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Neuroscience Perspectives on Adaptive Manual Control with Pursuit Displays

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Abstract: Cyberneticists develop mathematical human control models which are used to tune manual control systems and understand human performance limits. Neuroscientists explore the physiology and circuitry of the central nervous system to understand how the brain works. Both research human visuomotor control tasks, such as the pursuit tracking task. In this paper we discuss some commonalities and differences in both approaches to better understand the adapting human controller. Special attention is given to Adaptive Model Theory, which studied adaptive human control using several linear and nonlinear control engineering techniques. The insights gained yield schemes and concepts which pave the way for key future work on this topic.

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Keywords: Modeling of human performance, Adaptive system and control, Manual Control

1. INTRODUCTION

Modeling human behaviour in manual control has been studied for over 70 years, see review papers by McRuer and Jex (1967) and Mulder et al. (2018). Krendel and McRuer (1960) distinguish three stages of human control: compensatory, pursuit and precognitive. Depending on the variables that describe the task, mainly the type of display (compensatory, pursuit, preview, see Fig. 1), the controlled element (CE) dynamics, and the spectral properties of the target signal to be followed (f_t), the human controller (HC) *systematically adapts* to balance high tracking performance with limited control effort.

The systematic HC adaptation to task variables in compensatory tracking has been captured – in simple control engineering terms – with the *crossover model* (McRuer and Jex, 1967). This model has served for decades to tune manual control devices and to understand human bio-dynamics and other phenomena. Mulder et al. (2018) argue, however, that research has focused too much on modeling feedback-only (FB) compensatory tracking, the *exception* in human control. More efforts are needed to study the *rule* of human control, that is, to model the versatile, *adapting*, biological system, using more relevant pursuit and preview displays (Drop, 2016; Van der El, 2018). Being able to understand and model the human capabilities to *adapt* to changing circumstances may pave the way for better support systems, and human-like automation. But strikingly, our understanding and modeling capabilities of the *adaptive* HC has not progressed much since the seminal paper by Young (1969), reviewing a decade of work on adaptive manual control in compensatory tracking.

This paper discusses insights gained when studying the neuroscience literature on adaptive manual control in *pursuit* tracking. Work on this topic has progressed in both neuroscience and engineering communities, however,

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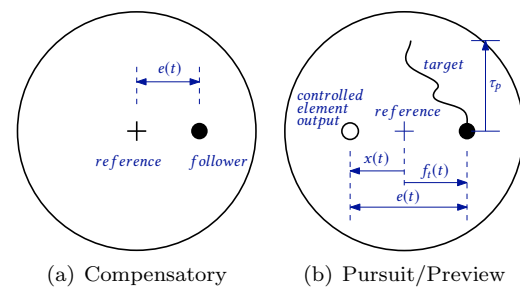


Fig. 1. Compensatory, Pursuit and Preview displays.

with only sporadic and limited interchange. Much can be gained from a joint perspective, for which this overview, written for control engineers, is a first attempt. We start in Section 2 with a summary of key neuroscience concepts and definitions. Adaptive Model Theory (AMT) will be discussed in Section 3, and re-engineered for the pursuit tracking task in Section 4.

2. BASIC NEUROSCIENCE CONCEPTS

The ‘comparator model’ illustrated in Fig. 2 provides a good starting point for studying the vast literature on human motion control in neuroscience. Introduced in (Frith et al., 2000) (page 1773, as Figure 1), it shows the “*basic components of a motor control system based upon engineering principles*”. The diagram is adapted to fit the purpose of the current paper, see also the figure caption. It is used here to introduce principles of neuroscience rationale, definitions and nomenclature to engineers.

The reader should note that this, like many other models in neuroscience, is a ‘conceptual model’, used to explain the *possible* processes in the brain and body that account for body movement tasks such as ‘to grab an object’, ‘to turn a dial’, etc. Useful reviews can be found in (Wolpert, 1997; Wolpert et al., 1998). In our application of pursuit tracking, the movement under study is ‘how the brain

