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The role of action plans and other cognitive factors in motion extrapolation: A modelling study

Wolfram Erlhagen
Departamento de Matemática para C&T, Universidade do Minho,
Guimarães, Portugal

Dirk Jancke
Institut für Zoologie und Neurobiologie, Ruhr-Universität Bochum, Germany

When observers are asked to remember the final location of an object undergoing apparent or implied motion, a forward displacement is observed. The magnitude of this form of motion extrapolation is known to depend on various factors including stimulus attributes, action plans, and other cognitive cues. Here we present a modelling approach that aims at bridging different existing theories of displacement within a single theoretical framework. A network model consisting of interacting excitatory and inhibitory cell populations coding for stimulus attributes like position or orientation is used to study the response to motion displays. The intrinsic network dynamics can be modulated by additional information sources representing action plans directed at the moving target or cognitive cues such as prior knowledge about the trajectory. These factors decide the extent to which the dynamic representation overshoots the final position. The model predictions are quantitatively compared with the experimental findings. The results are discussed in relation to theoretical ideas about processing principles underlying motion extrapolation and a comparison with neurophysiological findings linked to movement prediction is made.

How does the brain cope with dynamic events in the world? In everyday life, we are frequently faced with the problem to plan or avoid contact with objects undergoing smooth change, for instance in location or orientation. Our perceptual system must in some way represent these events that unfold over time. Valuable insights about the mechanisms underlying the processing of dynamic information have been gained by analysing errors that observers share in

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Please address correspondence to: Wolfram Erlhagen, Departamento de Matemática para C&T, Universidade do Minho, 4800-058 Guimarães, Portugal. Email: wolfram.erlhagen@mct.uminho.pt

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common. When observers are asked to remember the final position of an object presented in motion (including implied motion and apparent motion) they typically misremember it as further along the implied trajectory (for reviews see Freyd, 1987; Hubbard, 1995). In analogy to classical mechanics this form of motion extrapolation has been labelled ''representational momentum'' (Freyd & Finke, 1984). The momentum metaphor refers to the notion that the internal representation of target position may itself be dynamic (Freyd, 1987). Much like the inertia of a moving physical object, it suggests that the internal representation cannot be halted instantaneously upon stimulus offset but continues for some time. The observations that the magnitude of the forward displacement is impervious to error feedback and increases with higher (implied) stimulus velocity have been taken as support for this conceptualization.

However, subsequent studies have directly addressed the question to which extent this extrapolation process is indeed unconscious and effortless. A central piece of evidence that representational momentum may be subject to ''cognitive penetrability'' (Pylyshyn, 1981) was the finding that expectations and beliefs regarding the direction of the motion affected memory distortions. Hubbard and Bharucha (1988) presented observers with a linear motion display in which the target appeared to bounce off a wall. When the target vanished just prior to or at the moment of collision, the displacement was in the direction of anticipated motion, rather than in the direction of current motion (see also Verfaillie & d'Ydewalle, 1991). Even more direct evidence for a top-down penetration of the extrapolation process came from studies showing that background knowledge from verbal instructions (Hubbard, 1994) and object-specific constraints (Reed & Vinson, 1996) may influence the magnitude of the displacement.

Functionally, the prediction of movement is of particular importance whenever an ocular or manual motor action is directed at a moving target. There are sizeable delays within the visuomotor pathway, which have to be compensated for to guarantee for a successful action. It has been suggested that the compensation is at least in part based on visual extrapolation of past trajectory information (Nijhawan, 1994; Nijhawan, Watanabe, Khurana, & Shimojo, 2004). Converging lines of experimental evidence suggest that the integration of action plans into the processing of positional information greatly enhances our capacity to predict future positions of a moving object.

Wexler and Klam (2001) compared the position judgement for a target disappearing behind an occluder when the target movement was action-generated (by controlling a manipulandum) with a passive viewing condition. They found that the prediction was systematically more advanced in the active compared to the passive condition. This was the case despite the fact that an exact copy of the actively produced trajectory was used for the passive movement prediction.

Motor tracking is another example showing that actions may become resident in spatial perception. Kerzel, Jordan, and Müsseler (2001) investigated systematically the influence of eye movements on representational momentum. Observers were instructed to either fixate a fixation point or to actively track the target in linear motion with the eyes. An important finding of this study was that representational momentum occurred only with pursuit eye movements. This outcome strongly supports the idea that motor plans caused the overshooting since expectations about the future trajectory have to be created in order to guarantee for a successful tracking behaviour.

In a series of experiments Stork and Müsseler (2004; see also Jordan, Stork, Knuf, Kerzel, & Müsseler, 2002) showed that under the condition of smooth pursuit the localization error appeared to be significantly reduced when the stimulus offset was itself action generated. The intention to stop the target seems to counterbalance the tendency for extrapolation due to the ocular motor plan. This finding suggests that more than one action plan may simultaneously be integrated into the processing of position.

In this paper we present a modelling approach which aims at bridging the various theories about the processing principles underlying the displacement within a single theoretical framework. We use a network model to study its response to dynamic targets. The network consists of interacting excitatory and inhibitory cell populations coding for stimulus attributes such as position or orientation. In response to an apparent motion display the network develops a wavy activity pattern in parametric space. The fundamental assumption behind our modelling work is that recurrent interactions within the network may sustain the dynamic transformations for some time upon stimulus offset. Cognitive factors such as prior knowledge about the task setting and action plans directed at the moving target are modelled as additional dynamic inputs to the network. They may influence the extent to which the population response overshoots the final target position.

A second purpose of this paper is to discuss within our theoretical framework differences and similarities between dynamic representations of targets undergoing apparent motion and targets undergoing implied motion. This question is important to address for understanding the functional nature of motion extrapolation. The large interstimulus intervals (typically 250 ms) used in implied motion displays prevent the network from triggering a coherently travelling activity wave. Instead, the individual frames of the stimulus train are processed independently, resulting in localized but stationary activity patterns in parametric space. However, we have recently argued that under appropriate conditions the bottom-up signal may be continuously compared with a stored internal model that predicts future states of the moving stimulus (Erlhagen, 2003). The notion of an interaction between external sensory events and an internal modelling process is in line with a growing body of empirical evidence that emphasizes the role of top-down information for the recognition of familiar dynamic sequences (e.g., Cavanagh, Labianca, & Thornton, 2001). We shall show that the integration of a predictive model into the processing of parametric information about position or orientation may cause a drift of the dynamic representations in the direction of implied motion.

