{X}_{\text{ip}}$, and A_{BS} are presented in the left panels of Fig. 5. T_{ini} was significantly influenced by ball velocity ($F(2, 18) = 31.98$; $p < 0.001$); post hoc analyses showed that T_{ini} differed significantly over all ball velocities (i.e., the higher the ball velocity, the later the initiation). $T_{\text{FS-ini}}$ was also significantly influenced by ball velocity ($F(2, 18) = 19.60$; $p < 0.001$); post hoc analyses showed that the front swing was initiated significantly later for a ball velocity of 2.0 m s^{-1} than for ball velocities of 1.0 and 1.5 m s^{-1} . Moreover, the RM ANOVA revealed a significant goal distance $\times$ ball velocity interaction ($F(2, 18) = 6.14$; $p < 0.01$); post hoc analyses revealed a significantly later front swing initiation for the far compared to the near goal, but only for a ball velocity of 1.5 m s^{-1} . A_{BS} was significantly influenced by goal distance ($F(1, 9) = 68.95$; $p < 0.001$) as well as ball velocity ($F(2, 18) = 34.86$; $p < 0.001$). Post hoc analyses showed that A_{BS} was significantly larger for the far compared to the near goal and differed significantly over all ball velocities (i.e., the higher the ball velocity, the smaller the A_{BS}). Again, as required by the task, $\dot{X}_{\text{ip}}$ was significantly influenced by goal distance ($F(1, 9) = 513.65$; $p < 0.001$), with a higher $\dot{X}_{\text{ip}}$ being observed for the far goal than for the near goal.

The right panels of Figs. 4 and 5 present the results as obtained for the first set of simulations. There is a good correspondence between the data (left panels) and the simulation results (right panels); however, several minor differences can still be delineated. The pattern for $\dot{X}_{\text{ip}}$ generated by the model did not correspond to the significant

goal distance $\times$ ball velocity interaction for $\dot{X}_{ip}$ in the experimental data (although both in the model and the data the differences in $\dot{X}_{ip}$ between the different ball velocities were very small and hardly visible in Fig. 4). For the task with the hand initially positioned at the IP the difference between T_{FS-ini} for ball velocities of 1.0 and 1.5 $m s^{-1}$ in the data was small (and not significant), whereas the simulations showed a monotonic effect of ball velocity on T_{FS-ini} (Fig. 5, top panels). Despite these two small discrepancies, the hit-RVITE model could account for all other effects present in the data of Caljouw et al. (2004b, c).

To examine the model's ability to produce adequate planned trajectories, the average experimentally observed lateral hand position and velocity profiles are presented for individual participants of Caljouw et al. (2004b, c) and Caljouw et al. 2004a in Figs. 6 and 7, respectively, together with the corresponding PPV and DVV profiles generated with the hit-RVITE model. These figures demonstrate the model's ability to capture individual differences that were related to the different T_{ini} s and $\dot{X}_{ip}$ s of these participants. It should be noted that these figures do not represent the best possible correspondence between model and data; we focused on the qualitative aspects and refrained from varying the parameters between participants within a single experiment. As averaging the kinematic profiles for each participant might have introduced discrepancies that are not related to the actual kinematic performance, we also examined whether the variations in T_{FS-ini} , A_{BS} , and $\dot{X}_{ip}$ evident in the averaged empirical kinematic profiles corresponded qualitatively to the participants' individual averages. Only one average profile of one participant showed a discrepancy in this respect; this case is discussed below.

Figure 6 shows the average empirically observed and simulated planned kinematics for two participants of Caljouw et al. (2004b). Participant 1 (Fig. 6, upper panels) initiated markedly earlier for the far goal (0.647, 0.582, and 0.546 s for a ball velocity of 1.0, 1.5, and 2.0 $m s^{-1}$, respectively) than for the near goal (0.478, 0.364, and 0.504 s for a ball velocity of 1.0, 1.5, and 2.0 $m s^{-1}$, respectively). This early initiation for the far goal was accompanied by considerable backswing movements (this participant's behavior was most extreme in this regard). The model also shows backswings for the far goal that are, however, much larger and modulated by ball velocity. These backswings delay T_{FS-ini} such that it occurs later for the far goal. Qualitatively the model captures the kinematic performance of this participant but with some sizeable quantitative differences. Participant 8 (Fig. 6, lower panels) initiated earlier for the near (0.418, 0.492, and 0.394 s for a ball velocity of 1.0, 1.5, and 2.0 $m s^{-1}$, respectively) than for the far goal (0.249, 0.306, and 0.274 s for a ball velocity of 1.0, 1.5, and 2.0 $m s^{-1}$, respectively). Except for some discrepancies in the DVV profile close to contact (with the peak occurring too early and being too high for the far goal), the hit-RVITE model accurately reproduces the key features of this participant's kinematics.