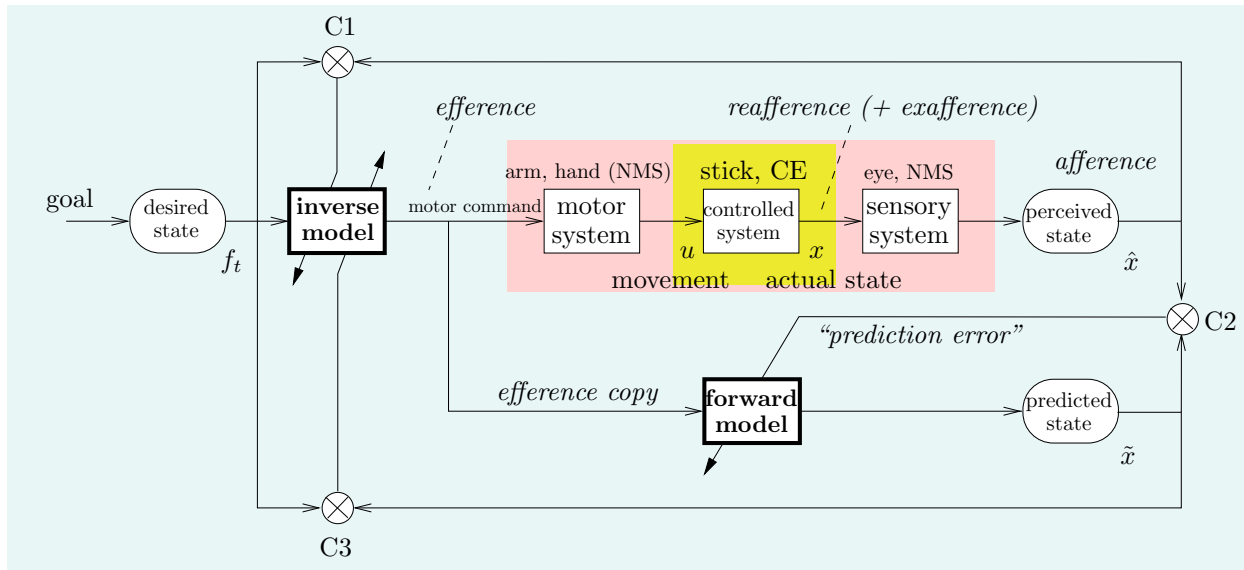


Fig. 2. Comparator model, our interpretation of (Frith et al., 2000), adapted to pursuit tracking. The yellow block reflects ‘what is to be controlled in the world’, the pink block reflects the peripheral nervous system, the remainder in blue the CNS (cerebrum, cerebellum, brainstem, spinal cord). CE stands for Controlled Element, NMS for Neuromusculoskeletal System and C1, C2, C3 for the three ‘comparators’ discussed in the text. Arrows crossing blocks indicate possible adaptation of these blocks. Desired, predicted and perceived states are shown in rounded boxes to make them stand out more. Several plausible internal loops (e.g., muscle tension, muscle lengths) and a disturbance signal f_d acting on the CE are not shown; the boundaries of the colored boxes are a bit arbitrary.

controls the hand to move the stick (u) and controls the CE output (x) such that it follows the target signal (f_t) as close as possible’. Or, perhaps better stated, ‘how the brain controls the CE output x to follow f_t ’, as ultimately, moving the hand and stick is a means to an end.

The comparator model includes the components assumed to be working together in the brain and body to perform bodily motions and interact with the world. It illustrates the vast challenge in understanding visuomotor control, with most of the diagram elements (blocks, states, signals, feedback loops, etc.) *assumed* to be present in the human body and brain and only a small part (yellow block) that allows for direct inspection or manipulation by an experimenter. Clearly, one can measure more than just the input u to the CE (here, stick position) and the output of that system x , e.g., EMG, muscle tension, muscle forces, etc.; and in pursuit tracking we perfectly *know* (and show) the desired state f_t . Many if not all signals, loops and adaptation processes, however, have to be *inferred* from experimental data. Both neuroscientists and cyberneticists cleverly develop tasks and experiments to disentangle these relationships, and with that try to find evidence for their models. The lack of observability of brain and body processes remains a formidable research problem.

Based on the ‘desired state’ (f_t) the HC uses an inverse model to generate a motor command (*efference*, the CNS output) that is sent to the motor system (arm, hand) moving the stick position (u , ‘movement’) which drives the CE output (x , ‘actual state’). The eyes sense the output (in pursuit tracking also f_t), the ‘perceived state’ (the NMS provides kinesthetic feedback to the CNS regarding arm and hand positions (not shown)). In this diagram, which does not have a disturbance signal (f_d) acting on the CE, the actual state is the *reafference* (defined as

‘the effect on an organism’s sensory mechanism due to the organism’s own actions’). In case f_d would be there, also acting on the CE, the actual state would reflect both the reafference and the *exafference* (defined as ‘the effect on an organism’s sensory mechanism due to factors external to the organism’). Hence, the *afference* (the input to the CNS) equals the reafference and exafference combined.