The paper is organized as follows: We first present the architecture and dynamics of our network model. The main part of the paper deals with a comparison of model predictions and experimental data. We focus on the role of action plans and other cognitive factors in the extrapolation of linear apparent motion and present the fundamental findings for implied motion displays separately. We finish the paper with a discussion of the functional consequences of our results for the processing of dynamic events. We also compare the processing principles implemented in our network model with recent neurophysiological findings linked to trajectory prediction.

THE DYNAMIC MODEL

The model network consists of an excitatory and inhibitory population of neurons that code for the dimensions tested in the experiments. For the present discussion of the representational momentum these dimensions are stimulus position or stimulus orientation. Each neuron is parameterized by its visual receptive field centre x. It is driven by external inputs representing bottom-up information about the retinal location or the orientation of the visual stimulus but its activity can be modulated also by top-down signals. The structure of the recurrent connections within the network resembles an architecture first studied by Wilson and Cowan (1973). Each excitatory neuron, x, integrates activity from neighbouring neurons and projects via local connections to neurons of the inhibitory population which belong to the same functional column and via lateral connections to inhibitory neurons, x', with distinct visual receptive field centres ($x \neq x'$). Each inhibitory neuron is assumed to laterally integrate the incoming excitation but to project back to the excitatory population locally only (see Jancke et al., 1999, for details). For large neuronal populations the excitatory and inhibitory activity at time t in the network can be described by two continuous functions, $u(x, t)$ and $v(x, t)$, respectively (Amari, 1977). The temporal evolution of these activities is governed by the following mean-field equations:

$$\tau\dot{u}(x,t) = -u(x,t) + S_{ex}(x,t) + h + g(u(x,t))\left[\int w_u(x-x')f(u(x',t))dx' - v(x,t)\right]$$

$$\tau\dot{v}(x,t) = -v(x,t) + S_{in}(x,t) + \int w_v(x-x')f(u(x',t))dx'$$

where $S_{ex}(x, t)$ and $S_{in}(x, t)$ are transient afferent inputs from sources external to the network and $h < 0$ defines the resting level to which field activity relaxes without further stimulation. Gaussian profiles have been chosen for $S_{ex}(x, t)$ and $S_{in}(x, t)$. Their amplitude, A_s, and space constant, σ_s, reflect the strength and half-width of the localized stimulations. The parameter τ defines the time constant of the dynamics. It is adjusted to reproduce the experimentally observed time scales. The response function f, which gives the expected portion of neurons at position x firing for a given level of excitation, is taken as a monotonically increasing function of typical sigmoid shape:

$$f(u) = 1/(1 + exp(-\beta(u - u_f)))$$

with threshold u_f and slope parameter β. The strength of the lateral interactions, $w_u(x, x')$ and $w_v(x, x')$, is assumed to decay as a function of the distance between sites x and x' in feature space. Gaussian decay functions with amplitude parameters A_u and A_v and spatial constants σ_u and σ_v are chosen for the excitatory and inhibitory population, respectively. In addition, as in many other field models it is assumed that the effective interaction strength in the network is inhibitory for sufficiently large separations between any two sites x and x' (e.g., Wilson & Cowan, 1973). Finally, the interaction term in the excitatory field is multiplied by a nonlinear function $g(u)$ leading to a network of shunting type (for a review see Grossberg, 1988). $g(u)$ is assumed to be also of sigmoid shape with threshold u_g and slope β. Functionally, this state-dependent nonlinear signal serves to gate the lateral interactions by feedforward activation. For a sufficiently large threshold u_g the response properties of a neuron can only be influenced by interactions if the neuron receives direct bottom-up input. Important to the present paper is the fact that the gating mechanism influences the extent to which the internal network dynamics may lead to an extrapolation of past trajectory information into the future.

The link to the position judgement data reported in the experiments is brought about by our basic assumption that localized activity patterns in parametric space represent instances of the stimulus dimensions position or orientation tested in the experiments (see Erlhagen & Schöner, 2002; Schöner, Kopecz, & Erlhagen, 1997, for a similar conceptualization in the domain of motor planning).

The presentation of a brief localized stimulus $S_{ex}(x, t)$ of adequate intensity leads to a model response known as an active transient. After stimulus offset the activity in the excitatory layer at stimulated sites continues to increase, reaches a maximum level and then decays back to resting level due to the increasing inhibition in the network (Figure 1A). The localized response is centred over the position x_c throughout the whole evolution (Figure 1B). We have chosen the time constant τ = 35 ms to assure that the duration of the active response matches the visual persistence of a flashed stimulus (about 100 ms; Coltheart, 1980).

Importantly, there is a threshold for the ignition of this active response. The external stimulation must be strong enough to trigger the self-stabilizing feedback loops. In the following we refer to this threshold activity level as u_{TH} and to the corresponding stimulus intensity as A_{TH}.

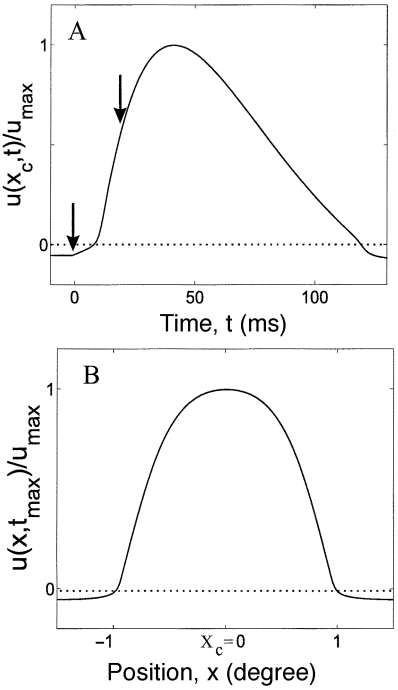

Figure 1. Active transient response to a brief stimulus $S_{ex}(x, t)$ centred at position x_c. (A) The time course of activation of the field element at x_c is shown. The arrows indicate stimulus onset and offset, respectively. The dotted line indicates the threshold u_{TH} for the active response, it is set to zero for convenience. (B) A snapshot of the localized pattern at the moment of maximum activation is shown. The response remains centred over position x_c throughout the whole evolution. Stimulus parameters were: $A_s = 2.0$, $\sigma_s = 0.4$ deg for the Gaussian profile and $\Delta t = 15$ ms for the stimulus duration. Model parameters were: $\tau = 35$ ms, $h = -3$, $\beta = 1.0$, $u_f = 0$, $u_g = -0.25$, $A_u = 2.33$, $\sigma_u = 0.3$ deg, $A_v = 1.99$, $\sigma_v = 0.4$ deg. To adjust the spatial scale in the model to the experimental units we have chosen 10 pixel = 0.1 deg.