Figure 7 shows the average empirically observed and simulated planned kinematics for two participants of Caljouw et al. (2004c): participant 5 (Fig. 7, upper panels) initiated relatively early (near goal: 0.760, 0.695, and

Fig. 6. Average experimental (left column) and simulated planned kinematics (right column) for two participants in the experiment with the hand initially located 0.30 m to the right of the IP. Participant 1 (upper panels) initiated earlier for the far than for the near goal, whereas participant 8 (lower panels) initiated earlier for the near than for the far goal

0.641 s; far goal: 0.779, 0.689, and 0.597 s for ball velocities of 1.0, 1.5, and 2.0 $m s^{-1}$, respectively), and participant 6 (Fig. 7, lower panels) initiated relatively late (near goal: 0.579 s, 0.578 s, and 0.472 s; far goal: 0.522, 0.478, and 0.428 s for ball velocities of 1.0, 1.5, and 2.0 $m s^{-1}$, respectively). For this task, the simulated kinematics contains only one discrepancy: for participant 5 the A_{BS} for a ball velocity of 1.0 $m s^{-1}$ and the far goal is too large (compared to a ball velocity of 1.5 $m s^{-1}$). A similar discrepancy seems to be present for participant 6, but this is due to the averaging of the profiles: the average A_{BS} for this participant does show a decrease over all ball velocity levels (as does the model). All other key features of these participants' kinematics are adequately reproduced by the hit-RVITE model.

Fig. 7. The average experimental (*left column*) and simulated planned kinematics (*right column*) for two participants in the experiment with the hand initially located at the IP. Participant 5 (*upper panels*) initiated earlier than participant 6 (*lower panel*)

4 Discussion

The proposed hit-RVITE model for the neural control of hitting describes the planning of the effector trajectory in view of spatiotemporal (i.e., being at the right place at the right time) as well as interception constraints (i.e., controlling $\dot{X}_{ip}$, and thus object velocity after interception). In particular, the latter aspect has received little attention in the literature. The new feature of the hit-RVITE model, relative to the original VITE and RVITE models, involved an inhibition of the DVV that depends on $\dot{X}_{ipdes}$, as explained in Fig. 2. Analyses of the model equations (see Appendix) showed that the model possesses TC^{-1} -scaled position- and velocity-servo properties without requiring explicit control of effector acceleration. An interesting property of the model is the backswing generated when the effector is initially positioned close to the IP: the complete backswing emerges in real time from the neural dynamics

and does not involve biphasic planning, that is, there are no separate TPVs for back and front swing. Moreover, when the effector does not start at the IP, a much smaller backswing may also emerge from the model, depending on $\dot{X}_{ipdes}$ and T_{ini} . This task-specific adaptation emanating from the hit-RVITE model underscores Bullock and Grossberg's (1988) argument that many variant and invariant properties of human movements can emerge in real time from sensory, neural, and musculoskeletal dynamics (and their interactions) without being explicitly represented in the motor control system as such.

To evaluate the hit-RVITE model's performance, the planned trajectories were compared to the trajectories recorded by Caljouw et al. 2004b, c. One set of simulations focused on the average values of several kinematic variables extracted from the empirical data (i.e., T_{FS-ini} , A_{BS} , and $\dot{X}_{ip}$), while another set focused on individual position and velocity profiles. The simulations showed that the hit-RVITE model accounts for nearly all effects present in the average data, as well as for most individual kinematic differences. Thus, given a very straightforward control of $\dot{X}_{ip}$, the hit-RVITE model provides an adequate account for the data of Caljouw et al. 2004b, c.