The inverse model should include both the dynamics of the human motor system and the CE, as the motor command should be such as to make the actual state x follow the desired state f_t : $e = f_t - x = 0$ (the error $e(t)$ in Fig. 1). The first ‘comparator’ (C1) in Fig. 2 compares the difference, the C1 error, between the *perceived* state \hat{x} and *perceived* desired state \hat{f}_t . Both are perceived visually, which means that this first comparator loop is relatively slow (typical visual delays are 150-250 ms). Frith et al. (2000) state that the CNS can use the C1 error signal to “improve the performance of the controllers”, that is, the quality of the inverse model. Whether an actual *feedback* loop is closed is unclear, but appears not to be the case.

A copy of the motor command, the *efference copy*, is sent to the forward model which predicts the sensory consequences of the action, the ‘predicted state’, \tilde{x} . Similar to the inverse model, the forward model should include the dynamics of both the human motor system and the CE dynamics. The second comparator (C2) compares the predicted state \tilde{x} and perceived state \hat{x} , yielding a ‘prediction error’ of the forward model, used to “improve the performance of the predictors” (Frith et al., 2000). Since the perceived state \hat{x} includes both the reafference and exafference, and the predicted state \tilde{x} only the (predicted) reafference, one could see this C2 error as a means for the CNS to disentangle the effects on the CE due to the HC (reafference) and external factors (exafference). Literature

is not very clear on this, however. Often this feedback loop is described as a ‘process of attenuation’, such as in cancelling the sensory effects of the self-generated movement (resulting in the inability to ‘tickle ourselves’) (Swiney and Sousa, 2014). The forward model is adapted based on the attribution of the C2 error to internal or external causes, then recalibrating for the *internal* causes only.

Of course, the C1 and C2 errors can have many causes. Examples are an inaccurate inverse model (e.g., when the HC is still learning to control the CE), effects due to an (unknown) disturbance f_d acting on the CE (e.g., an aircraft flying through turbulence) (not shown here), a sudden or gradual change in the CE dynamics (e.g., when controlling a time-varying CE), and effects of inaccuracies in the HC motor and sensory systems. The problem for the CNS is to disentangle all these causes, and act appropriately: the core of the learning, adaptive HC.

The third comparator (C3) compares the predicted state \tilde{x} with the desired state f_t , resulting in a third ‘error’ used to update the inverse model only. Swiney and Sousa (2014) refer to this loop as a means for “allowing the motor command to be checked even before it is issued” (page 2). Hence, this loop is used for ‘mental simulation of possible control actions’, the purpose of which for pursuit tracking may be limited, except perhaps when the error $e = f_t - x$ is large, leading the HC to exert a ‘ballistic’ control input to rapidly move the CE output back to the target.

Let’s reflect on the summary so far. First, the model has three ‘error’ loops, but a feedback loop in the engineering sense, one that ‘feeds back the error’ to HC output u , seems absent. The C1/C2/C3 errors in Fig. 2 all appear only to update the inverse and forward models. Since there will always be some error between desired and actual state, due to the non-linearities, inaccuracies and the time-varying nature of the HC, it is odd that nothing seems to actually ‘feed back’ the error in some way into the HC control signal u . Second, the inverse and forward models appear as separate models, updated through different loops (C1 and C3 for the inverse model, C2 for the forward model). Although the *same dynamics* H^{-1} and H play a role in the inverse and forward models, respectively, these are believed to be coded separately in the CNS. Third, the ‘prediction error’ only affects the forward model and not the inverse model, emphasizing their separation.

In the next section a neuroscience model specifically developed for pursuit tracking will be discussed, in the ‘adaptive model theory’ (AMT) project that ran for several decades. Other reviews and models, providing a wealth of material on adaptive human visuomotor control, can be found in (Kawato and Gomi, 1992; Tin and Poon, 2005; Shadmehr et al., 2010; Gawthrop et al., 2011; Gollee et al., 2017).

3. ADAPTIVE MODEL THEORY

Adaptive Model Theory is the umbrella term for a significant body of research conducted by Neilson and others, defined as “a computational theory of the information processing performed by the human nervous system in control of movement” (Neilson et al., 1993) (page 85). This team investigated the neuroscience of pursuit tracking from several perspectives, often using theories and terminology

from control engineering. Starting with a classical ‘system identification’ approach on pursuit tracking data (Neilson et al., 1988a,b), the team developed AMT-based computer simulations (all in discrete time) involving adaptive neural circuits (Neilson et al., 1993), adaptive optimal control (Neilson et al., 1995) and optimal control using adaptive filter neural networks (Neilson and Neilson, 1999). Davidson (2001) provides a review of much of the later AMT work and extends it to the control of nonlinear systems.