In response to a continuously displaced stimulus of adequate intensity (apparent motion paradigm), the network develops a localized wavy activity pattern (Figure 2). The peak of the wave travels with the velocity of the inducing display but spatially lags behind the actual stimulus position (Erlhagen & Jancke, 2002). We have adjusted the parameters describing the interaction kernels to guarantee that the balance between excitation and inhibition within the network allows for the whole range of experimentally tested velocities for a continuously travelling wave. The only model parameter which is changed throughout this study is the threshold u_g controlling the gating of the recurrent interactions. For a sufficiently low threshold the cooperative forces within the network may be strong enough to maintain the travelling wave without further

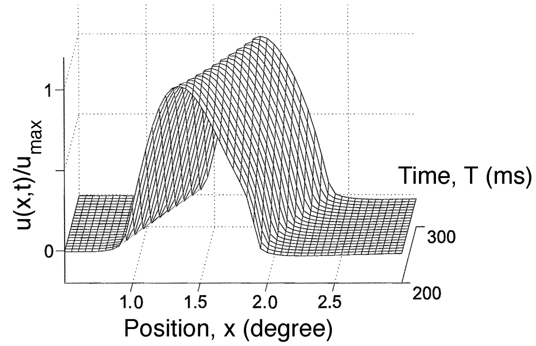

Figure 2. Field response to a stimulus $S_{ex}(x, t)$ that is continuously displaced by a distance Δx along a horizontal line. Each frame is presented for a time interval Δt leading to an apparent velocity $v = \Delta x/\Delta t$ of the stimulus train. Only a part in the middle of the trajectory is shown. Stimulus parameters were: $A_s = 2.0$, $\sigma_s = 0.4$ deg for the Gaussian profile, $\Delta t = 10$ ms for the frame duration and $\Delta x = 0.1$ deg for the displacement. Model parameters were as in Figure 1.

bottom-up stimulation (Erlhagen, 2003). The parameters of the afferent input are chosen to match as close as possible the spatiotemporal characteristics of the experimental displays.

FORWARD SHIFT OF THE INTERNAL REPRESENTATION

What happens with the dynamic representation of the moving stimulus when the external input abruptly vanishes? Due to the nonlinear interactions within the network the population response continues to travel in the direction of motion. Recurrent excitation may trigger an active response also at positions, which have not been directly stimulated. However, the amplitude and the velocity of the propagating activity are predicted to continuously decrease since the excitatory interaction forces are not strong enough to maintain the wavy activity pattern without bottom-up stimulation. At a certain position forward to the vanishing point the population response stops to travel and decays back to resting level. Figure 3A illustrates this behaviour by showing the activity pattern at the time when the stimulus vanishes at position $x = 0$ (dashed line) and at the time when the pattern stops to propagate in the direction of anticipated motion. In the following we use the peak position of the latter pattern to quantitatively compare model predictions with the memory distortions typically observed when subjects judge the vanishing point (by positioning a crosshair, for instance).

As illustrated in Figure 3B, the magnitude of the forward shift critically depends on the gating mechanism for the recurrent interactions. Lowering the threshold u_g results in a larger extrapolation of past trajectory information into the future. For sufficiently high thresholds u_g, on the other hand, the spread of

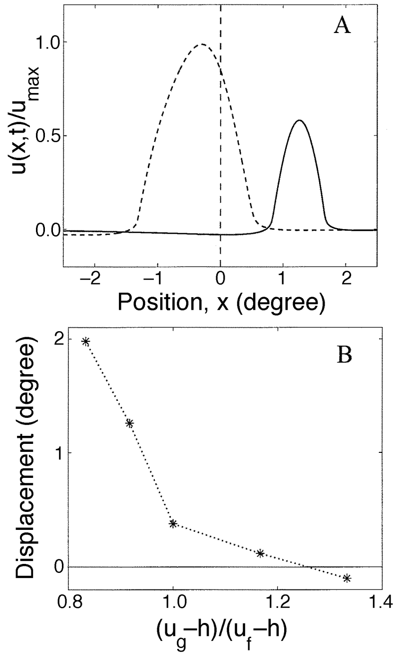

Figure 3. Overshooting of the dynamic representation. (A) Two snapshots of the population response are shown. The left pattern represents the response at the time of stimulus offset, the right pattern the response when it stops to travel in the direction of implied motion. The forward displacement is defined as the distance between the peak of the latter pattern and the final stimulus position $x = 0$. (B) The magnitude of the forward displacement as a function of the shunting threshold u_g is shown. It is plotted as a function of the dimensionless variable $(u_g - h)/(u_f - h)$. Negative displacements indicate that the dynamic representation dies out before it reaches the final stimulus position. The rest of the model parameters were as in Figure 1. The stimulus parameters were: $A_s = 9.97$, $\sigma_s = 0.4$ deg, and the apparent velocity was chosen as $v = 20$ deg/s.

excitatory activation to subsequent positions appears to be completely suppressed. Recurrent inhibition within the network may even prevent the wave from reaching the final stimulated site, leading to a negative displacement (compare the rightmost data point in Figure 3B).

The observed overshooting of the internal representation is in complete agreement with the momentum metaphor introduced by Freyd and Finke (1984). The transformations evolve along the time dimension in a way consistent with a moving physical object to which a stopping force has been applied. Moreover, the postulation of an adaptive gating mechanism allows the incorporation of other regularities that are invariantly present with moving objects without changes in the spatial interaction structure of the network. For instance, a gravity-like effect has been described in memory displacement. A stimulus moving downwards produced a larger forward shift than did a stimulus moving upward (''representational gravity''; Hubbard, 1995).