The motor outflow commands issued by the hit-RVITE model are generated continuously during the ball approach, without being programmed beforehand. The good correspondence between model and data therefore suggests that many aspects of fast hitting movements are consistent with a continuous generation of movement trajectories. Patently, continuous control critically depends on the continuous availability of the various informational inputs; in its current form, the hit-RVITE model breaks down if vision of the ball is prevented at some point in the ball approach. However, in this situation, successful hitting is still possible (cf. Brouwer et al. 2002; Sharp and Whiting 1974), which might be accounted for by extending the hit-RVITE model with an internal model of the ball's motion, predicting (part of) the time course of the informational variables on the basis of earlier informational inputs. In this manner, continuous control of even very fast hitting movements is still viable (cf. Desmurget and Grafton 2000).

An interesting emergent feature of the hit-RVITE model was the generation of backswing movements. When the effector starts at the IP, a backswing is not only necessary to meet the task requirement (since the effector cannot instantaneously reach a desired velocity), but it is also advantageous from a mechanical point of view: during the backswing elastic energy is stored in the tendons of the arm flexors, and these muscles are given time to build up active state, both increasing power output during the front swing (e.g., Anderson and Pandy 1993; Bobbert et al. 1996). Another interesting feature in this respect is that the small backswings that occur when the effector does not start at the IP effectively delay T_{FS-ini} in a task-dependent manner. An important implication of this prediction (which was consistent with the data of Caljouw et al. 2004b) is that, due to the dynamics of movement generation, variations in movement initiation (as typically determined on the basis of kinematic considerations regarding the front

swing) might not always reflect variations in the start of movement generation.

The hit-RVITE model uses three external sources of information to ensure successful hitting performance, which are presumably all available visually: spatial (i.e., TPV) and temporal information (i.e., TC) and information about the goal distance. On the basis of the perceived goal distance, which specifies the required object velocity directly after interception, the actor has to determine $\dot{X}_{ipdes}$. This “transformation” is simply presumed in the model since it was not the primary focus of this study. With regard to the model’s TPV it should be noted that this variable may correspond to the lateral ball position or to a prediction of the IP. Evidently, different sources of visual information might be used for these two options. However, since the experiments of Caljouw et al. (2004b and c) involved head-on approaches with lateral ball position always coinciding with the future IP, these two options could not be dissociated in the present study.

Besides its informational basis, the neurophysiological basis of hit-RVITE also remains to be unraveled. As it stands, there are only very little neurophysiological data on interceptive actions (Lee et al. 2001; Port et al. 2001; Merchant et al. 2004), and to our knowledge neurophysiological data on hitting (i.e., the control of $\dot{X}_{ip}$) are completely lacking. Although the original formulation of the RVITE model (Dessing et al. 2002; see also Beek et al. 2003) was consistent with available neurophysiological data, the hit-RVITE model makes predictions for future neurophysiological observations. In the following discussion, several tentative implications of hit-RVITE are discussed in the form of possible neural correlates of the IVV.

Given the mathematical formulation of the hit-RVITE model, basically two architectures are possible, which are depicted in Fig. 8. The most literal translation of (6) and (7) yields architecture A, which preserves the TC^{-1} scaling at the GO signal by also incorporating a TC scaling of the IVV. In architecture B the DVV receives excitatory inputs from a population encoding the required velocity (ReqVV) and inhibitory inputs from the IVV. Thus, contrary to the original RVITE model, the TC^{-1} scaling in this architecture occurs not at the GO signal, but at the ReqVV. Projections exist from the lateral posterior and pulvinar thalamic nucleus (LP-PUL, the proposed origin of the TC signal: cf. Dessing et al. 2002; see also Sun and Frost 1998) to the GO site (globus pallidus; e.g., Butler and Hodos 1996), as well as to cortical areas 5 and 7 (e.g., Brooks 1986; Mesulam 1983), where a ReqVV might be coded. Although it remains to be determined to what extent the latter assumption is realistic, the fact that cortical areas 5 and 7 project to the hypothesized DVV site, area 4; e.g., Babb et al. 1984) means that architecture B cannot be rejected on the basis of the available neuroanatomical data.