For the sake of brevity, only an earlier AMT human control *simulator* model (running in discrete time at 20 Hz) is discussed using Fig. 3, our interpretation of Figure 3 (page 105) of (Neilson et al., 1995) with the nomenclature altered to match our current paper. A three-stage model of movement control is assumed: (i) sensory analysis (SA), (ii) response planning (RP) and (iii) response execution (RE). These stages run sequentially, in parallel and independently, communicating using memory buffers, from SA to RP to RE. A fixed time of 150 ms for RP processing introduces intermittency. The resulting simulator is “adaptive and alters its behavior in response to changes in the dynamics of the tracking system or variations of the statistical properties of the target and disturbance signals” (Neilson et al., 1995) (page 104). These are exactly the capabilities called for in future cybernetics models (Mulder et al., 2016, 2018).

Although Fig. 3 has a similar structure as the comparator model, Fig. 2, with at its center the (adaptive) inverse and forward models, the CE, the efference, afference and efference copy, there are also many differences. The peripheral motor and vision parts of the nervous system are left out (later versions of AMT include the NMS (Neilson and Neilson, 1999)), the HC output u (stick position, efference) and input x (CE output y perturbed with disturbance f_d , afference) are simply ‘known’ to the HC. Also, comparator C3 is not present, comparator C1 exists in the Response Planning (RP) stage, comparator C2 indeed compares the expected reafference x' (the predicted state in Fig. 2) with the afference x (the perceived state in Fig. 2), but feeds the difference – which one can interpret as the HC’s *estimate* of the exafference (here we deviate from (Neilson et al., 1995)), the effects of an (unknown) f_d on x – back to the central ‘Modelling Circuitry’ element.

Neilson et al. (1995) describe the Sensory Analysis (SA) stage as having three inputs (f_t, u, x) and three outputs ($\tilde{f}_t, \tilde{f}_d, \tilde{x}$). It incorporates three adaptive *self-tuning* digital filters, shown as circles 1, 2 and 3 in Fig. 3. The first two filters process f_t and f_d' and are driven by autocorrelations of these signals to generate the best possible predictions \tilde{f}_t and \tilde{f}_d . The third filter *automatically tunes itself* to maintain an accurate internal model of the relationship between u and x , i.e., an internal model H_m of the CE dynamics H . The fourth element of SA is the predictor for x , which is *not* adaptive, it predicts the movement of the target \tilde{x} based on the current target x and the previously planned x^* trajectory kept in memory awaiting execution.

The Response Planning (RP) stage uses the three SA outputs ($\tilde{f}_t, \tilde{f}_d, \tilde{x}$) to generate one output: a new x^* trajectory. Basically, x^* is an S-shaped trajectory (some function $\sigma(T)$ which runs from 0 to 1 in T seconds) from \tilde{x} to \tilde{f}_t , including a compensatory component equal to the negative of \tilde{f}_d ,