A central piece of evidence for the physical analogy was the dependence of the magnitude of displacement on stimulus velocity. Larger memory shifts were found for targets moving at faster velocities. In Figure 4 we compare for apparent velocities in the range between 10 and 20 deg/s modelling results (asterisk) and experimentally observed displacements (plus) as reported in Hubbard (1990) and Hubbard and Bharucha (1988). The nonlinear interaction processes underlying the motion extrapolation in the model can explain qualitatively very well the experimental data. Interestingly, the peak of the population response lags behind the actual vanishing point at the time of stimulus offset (compare Figure 3A). Since this spatial lag increases with higher apparent velocity of the inducing display (Erlhagen & Jancke, 2002), the velocity dependence of the travelled distance after the target vanished appears to be even more pronounced. However, for the spatial interaction ranges used in the simulations the capacity to extrapolate turns out to be reduced when a stimulus train with lower apparent velocity is applied. For velocities below about 9 deg/s the localized activity pattern starts to travel less coherently, resulting in a reduced drift in the direction of implied motion. Very likely, several pools of neurons with spatial interactions covering different velocity ranges coexist within the visual system (for a detailed discussion of the relation between the spatial ranges of interactions and the wave velocity see Ben-Yishai, Hansel, & Sompolinsky, 1997).

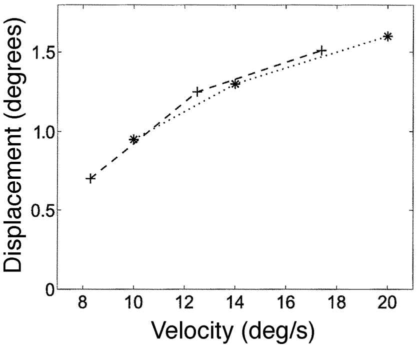

Figure 4. The velocity dependence of the forward shift is shown for the model with fixed value $u_g = -0.3$ (asterisk) and compared with the experimental findings (plus). The values for $v = 8.3$ deg/s and $v = 12.5$ deg/s are estimated from Figure 1 in Hubbard (1990), the value for $v = 17.4$ deg/s from Figure 1 in Hubbard and Bharucha (1988). As in the experiments, different apparent velocities were achieved by holding the frame duration, Δt, constant and adapting the displacement, Δx, accordingly. The stimulus width $\sigma_s = 0.4$ deg ($A_s = 9.97$) approximately matched the radius of the circular target used in the experiment. The model parameters were as in Figure 3.

PREDICTABLE CHANGES IN MOVEMENT DIRECTION

Thus far, we have shown that depending on the model parameters the presentation of a coherently displaced target may trigger a process of an automatic extrapolation of prior trajectory information into the future. This process can be stopped only by actively applying an opposing force to the network. The findings reported in Hubbard and Bharucha (1988) suggest that observers' beliefs and expectations concerning the future behaviour of the target may represent such a force. Hubbard and Bharucha presented a circular target in linear motion, which bounced off a wall at a predictable position. In the collision condition the target vanished at the moment of impact with the wall. The fundamental finding was that the displacement was negative with respect to the motion direction prior to contact. In other words, the subjects anticipated the change in movement direction. In our model, we incorporate this additional, cognitive contribution as a localized input, $S_{in}(x)$, to the inhibitory population at the field site representing the location of the wall. As a result, the neurons coding for positions in the neighbourhood of the barrier become hyperpolarized. The recurrent interactions may thus not be sufficiently strong to guarantee for a dynamic representation reaching the vanishing point. The spatial range of this active inhibition can be estimated by considering also the ''precollision'' condition of the experiments. For a vanishing point at a distance of about 1.6 deg to the wall a much smaller but still significant negative displacement was found. We have adjusted the width parameter, σ_s, of the input signal $S_{in}(x)$ to quantitatively account for the experimental data (Figure 5). It is important to stress again that for a negative displacement to occur the observer must know in advance that the target bounces off the wall. Hubbard and Bharucha tested also the collision condition when the target was expected to crash through the barrier. Compared with the target motion without obstacle the displacement appeared to be reduced, but it did not reverse direction. For the tested velocity of 14.5 deg/s we expect a shift of more than 1 deg (Figure 4), which has to be compared with the reported 0.2 deg (rightmost data point in Figure 5). The physical presence of the wall affects the magnitude of the displacement. The presence *per se*, however, does not explain the anticipation pattern. The model network may account for this finding in the ''collision-crash'' condition by appropriately reducing the strength, A_s, of the signal $S_{in}(x)$ (Figure 5). This changes the relative weight of the different contributions for the processing towards the bottom-up input stream. Moreover, assuming that the signal may be itself subject to cognitive penetrability allows the explanation that verbal instructions may alter the displacement pattern in otherwise identical displays. In the experiments reported in Hubbard (1994) subjects were visually presented with the cue word ''bounce'' or ''crash'' in the collision condition. The precue could be valid or invalid. In valid crash trials the forward displacement was

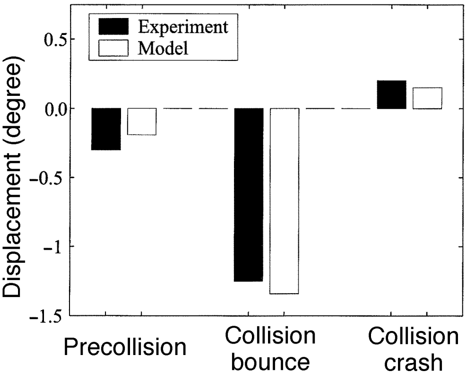

Figure 5. Comparison of model prediction and experimental findings for a linear motion paradigm with a change in direction at a predictable position (''bouncing off a wall''). In the precollision condition the target approached the wall and vanished about 1.6 deg away from the wall, in the collision-bounce condition the target vanished at the moment of impact with the wall. The observed negative displacement pattern is captured by the model when assuming an additional input $S_{in}(x)$ ($A_s = 4.43$, $\sigma_s = 0.9$ deg) to neurons of the inhibitory population representing the position of the wall. In the collision-crash condition observers expect the target to crash through the wall. A small forward displacement was observed when the target vanished at the moment of impact with the wall. A reduction of the input strength A_s of $S_{in}(x)$ to 20% of its original value allows explaining also this observation. The moving stimulus ($A_s = 1.99$, $\sigma_s = 0.4$ deg) matched the apparent velocity, $v = 14.5$ deg/s, used in the experiments. Model parameters were as in Figure 4.

systematically larger compared to the invalid trials, suggesting the application of a weaker stopping force.