Both architectures involve inhibitory projections from the IVV to the DVV locus (primary motor cortex). Architecture A additionally assumes a projection from the TC locus to the IVV locus. Given that no neurophysiological

Fig. 8. Two possible architectures implementing the hit-RVITE model. Architecture A incorporates a TC scaling of the IVV and thus maintains the TC^{-1} scaling of the GO signal. Architecture B separates a required velocity vector (ReqVV) and interception velocity vector (IVV) input to the desired velocity vector (DVV). As such, the TC^{-1} scaling of the GO signal, as proposed in the original RVITE model, is no longer present (see text and Fig. 1 for further details)

data are available to determine a neural correlate of the IVV, the latter difference between the architectures is insufficient to motivate a principled choice between them. However, a tentative hypothesis about the IVV locus can be formulated on the basis of neurophysiological studies on “normal” reaching. The dorsal premotor cortex (PMd) is an interesting candidate because it is known to associate particular sensory events with specific movements. The PMd has been implicated in the programming of motor output parameters such as direction, amplitude, and velocity (e.g., Johnson et al. 1999; Turner et al. 1998). As such, the PMd seems well suited for providing a form of velocity control as proposed in the hit-RVITE model. Notably, the premotor cortex projects to area 4 as well as directly to the spinal cord (e.g., Dum and Strick 2002) but does not receive projections from LP-PUL (Darian-Smith et al. 1990b; although these projections are present in early development; Darian-Smith et al. 1990a). Thus, under the hypothesis that the IVV is coded in PMd, architecture A should be rejected due to the absence of TC input to the IVV.

An aspect of the RVITE architecture that deserves special mention is the interaction between the GO signal and the DV at the DVV. This interaction is multiplicative, while most local neural operations can be understood in terms of addition and subtraction (through excitation and inhibition). Recently, however, plausible neural operations acting effectively as multiplication have been identified (Chance et al. 2001; Murphy and Miller 2003). The gain modulation (i.e., multiplicative scaling of neural activity) reported in these studies has been observed throughout the parietal cortex (see Salinas and Abbott 2001) and has been implicated in sensorimotor coordinate transformations (e.g., Ajemian et al. 2001; Salinas and Abbott 1995). Thus, it may be suggested that the multiplicative interactions in the hit-RVITE model (and related VITE extensions) are brought about by such gain modulation.

5 Conclusion

We proposed a neural network model, by extending the RVITE model, to account for the control of $\dot{X}_{ip}$ in hitting. The model effectively operates as parallel TC^{-1} -scaled position and velocity servos and can account for nearly all the qualitative effects present in the hitting data of Caljouw et al. 2004b, c. Interestingly, the predicted small back swings in situations for which such movements had not been presented before in the literature were indeed observed in the empirical data of Caljouw et al. (2004b). Whereas the original RVITE model was consistent with available neurophysiological data, no neurophysiological data about velocity control in hitting tasks are available to substantiate the present extension. However, on the basis of the proposed model, architecture-specific hypotheses were formulated with regard to the instantiation of the proposed IVV in the hit-RVITE model.

Appendix

By means of the time derivative of (6) it is shown that the hit-RVITE model implicitly operates as an integrated TC^{-1} -scaled position and velocity servo. To this end, the dynamics of the DV is neglected (i.e., using $V = T - P$), which is justified given its fast integration rate. Also, the TPV is assumed not to change (i.e., $\dot{T} = 0$), given the head-on ball approaches used in the modeled experiment.

$$I = TC \cdot \dot{X}_{ipdes} . \quad (9)$$

Combining (9) with (6) yields

$$TC \cdot \dot{P} = G (V - TC \cdot \dot{X}_{ipdes}) , \quad (10)$$

which, after differentiation, yields

$$TC \cdot \ddot{P} - \dot{P} = G (-\dot{P} + \dot{X}_{ipdes}) + \dot{G} (V - TC \cdot \dot{X}_{ipdes}) \quad (11)$$

which equals

$$\ddot{P} = (G - 1) \left(\frac{\left(\frac{G}{G-1} \right) \dot{X}_{ipdes} - \dot{P}}{TC} \right) + \dot{G} \left(\frac{(T - TC \cdot \dot{X}_{ipdes}) - P}{TC} \right) . \quad (12)$$

The first term of (12) is a velocity servo (stable for $G > 1$) that has a set point equaling $(G / (G - 1)) \dot{X}_{ipdes}$, suggesting that (9) should be replaced by

$$I = \left(\frac{G - 1}{G} \right) \cdot TC \cdot \dot{X}_{ipdes} . \quad (13)$$

The second term of (12) is a position servo, of which the set point $(T - TC \cdot \dot{X}_{ipdes})$ is time dependent (due to the TC term).