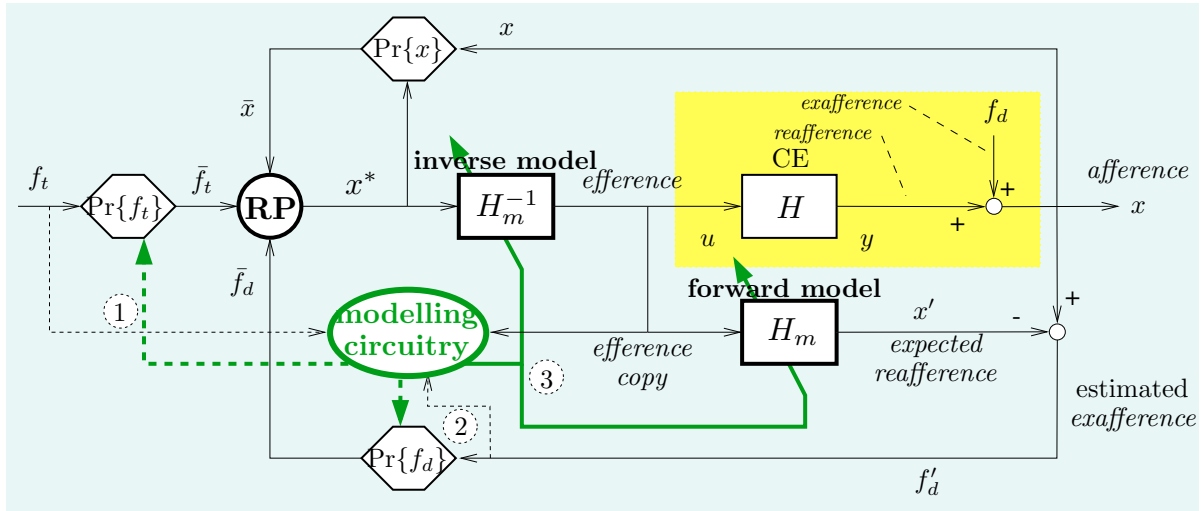


Fig. 3. AMT simulator of (Neilson et al., 1995), adapted to the current paper nomenclature and omitting the ‘memory’ blocks. The yellow and blue blocks indicate the same as in Fig. 2. The CE output y (the refference) is perturbed by an unknown disturbance f_d (the exafference), yielding the afference $x = y + f_d$. Three hexagons represent the Predictors for f_t , f_d and x . The ‘modelling circuitry’ adapts the HC predictors for f_t and f_d using loops 1 and 2, and the *linked* HC inverse and forward models through loop 3. Response Planning (RP) is explained in the text. Again, several plausible internal loops (e.g., muscle tension, muscle lengths) are not shown.

i.e., $x^* = \bar{x} + \sigma(T)(\bar{f}_t - \bar{x}) - \bar{f}_d$. Hence, a proportional ‘1’ feedback on predicted error, compensating for the predicted effect of the estimated disturbance. Using the S-shaped function $\sigma(T)$, the simulator can mimic operators who track with a ‘high or low gain’, i.e., balancing tracking performance (minimize error) with HC control effort.

The Response Execution (RE) stage uses x^* to generate the HC output u using inverse model H_m^{-1} . This adaptive filter is *slaved* to the internal model of the forward dynamics H_m (obtained in SA): “*any change in the dynamic response characteristics of the tracking system H leads to an automatic adaptive retuning of the forward model H_m and of the inverse model H_m^{-1} employed using response execution*” (Neilson et al., 1995) (page 108).

The AMT simulator of human tracking is used to mimic experimentally-measured HC behavior (primarily studying signals u , x and $e = f_t - x$ in the time and frequency domains), and successfully demonstrated effects of adaptation to CE dynamics, prediction of target and disturbance signals, speed of adaptation, and accuracy/effort trade-offs. AMT provides evidence for the CNS capabilities to: (i) compensate for CE dynamics through inverse models, (ii) compensate for time delays by predicting the target, and (iii) attempts to compensate for reaction time by predicting the disturbance, overall behaving as an adaptive *optimal* neural controller (Neilson et al., 1995).

Neilson and Neilson (1999) extend the discussed AMT model to obtain a neuroengineering view on optimal tracking, accounting for adaptation to task variables (CE dynamics, f_t and f_d characteristics) and HC-centered variables (“*multivariable, nonlinear, time-varying characteristics of neuromuscular and biomechanical systems internal to the human operator*” (page 155)). Where in (Neilson et al., 1995) the inverse and forward models do not include NMS dynamics, Neilson and Neilson (1999) present an optimal transformation of a 58-dimensional (!) muscle

system to yield a two-dimensional response (as this later paper studies 2D pursuit tracking). A linearized linear matrix approximation of the multi-dimensional adaptive filter nonlinear neural networks (using Volterra equations) is presented that resembles, significantly extends, the Optimal Control Model (OCM) of (Kleinman et al., 1970a,b).

Neilson et al. (1995) admit that their AMT models need more neurobiological data than available for proper verification. They argue, however, that the AMT simulators provide a means to suggest and check theories about the neurobiological processes involved in tracking, leading to predictions on HC behaviour that can be experimentally tested. In the engineering community, the above-mentioned OCM has found little traction. It has a solid theoretical basis – LQR/LQG theory – and appeals to an engineer’s intuitions regarding manual control, but it has too many parameters and cannot be identified from experimental data (Kok and van Wijk, 1978). But perhaps also here cyberneticists can learn something from neuroscientists, and that is that a good computational model that mimics HC behavior is still worthy to pursue.