THE INTEGRATION OF ACTION PLANS

Visual motion extrapolation as revealed, for instance, by the representational momentum has predominately been studied under conditions in which a direct binding of the moving object in an action plan was not required. However, in paradigms, which demand a strong perception–action coupling, the need for some from of predictive behaviour becomes even more evident. When trying to catch an object in motion the accurate timing of the hand movement is crucial. There are significant processing delays both along the visual and the motor pathway, which have to be compensated for in order to guarantee for a successful action. It has been suggested that the central nervous system uses forward models to predict the sensory consequences of motor commands sent to an effector, such as the hand (Wolpert, Ghahramani, & Jordan, 1995). This would allow the provision of the missing feedback information with negligible delays, thus maintaining stability. Furthermore, it has been argued that motor learning, which includes an adaptation of the forward model, would be sufficient to compensate for all visuomotor delays (Eagleman & Sejnowski, 2000; Wolpert

& Ghahramani, 2000). However, we agree with the argumentation of Nijhawan and colleagues (2004) that there is no a priori reason to restrict predictive mechanisms exclusively to the motor side. In what follows we will show that the integration of motor plans in our model network coding for position may lead to visual motion extrapolation. The modelling results thus support the notion that beside perceptual history (Nijhawan, 1994) additional information sources may be used by the visual system to actively compensate for processing delays. It is yet not completely clear where in the distributed sensorimotor system the integration process may take place. However, several lines of recent experimental evidence indicate that the parietal lobe plays a crucial role (see the Discussion).

Actively produced movements

Intuitively, one would expect that the link between action and perception is closest whenever the attended object motion is self-produced, for instance, by controlling the motion with a joystick. In a recent study, Wexler and Klam (2001) directly compared the prediction of future positions for actively produced and passively observed motion trajectories. They asked subjects to estimate after a variable delay the position of a moving target that disappeared behind an occluder. Despite the fact that in the passive condition the exact spatiotemporal trajectory produced in the active case was used, the prediction appeared to be systematically more anticipatory when the motion was self-generated.

To illustrate the impact of a predictive motor signal on the processing of positional information, we compare in Figure 6 the network response in the passive case (A) and the active case (B) using a typical representational momentum paradigm with externally controlled stimulus offset. The process of integration of the motor signal is constraint by two basic assumptions. First, the motor input to the position field is predicted to continuously precede the onset of the bottom-up stimulation by a constant time interval ΔT. It is generally believed that a more centrally generated planning signal triggered by motor outflow does not suffer the same processing delays as the retinal information. Second, the motor planning signal is assumed to be subthreshold, that is, it does not trigger an active response when presented alone. In psychological terms, the effect of this signal can be best described as a predictive priming of the position field. However, the subthreshold activation appears to be sufficient to shift the whole population response forward (compare the position of the leftmost distributions). Moreover, the priming also causes the observed displacement in the direction of implied motion. This can be clearly seen by comparing the network response in the active and the passive case at the time of stimulus offset (dashed lines) and at the time when the responses stop to travel (dotted lines). In the simulation shown, the gating mechanism for the recurrent interactions was

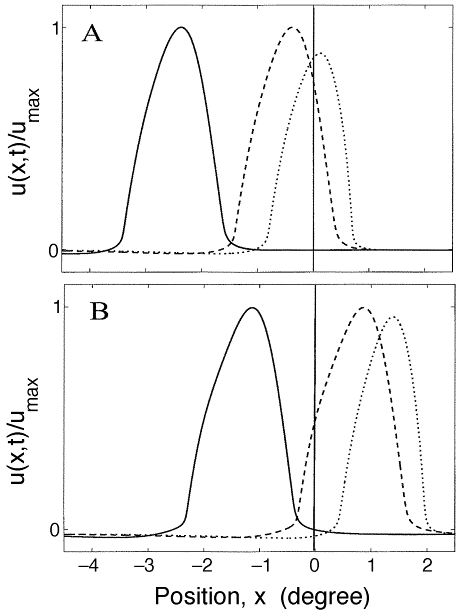

Figure 6. Integration of an action plan, $S_{act}(x, t)$, into the processing. (A) Three snapshots of the travelling wave are shown: The solid line plots the activity at a time before the last stimulus of the sequence reaches the position field, the two other activity patterns represent the response at the time of stimulus offset and the time when the wave stops to travel in the direction of implied motion. Compared to the simulation in Figure 3A, the internal dynamics is less predictive due to a larger threshold ($u_g = +0.5$) of the gating mechanism for the recurrent interactions. The rest of the model parameters were as in Figure 3. (B) The predictive action signal is modelled as an additional input, $S_{act}(x, t)$, which travels with the velocity of the inducing display, but precedes the onset of the bottom-up stimulation by a constant time interval $\Delta T = 90\,\text{ms}$. The population response to the stimulus train used in (A) now appears to be shifted in the direction of motion. For simplicity, we modelled $S_{act}(x, t)$ as a continuously displaced Gaussian profile ($\sigma_{act} = 0.4$ deg, $A_{act} = 1.52 < A_{TH}$).

adjusted to guarantee that only a very modest displacement forward to the vanishing point $x = 0$ can be observed when the bottom-up signal exclusively drives the network. In the active case, on the other hand, the population response appears to be already ahead of the vanishing position at the time when the last stimulus reaches the position field.

In conclusion, the modelling results strongly suggest the application of a classical representational momentum paradigm in the case of an actively produced movement. We expect a significant forward displacement also in a fixation condition. It would be also interesting to use a relative judgement task with accompanying flash to further elucidate the impact of action plans on spatial perception. On the assumption that the action plan produced in relation to the moving stimulus does not affect the processing of position of the flash, we expect a significant larger flash-lag effect (Nijhawan, 1994) compared to the passive case with identical trajectory.

Motor tracking of the moving target

Although the potential role of eye movements for memory displacement has been discussed in the literature from the beginning on (see Hubbard, 1995, for a review), an eye movement account for the representational momentum has been systematically investigated only recently. As a motivation for their study, Kerzel et al. (2001) argued that a contribution of eye movement cannot be excluded, since in the original work of Hubbard and Bharucha (1988) no fixation dot was provided and eye movement was not controlled. The range of tested velocities in the linear motion paradigm, however, was mostly adequate for smooth pursuit eye movements.