Although the derivations described above refer to the desired hand acceleration ($\ddot{P}$), it should be noted that the hit-RVITE model does not specifically control hand acceleration: (6) corresponds to the actual model, which controls the desired hand velocity.

References

- Ajemian R, Bullock D, Grossberg S (2001) A model of movement coordinates in the motor cortex: posture-dependent changes in gain and direction of single cell tuning curves. *Cereb Cortex* 11:1124–1135
- Anderson FC, Pandy MG (1993) Storage and utilization of elastic strain energy during jumping. *J Biomech* 26:1413–1427
- Ashe J, Georgopoulos AP (1994) Movement parameters and neural activity in motor cortex and area 5. *Cereb Cortex* 4:590–600
- Babb RS, Waters RS, Asanuma H (1984) Corticocortical connections to the motor cortex from the posterior parietal lobe (areas 5a, 5b, 7) in the cat demonstrated by the retrograde axonal transport of horseradish peroxidase. *Exp Brain Res* 54:476–484
- Beek PJ, Bootsma RJ (1991) Physical and informational principles in modeling coordinated movements. *Hum Mov Sci* 10:81–92
- Beek PJ, Dessing JC, Peper CE, Bullock D (2003) Modelling the control of interceptive actions. *Philos Trans R Soc B* 358:1511–1523
- Bobbert MF, Gerritsen KG, Litjens MC, Van Soest AJ (1996) Why is countermovement jump height greater than squat jump height? *Med Sci Sport Excer* 28:1402–1412
- Bootsma RJ, Van Wieringen PCW (1990) Timing an attacking forehand drive in table tennis. *J Exp Psychol HPP* 16:21–29
- Bootsma RJ, Fayt V, Zaal FTJM, Laurent M (1997) On the information-based regulation of movement: What Wann (1996) may want to consider. *J Exp Psychol HPP* 23:1282–1289
- Brenner E, Smeets JBJ (1996) Hitting moving targets: co-operative control of ‘when’ and ‘where’. *Hum Mov Sci* 15:39–53
- Brenner E, Smeets JBJ, De Lussanet MH (1998) Hitting moving targets: continuous control of the acceleration of the hand on the basis of the target’s velocity. *Exp Brain Res* 122:467–474
- Brooks V (1986) The neural basis of motor control. Oxford University Press, New York
- Brouwer AM, Brenner E, Smeets JBJ (2002) Hitting moving objects: is target speed used in guiding the hand? *Exp Brain Res* 143:198–211
- Bullock D, Grossberg S (1988) Neural dynamics of planned arm movements: emergent invariants and speed-accuracy properties during trajectory formation. *Psychol Rev* 95:49–90
- Bullock D, Grossberg S (1991) Adaptive neural networks for control of movement trajectories invariant under speed and force rescaling. *Hum Mov Sci* 10:3–53
- Butler A, Hodos W (1996) Comparative vertebrate neuroanatomy. Wiley, New York
- Caljouw SR, Van der Kamp J, Savelsbergh GJP (2004a) The fallacious assumption of time-to-contact perception in the regulation of catching and hitting. In Hecht H, Savelsbergh GJP (eds) Time-to-contact. Elsevier, Amsterdam, pp 443–474
- Caljouw SR, Van der Kamp J, Savelsbergh GJP (2004b) Timing of goal-directed hitting: impact requirements change the information movement coupling. *Exp Brain Res* 155:135–144
- Caljouw SR, Van der Kamp J, Savelsbergh GJP (2004c) Bi-phasic hitting with constraints on impact velocity and temporal precision. *Human Mov Sci* (in press)
- Chance FS, Abbott LF, Reyes AD (2001) Gain modulation from background synaptic input. *Neuron* 35:773–782
- Chapman S (1968) Catching a baseball. *Am J Phys* 36:868–870