4. LESSONS LEARNED

Combining insights from neuroscience with our engineering intuitions yields a conceptual scheme for adaptive human control in pursuit tracking, Fig. 4. It directly extends the perspective put forward by Mulder et al. (2018), using the concept of an HC’s ‘internal representation’ (IR) of the task variables. Proficient HCs may detect the changes in the task variables (here: CE dynamics, (statistical) properties of the target and disturbance signals) because their *expectation* obtained from the IR does not match their *observation*. For example, the CE responds to the control commands differently than expected, with the expectation driven by the internal model of the CE dynamics H maintained in the IR, resulting in an *innovation* signal,

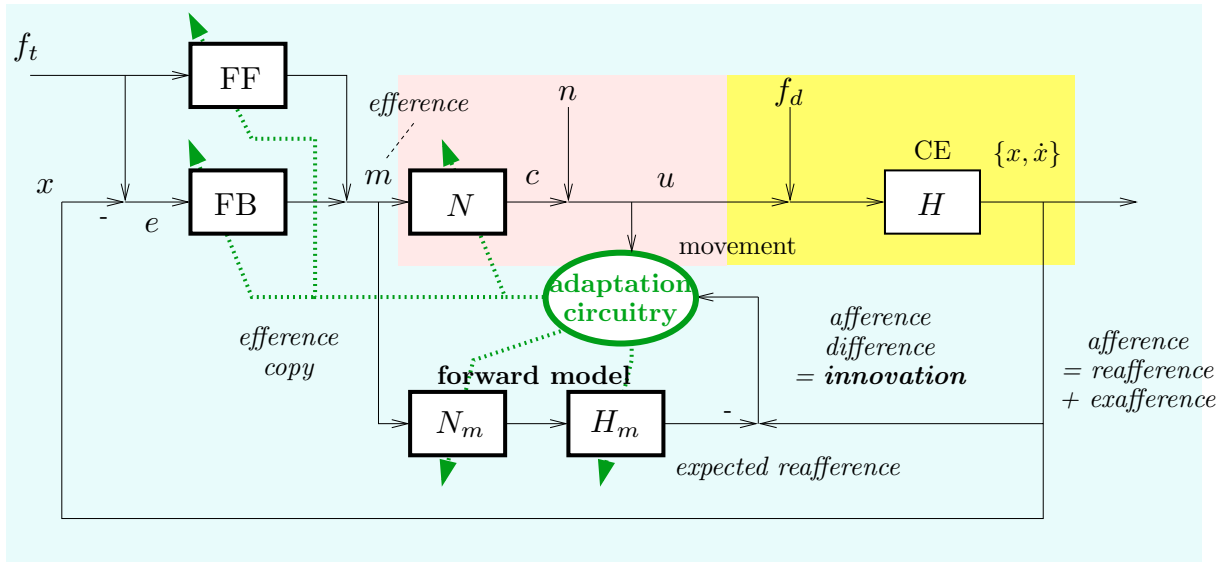


Fig. 4. Re-engineered scheme of the adaptive HC, using some neuroscience terminology and the same color-coding as before. N stands for the NMS+stick dynamics, H the CE dynamics and N_m and H_m the HC internal models of these dynamics. FF, FB, n , the adaptation circuitry and green arrows are all explained in the text. In this figure, when arrows come together they are added unless otherwise specified.

as shown by Mulder et al. (2018) (Figure 3, page 473). This mismatch then triggers (cognitive) adaptations in the HC's feedback (FB) and feedforward (FF) control dynamics, as well as physiological changes in the NMS. In the following, we only discuss adaptations to changes in the target signal f_t , and to the CE dynamics H and disturbance signal f_d .

4.1 Adaptation to target f_t

The pursuit display provides the HC a 'clear sight on f_t ' to study its characteristics. A skillful HC will learn its statistical properties, use these to predict f_t some time ahead, and adapt the IR of f_t to changes when they occur. Magdaleno et al. (1969) developed a scheme for levels of (subjective) predictability, some followed-up on this scheme (e.g. (Drop et al., 2016)), and Mulder et al. (2019) describe nonlinear HC strategies in pursuit tracking. An extended literature survey is needed, however, to study these aspects. In a preview tracking task, the predictability of f_t (and the effort for the HC to predict it) becomes irrelevant for sufficient preview times.

4.2 Adaptation to CE dynamics H and disturbance f_d

In our scheme, the 'classic' feedforward/feedback (FF/FB) scheme used in both neuroscience (Wolpert et al., 1998) and cybernetics (Drop et al., 2019) is adopted, irrespective of the fact that Van der El (2018) used a much simpler and equally effective scheme *without* a feedforward path based on inverse CE dynamics. But here we assume the FF component to include an inverse model of the HC's IR of the NMS and CE dynamics in series: $N_m^{-1}H_m^{-1}$. This is because the motor command m should be such that $x = N \cdot H \cdot m = f_t$, similar to (Neilson and Neilson, 1999). The FB component works on the difference e between f_t and x , such that integrator-like open loop dynamics of the crossover model are established: $N_m^{-1}H_m^{-1}\omega_c e^{-j\omega\tau_e}/(j\omega)$. The attentive reader notices the *same* inverse model as

in the FF, multiplied with an integrator, as suggested by Neilson et al. (1995) and also alluded to by Young (1969) (page 295) in his discussion of the crossover model. We explicitly include a feedback loop, operating on the 'C1 error' rather than only using this error to adapt the inverse model. We also include a remnant signal n to account for the inevitable HC 'noise' (McRuer and Jex, 1967).