Kerzel and colleagues (2001) utilized similar displays as Hubbard and Bharucha (1988) but, in addition, instructed the observers to either fixate a point slightly below the trajectory or to actively track the target with the eyes. The fundamental finding of their study was that a forward displacement occurred only with eye movements. This outcome is particularly surprising since the perceived speed of the moving target is known to be larger in the fixation condition (Aubert, 1886), suggesting also a larger inertia of the representation. The lack of a significant overshooting in the fixation condition may be interpreted as further experimental evidence that the integration of an action plan into the processing may cause motion extrapolation.

Conceptually, the study differ from the study of Wexler and Klam (2001) in that the ocular pursuit does not drive the target. However, it can be argued that during smooth pursuit perception and action are nevertheless very closely linked. To guarantee that the eyes point accurately at the physical position of the pursued stimulus, the motor signals must continuously specify a position that is ahead of the current gaze direction. To be sure, the idea that the integration of oculomotor plans and retinal information may cause localization errors has since long been discussed in the literature (e.g., Hazelhoff & Wiersma, 1924; van Beers, Wolpert, & Haggard, 2001). More specifically, a temporal misalignment of the visual input signal and the motor outflow has been proposed as an explanation of misperception phenomena during smooth pursuit (e.g. Brenner, Smeets, & van den Berg, 2001; for a recent review see Schlag & Schlag-Rey, 2002).

To explain the findings of Kerzel and colleagues (2001) we have used the model architecture with a predictive priming signal as an additional input. In the sense of a forward modelling, this signal specifies the position onto which the current motor command will bring the gaze. For the model, one intriguing question concerns the bottom-up input to the position field when the eyes are tracking the moving object. Assuming a perfect pursuit, the retinal image is constant. However, several brain areas including the parietal cortex have been identified with neurons coding for target location in head-centred coordinates (e.g., Andersen, Snyder, Bradley, & Xing, 1997). Taking into account an additional coordinate transformation (for a modelling approach see Pouget & Sejnowski, 1997) we can again assume an input stream, which matches the apparent velocity of the moving target.

The magnitude of the forward displacement which can be explained by the integration of the priming signal critically depends on the temporal misalignment ΔT. We have used an interval of 90 ms to quantitatively match the experimental findings. In Figure 7 we compare modelling results with the displacements reported for the two tested target velocities. Note that a fixed interval quite naturally explains the observed increase of the forward shift with higher velocities since a faster activity wave travels a larger distance within this time interval. The value of 90 ms is well in the range of the timing error proposed by Brenner et al. (2001) to explain the mislocalization of flashed targets during pursuit of a moving ring. The authors concluded from their position judgement data that the error corresponds to a distance of pursuit travelled in about 100 ms. Further experimental tests should manipulate the assumed time interval ΔT by either increasing the processing delays for the bottom-up information (by changing the target luminance for instance), or by using conditions that favour anticipatory smooth pursuit (Kowler, 1989).

Action control over the vanishing point

Thus far, we have discussed examples that illustrate that the price the visual system has to pay for a more accurate spatial percept of a moving stimulus may be an overshooting of the internal representation when the stimulus abruptly

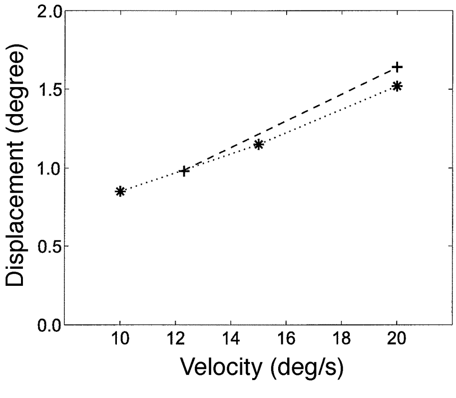

Figure 7. The dependence of the size of the forward shift on velocity is shown for the model (asterisk) and the experiment (plus). The experimental values are taken from Kerzel, Jordan, and Müsseler (2001, Exp. 3). The time interval $\Delta T = 90$ ms was constant for all three tested velocities.

stops. Inversely, one might expect that the planning of an action, which causes the offset of the moving stimulus at a self-defined position, will reduce the localization error at the end of the trajectory. Of particular interest for the present discussion is to what extent the intention to stop the target may counterbalance the tendency to extrapolate due to the tracking of the target.

In a series of experiments, Stork and Müsseler 2004 (see also Jordan et al., 2002) addressed this question. They designed a paradigm in which the vanishing point was either defined by a bottom press of the observer (intention) or externally by the computer (induction). Stork and Müsseler found that the forward displacement observed with smooth pursuit eye movements in the induction condition appeared to be significantly reduced when the observer intentionally stopped the target. In Figure 8 we show a model simulation that qualitatively reproduces this behaviour. To allow for a direct comparison, the simulation differs from the case ‘‘20 deg/s’’ in Figure 7 only in that an additional input, S_{int}, at the field side representing the intended stopping position, $x = 0$, is applied. The solid line plots a snapshot of the field activity well before the travelling wave reaches the vanishing position. Note that at this time the signal S_{int} has already triggered an active response localized at $x = 0$. The subsequent snapshots illustrate that the two activity distributions merge, but that the population response does not overshoot the vanishing point since the intentional input is strong enough to bind the representation at $x = 0$. To guarantee this

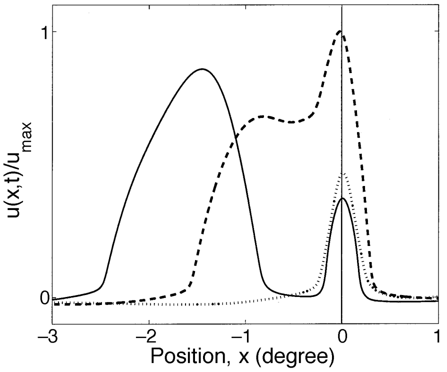

Figure 8. Influence of an action-generated vanishing point on motion extrapolation. The intention to stop a moving target, which is continuously tracked with the eyes, is modelled as a sustained input $S_{int}(x)$ centred at the intended vanishing position $x = 0$. Three snapshots of the temporal evolution are shown. The bimodal distribution (solid line) represents the travelling wave and the field response to the input S_{int}. At a later time these two responses merge (dashed line), but the activity pattern stops to travel and does not overshoot the position $x = 0$ (dotted line). The stimulus moving with 20 deg/s and the input S_{act} representing the predictive ocular motor signal were the same as in Figure 7. The parameters for S_{int} were $\sigma_{int} = 0.1$ deg and $A_{int} = 12$. Note that a weaker input S_{int} would lead to an overshooting.

binding over a longer time period, the input signal S_{int} must continuously activate the neurons representing the vanishing position since otherwise the lateral inhibition in the network will cause a decay to resting level. This suggests that the signal driving the cells must be actively stabilized (see the Discussion). The nature of such a signal, however, is unclear. It may simply code the attended location in space irrespectively of the action that stops the stimulus. Alternatively, it may represent the covert planning and suppression of a goal-directed motor act (for neurophysiological evidence supporting the existence of covert action plans see Snyder, Batista, & Andersen, 2000). This could be in principle tested by using different effectors to produce the offset of the movement.