- Darian-Smith D, Darian-Smith I, Cheema SS (1990a) Thalamic projections to sensorimotor cortex in newborn macaque. *J Comp Neurol* 299:47–63
- Darian-Smith D, Darian-Smith I, Cheema SS (1990b) Thalamic projections to sensorimotor cortex in newborn macaque: use of multiple retrograde fluorescent tracers. *J Comp Neurol* 299:17–46
- Desmurget M, Grafton S (2000) Forward modeling allows feedback control for fast reaching movements. *Trends Cogn Sci* 4:423–431
- Dessing JC, Bullock D, Peper CE, Beek PJ (2002) Prospective control of manual interceptive actions: comparative simulations of extant and new model constructs. *Neural Netw* 15:163–179
- Dum RP, Strick PL (2002) Motor areas in the frontal lobe of the primate. *Physiol Behav* 77:677–682
- Johnson MT, Coltz JD, Ebner TJ (1999) Encoding of target direction and speed during visual instruction and arm tracking in dorsal premotor and primary motor cortex neurons. *Eur J Neurosci* 11:4433–4445
- Kelso JAS, Fuchs A, Lancaster R, Holroyd T, Cheyne D, Weinberg H (1998) Dynamic cortical activity in the human brain reveals motor equivalence. *Nature* 392:814–818
- Lee DN (1998) Guiding movement by coupling taus. *Ecol Psychol* 10:221–250
- Lee DN, Young DS, Reddish PE, Lough S, Clayton TMH (1983) Visual timing in hitting an accelerating ball. *Q J Exp Psychol A* 35:333–346
- Lee D, Port NL, Kruse W, Georgopoulos AP (2001) Neuronal clusters in the primary motor cortex during interception of moving targets. *J Cogn Neurosci* 13:319–331
- McLeod P (1987) Visual reaction time and high-speed ball games. *Perception* 16:49–59
- Merchant H, Battaglia-Mayer A, Georgopoulos AP (2004) Neural responses during interception of real and apparent circularly moving stimuli in motor cortex and area 7a. *Cereb Cortex* 14:314–331
- Mesulam MM (1983) The functional anatomy and hemispheric specialization for directed attention. *Trends Neurosci* 6:384–387
- Miall RC, Wolpert DM (1996) Forward models for physiological motor control. *Neural Netw* 9:1265–1279
- Michaels CF, Zeinstra EB, Oudejans RD (2001) Information and action in punching a falling ball. *Q J Exp Psychol A* 54:69–93
- Murphy BK, Miller KD (2003) Multiplicative gain changes are induced by excitation or inhibition alone. *J Neurosci* 23:10040–10051
- Peper CE, Bootsma RJ, Mestre DR, Bakker FC (1994) Catching balls: how to get the hand to the right place at the right time. *J Exp Psychol HPP* 20:591–612
- Port NL, Kruse W, Lee D, Georgopoulos AP (2001) Motor cortical activity during interception of moving targets. *J Cogn Neurosci* 13:306–318
- Regan D (1992) Visual judgments and misjudgments in cricket, and the art of flight. *Perception* 21:91–115
- Salinas E, Abbott LF (1995) Transfer of coded information from sensory to motor networks. *J Neurosci* 15:6461–6474
- Salinas E, Abbott LF (2001) Coordinate transformations in the visual system: how to generate gain fields and what to compute with them. *Prog Brain Res* 130:175–190
- Savelsbergh GJP, Whiting HT, Bootsma RJ (1991) Grasping tau. *J Exp Psychol HPP* 17:315–322
- Sharp RH, Whiting HTA (1974) Information-processing and eye-movement behavior in a ball-catching skill. *J Hum Mov Stud* 1:124–131
- Smeets JBJ, Brenner E (1995) Perception and action are based on the same visual information: Distinction between position and velocity. *J Exp Psychol HPP* 21:19–31
- Sun H, Frost BJ (1998) Computation of different optical variables of looming objects in pigeon nucleus rotundus neurons. *Nat Neurosci* 1:296–303
- Turner RS, Grafton ST, Votaw JR, DeLong MR, Hoffman JM (1998) Motor subcircuits mediating the control of movement velocity: a PET study. *J Neurophysiol* 80:2162–2176
- Tresilian JR (1994) Perceptual and motor processes in interceptive timing. *Hum Mov Sci* 13:335–373
- Tresilian JR (1999) Visually timed action: time-out for ‘tau’? *Trends Cogn Sci* 3:301–310
- Tresilian JR, Lonergan A (2002) Intercepting a moving target: effects of temporal precision constraints and movement amplitude. *Exp Brain Res* 142:193–207
- Tyldesley DA, Whiting HTA (1975) Operational timing. *J Hum Mov Stud* 1:172–177
- Van der Kamp J (1999) The information based regulation of interceptive timing. Published doctoral dissertation, Vrije Universiteit, The Netherlands