The classic scheme is extended with the efference copy m (the CNS motor command to the NMS) to predict the CE response to that input using the forward model. This includes internal models of both the NMS and the CE, N_m and H_m . The CNS compares the expected refference with the perceived affectance and based on weighing the difference (the 'innovation') may adapt the IR of the inverse and forward models. As stated in Section 2, the crucial question then is *how* exactly the CNS disentangles the (many possible) causes for this difference, especially in the presence of an (often barely/unpredictable) CE disturbance f_d , and the HC remnant, together causing the exaffectance. But also *changes* in CE dynamics and a *learning* HC (imprecise IR) can lead to differences between what the HC expects and what she sees on the display.

The challenge may seem daunting, for the CNS but also for us, the CNS modelers, neuroscientists and cyberneticists alike. A first idea to be investigated is the limited equalization possibility that the HC has, given that humans can only visually perceive position and velocity, $\{x, \dot{x}\}$ (McRuer and Jex, 1967). Model-free nonlinear dynamic inversion techniques, developed recently for automated control systems, appear to work on what *derivative* (here \dot{x}) 'returns' based on a known input (here m) by that controller. Indeed, engineering intuition tells us that also the HC may put most attention on 'what CE symbol movement one gets back' when controlling the CE. Including the lead term (the HC acting on the *derivative*) in the crossover model, or not, is the crucial parameter selection for the class of $K/s - K/s(1 + \tau s) - K/s^2$ CE dynamics.

A second – related – idea is that stick position u provides useful information to the HC, hence the arrow feeding u into the adaptation circuitry of Fig. 4. With a pursuit display, the HC can directly perceive the CE response to stick input u . Disregarding the often small(er) effects of f_d on $\{x, \dot{x}\}$, the HC can ‘test’ the CE dynamics by feeding it with, e.g., small impulse-like inputs. The differences between K , K/s and K/s^2 dynamics would quickly become clear to an (experienced) HC, as with these dynamics the stick position u is directly linked to, respectively, the perceived position, velocity or acceleration of the CE output x . Any proficient HC will then be able to quickly switch between different inverse/forward models, as proposed by McRuer and Jex (1967). This is the crucial difference with the extensively studied (e.g., (Young, 1969)) compensatory display, which does not allow the HC to distinguish between reafference and exafference.

5. CONCLUSIONS

Lessons learned from a neuroscience literature review on pursuit tracking were applied to develop a new model for the adaptive HC. A key addition is the inclusion of a forward model path that captures the HC’s hypothesized capability to adapt, based on differences between what one expects to happen, and what actually happens.