When observers had to fixate, Stork and Müsseler (2004) found no difference in the position judgement for the action-generated and the computer-generated condition. Importantly, the localization errors appeared to be consistently negative, that is, opposite to the movement direction (but see Müsseler, Stork, & Kerzel, 2002, for conflicting data). In the model, a high threshold u_g for the recurrent interactions leads to a travelling wave that does not reach the vanishing point (Figure 3). Our model simulations reveal that the activity may even die out before it reaches the border of the excitation triggered by the intention signal S_{int} (not shown). This finding suggest that all stimulus parameters that are known to affect motion extrapolation in the experiments and also in the model to some extent (e.g., contrast, shape, or velocity; Fu, Shen, & Dan, 2001) might be used to test the spatial range of this intentional attraction.

IMPLIED MOTION DISPLAYS

Memory distortion at the end of a trajectory was first observed with implied rather than apparent motion displays. In their seminal work, Freyd and Finke (1984) presented observers with a sequence of three discrete positions of an object consistent with the rotation of that object around its centre. In a typical experiment, the large interstimulus intervals prevented from perceiving the inducing display as a smooth rotation. The judged vanishing positions nevertheless support the notion of a mental extrapolation of the stimulus' trajectory. A comparison with the orientation of a probe stimulus presented after a retention interval was used to quantify the forward shift and not a direct localization by mouse pointing like, for instance, in the study of Hubbard and Bharucha (1988). But this difference in methodology is not central for the purpose of this paper. From a theoretical point of view a more important question concerns whether the forward displacements observed with implied or apparent motion reflect the same principles of representation. An answer to this question would broaden our understanding of how the brain copes with dynamic events to predict future states of the environment.

A hallmark of Freyd's theory of dynamic mental representations (Freyd, 1987) is the assumption that dynamic information should be mentally represented even when there is clearly no sensory basis to detect changes. In the model, the spatiotemporal characteristics of a typical implied motion display do not promote the interactions between the dynamic representations of individual stimulus frames. As we have seen, these interactions are necessary to establish and stabilize a population response, which propagates in the direction of change. We have recently proposed that a stored internal model of the moving stimulus might be used by the visual system to allow for object permanence following occlusion. The integration of such a top-down signal into the processing preserves the continuity of the wavy activity pattern in situations where the continuity of the bottom-up information is temporarily disrupted (Erlhagen, 2003). Similarly, we hypothesize here that a stored predictive model associated with the stimulus ‘‘animates’’ the sequence of static stimuli by filling-in dynamic information (see the Discussion for an interpretation of this predictive signal in terms of a covert action plan). Figure 9 illustrates the model architecture with the bottom-up input, S_{Bot}, and the top-down input, S_{Top}, to the neural field spanned over the parameter orientation. For our modelling work we applied a bottom-up input with the spatiotemporal characteristics of the display used by Freyd and colleagues (e.g., Freyd & Finke, 1984). Each stimulus was presented with a 250 ms duration, and successive presentations were separated by a blank interval of 250 ms and an angular disparity of 17 deg. The travelling activity pattern representing the subthreshold top-down signal matched the implied velocity of the inducing display.

In Figure 10 we compare snapshots of the dynamic representation at the position of the last stimulus without (A) and with (B) integration of the internal model. It can be clearly seen that the predictive top-down information causes a drift of the representation in direction of implied motion. It is important to note that this happens despite the continuous stimulation of the position $x = 34$ through the bottom-up signal.

The magnitude of the observed shift depends on the strength, A_{Top}, of the top-down contribution to the orientation field. A relative weak subthreshold contribution is sufficient to explain the experimentally observed memory displacements (typically about 2–3 deg, e.g., Freyd, 1987). However, as shown in Figure 11, much larger forward displacements can be achieved when increasing the strength A_{Top} to a level closer to the threshold A_{TH}.

A detailed discussion of the dynamics of the shift goes beyond the scope of this paper. It depends on the time scale, τ, of the dynamics but also on the relative timing of the two input signals (Erlhagen, 2003). Interestingly enough, since the stimulus duration is longer than the persistence of the population response (about 100 ms) a second active response is triggered. This activity pattern, however, lacks the interaction with the internal model and appears to be centred over the actual stimulus position throughout the whole evolution. This might contribute to the observed decrease of the displacement with sufficiently long retention intervals (Freyd & Johnson, 1987).

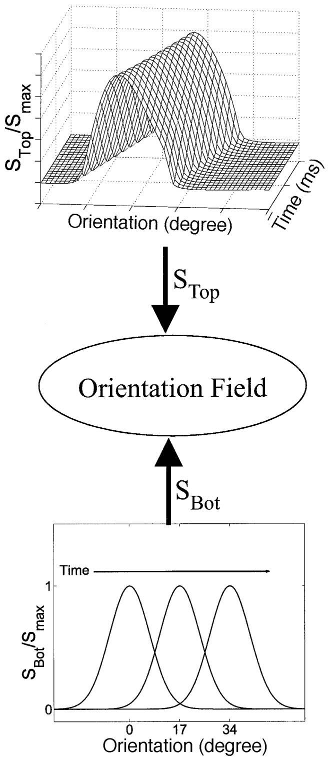

Figure 9. Sketch of the model architecture for implied motion displays. In addition to the bottom-up input stream, the neuronal population coding for orientation gets top-down information about the moving target. This top-down input is represented by a self-stabilized activity wave, which travels with the implied velocity of the inducing display (see Erlhagen, 2003, for details). The bottom-up information consists of a sequence of discrete inputs representing the three target orientations used in a typical implied motion paradigm (see text for more details).