REFERENCES

- Davidson, P.R. (2001). *Computational Modelling of the Human Motor Control System*. Diss., Un. of Canterbury.
- Drop, F.M. (2016). *Control-Theoretic Models of Feedforward in Manual Control*. Diss., TU Delft.
- Drop, F.M., De Vries, R., Mulder, M., and Bühlhoff, H.H. (2016). The Predictability of a Target Signal Affects Manual Feedforward Control. In *13th IFAC Symp. on Human-Machine Systems, Kyoto, Japan*, 177–182.
- Drop, F.M., Pool, D.M., Van Paassen, M.M., Mulder, M., and Bühlhoff, H.H. (2019). Effects of Target Signal Shape and System Dynamics on Feedforward in Manual Control. *IEEE Trans. on Cyb.*, 49(3), 2168–2267.
- Frith, C.D., Blakemore, S.J., and Wolpert, D.M. (2000). Abnormalities in the Awareness and Control of Action. *Phil. Trans. R. Soc. Lond. B*, 355, 1771–1788.
- Gawthrop, P.J., Loram, I.D., Lakie, M., and Gollee, H. (2011). Intermittent Control: a Computational Theory of Human Control. *Biological Cybernetics*, 31–51.
- Gollee, H., Gawthrop, P.J., Lakie, M., and Loram, I.D. (2017). Visuo-manual Tracking: Does Intermittent Control with Aperiodic Sampling Explain Linear Power and Non-linear Remnant without Sensorimotor Noise? *The Journal of Physiology*, 6751–6770.
- Kawato, M. and Gomi, H. (1992). A Computational Model of Four Regions of the Cerebellum based on Feedback-Error Learning. *Biological Cybernetics*, 68, 95–103.
- Kleinman, D.L., Baron, S., and Levison, W.H. (1970a). An Optimal Control Model of Human Response. Part I: Theory and Validation. *Automatica*, 6, 357–369.
- Kleinman, D.L., Baron, S., and Levison, W.H. (1970b). An Optimal Control Model of Human Response. Part II: Prediction of Human Performance in a Complex Task. *Automatica*, 6, 371–383.
- Kok, J.J. and van Wijk, R.A. (1978). *Evaluation of Models Describing Human Operator Control of Slowly Responding Complex Systems*. Diss., TU Delft.
- Krendel, E.S. and McRuer, D.T. (1960). A Servomechanics Approach to Skill Development. *Journal of the Franklin Institute*, 269(1), 24–42.
- Magdaleno, R.E., Jex, H.R., and Johnson, W.A. (1969). Tracking Quasi-predictable Displays Subjective Predictability Graduations, Pilot Models for Periodic and Narrowband Inputs. In *Proc. of the 5th Ann. NASA-University Conference on Manual Control*, 391–428.
- McRuer, D.T. and Jex, H.R. (1967). A Review of Quasi-Linear Pilot Models. *IEEE Trans. on Human Factors in Electronics*, 8(3), 231–249.
- Mulder, M., Pool, D.M., Abbink, D.A., Boer, E.R., Zaai, P.M.T., Drop, F.M., Van der El, K., and Van Paassen, M.M. (2018). Manual Control Cybernetics: State-of-the-Art and Current Trends. *IEEE Trans. on Human-Machine Systems*, 48(5), 468–485.
- Mulder, M., Pool, D.M., Abbink, D.A., Boer, E.R., and Van Paassen, M.M. (2016). Fundamental Issues in Manual Control Cybernetics. In *13th IFAC Symp. on Human-Machine Systems, Kyoto, Japan*, 1–6.
- Mulder, M., Pool, D.M., Van der El, K., Drop, F.M., and Van Paassen, M.M. (2019). Manual Control with Pursuit Displays: New Insights, New Models, New Issues. In *14th IFAC Symp. on Human-Machine Systems, Tallinn, Estonia*, 139–144.
- Neilson, P.D. and Neilson, M.D. (1999). A Neuroengineering Solution to the Optimal Tracking Problem. *Human Movement Science*, 18, 155–183.
- Neilson, P.D., Neilson, M.D., and O’Dwyer, N.J. (1988a). Intermittency in Internal Models; A Theoretical Account of Human Tracking Behavior. *Biological Cybernetics*, 58, 101–112.
- Neilson, P.D., Neilson, M.D., and O’Dwyer, N.J. (1993). What Limits High Speed Tracking Performance? *Human Movement Science*, 12, 85–109.
- Neilson, P.D., Neilson, M.D., and O’Dwyer, N.J. (1995). Adaptive Optimal Control of Human Tracking. In D.J. Glencross and J.P. Piek (eds.), *Motor Control and Sensory Motor Integr.: Issues and Directions*, 97–140.
- Neilson, P.D., O’Dwyer, N.J., and Neilson, M.D. (1988b). Stochastic Prediction in Pursuit Tracking: An Experimental Test of Adaptive Model Theory. *Biological Cybernetics*, 58, 113–122.
- Shadmehr, R., Smith, M.A., and Krakauer, J.W. (2010). Error Correction, Sensory Prediction, and Adaptation in Motor Control. *Annu. Rev. Neurosci.*, 33, 89–108.
- Swiney, L. and Sousa, P. (2014). A New Comparator Account of Auditory Verbal Hallucinations: How Motor Prediction can Plausibly Contribute to the Sense of Agency for Inner Speech. *Frontiers in Human Neuroscience*, 8(675), 1–15.
- Tin, C. and Poon, C.S. (2005). Internal Models in Sensorimotor Integration: Perspectives from Adaptive Control Theory. *J. Neural Eng.*, 2(3), S147–S163.
- Van der El, K. (2018). *How Humans use Preview Information in Manual Control*. Diss., TU Delft.
- Wolpert, D.M. (1997). Computational Approaches to Motor Control. *Trends in Cogn. Sc.*, 1(6), 209–216.
- Wolpert, D.M., Miall, R.C., and Kawato, M. (1998). Internal Models in the Cerebellum. *Trends in Cognitive Sciences*, 2(9), 338–347.
- Young, L.R. (1969). On Adaptive Manual Control. *IEEE Transactions on Man Machine Systems*, 10, 292–331.