DISCUSSION

When planning a motor action towards a continuously moving object the goal of the visual system becomes one of estimating the current state and predicting future states. It has been suggested that visual motion extrapolation is necessary to compensate for the sizeable processing delays between the retina and higher visual areas (Nijhawan, 1994; see also Nijhawan et al., 2004). But also when the timing issue is not the most important one (for instance, because the motion is only implied) it is functionally of advantage to create some expectation about possible future positions. Typically, the visual system has to handle multiple objects in the visual field, often in the presence of occlusion and background clutter.

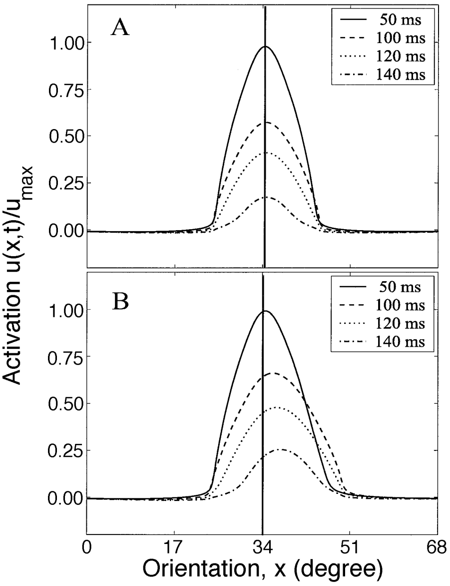

Figure 10. Effect of the top-down input on the spatiotemporal characteristics of the population response. (A) Four snapshots of the response after the presentation of the final stimulus at time $t = 0$ are shown. The response is centred over the position $x = 34$ deg, representing the final orientation of the target. Due to the long interstimulus intervals (250 ms) between successive presentations the active response of neurons coding for orientation $x = 0$ or orientation $x = 17$ deg has already decayed to resting level. The external stimulus ($A_s = 12$, $\sigma_s = 3.4$ deg) was presented for 250 ms. (B) The additional top-down signal caused a slight drift of the dynamic representation in movement direction. For simplicity, we used a Gaussian profile ($A_{Top} = 0.4$, $\sigma_{Top} = 10.2$ deg), which was displaced with the implied velocity of the display, instead of the actively generated signal used in Erlhagen (2003). Model parameters were: $\tau = 35$ ms, $h = -3$, $\beta = 1.0$, $u_f = 0$, $u_g = 0$, $A_u = 2.33$, $\sigma_u = 10.2$ deg, $A_v = 1.99$, $\sigma_v = 13.6$ deg. To adjust the spatial scale in the model to the experimental units we have chosen 1 pixel = 0.34 deg. Note that the drift of the response does not depend on the range parameters describing the lateral interactions. Larger values could have been chosen as well. This would lead to broader activity distributions in parametric space.

In the modelling work presented in this paper we have identified basically two distinct but not mutually exclusive mechanisms for motion extrapolation. One is based on nonlinear interactions among neurons coding for position. As shown in Figure 3, cooperative forces within the network may cause the continuation of the dynamic transformations upon offset of the moving target resulting in a significant overshooting of the dynamic representation. Moreover, they also lead to a partial compensation of processing delays, resulting in an activity wave that codes a position close to the actual stimulus position. This interaction-based mechanism can in principle take place at every processing level along the visual pathway that consists of lateral connections. In fact, there

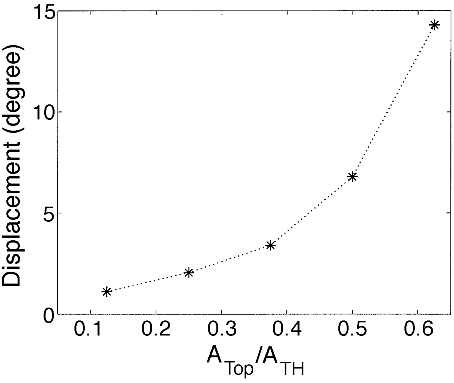

Figure 11. The forward displacement caused by the top-down signal in Figure 10B is plotted as a function of the input strength A_{Top} of S_{Top}. To allow for a quantitative comparison we have defined the displacement as the distance of the peak position to the stimulus position $x = 34$ at the time when the active response has decayed to 25% of its maximum level. The input strength is expressed as a fraction of the threshold activity A_{TH} necessary to trigger an active response.

is evidence that motion extrapolation begins already in the retina (Berry, Brivanlou, Jordan, & Meister, 1999).

In the model, the magnitude of the forward displacement is controlled by the threshold for the recurrent interactions. We hypothesize here that an adaptation of this threshold may account for experimental findings that show the influence of conceptual, path-independent knowledge on the forward displacement. This includes object-specific effects described by Reed and Vinson (1996; see also Vinson & Reed, 2002), but also motion invariants like gravity or friction, which are believed to be internalized into the representational system (Hubbard, 1995).

A second mechanism for motion extrapolation is based on an integration of additional information such as action plans into the processing of positional information. Our basic assumption is that the interaction with a fast moving target requires predictive models of both the motor apparatus *and* the attended object.

Several lines of experimental evidence suggest that the posterior parietal cortex (PPC) plays a crucial role in this predictive modelling. It is known that efference copy signals from motor areas and sensory information from a number of different neural systems do converge in PPC (for a review see Andersen et al., 1997). There is now clear evidence that activity in different subareas of PPC code for the intention to make saccades or reaches (Snyder et al., 2000). Importantly, it was shown that parietal cells might predict the retinal consequences of intended saccadic eye movements prior to the onset of the actual movement (Duhamel, Colby, & Goldberg, 1992). Eskandar and Assad (1999) found cells in PPC of macaques that seemed to monitor the trajectory of a temporarily occluded target whose movement was under the animal's control. We have recently shown that the integration of a sufficiently strong but still subthreshold signal into our model architecture may maintain the suprathreshold wave in the absence of direct sensory stimulation due to an occluder (Erlhagen, 2003). In the case of a self-generated movement this signal may represent the predicted position of, for instance, the hand controlling the manipulandum. Similarly, we argue here that also during smooth pursuit or other forms of motor tracking (e.g., with the index finger; Grafton, Mazziotta, Woods, & Phelps, 1992) a predictive representation of the trajectory may be used to cope with incomplete visual information and processing delays. However, it is unclear to which extent such a representation continuously monitors the motor outflow (e.g., a velocity signal) driving the eye or the hand. It might be that an initial motor command triggers a representation that is to a large extent self-stabilized. The prediction about future states would then continue until it is actively stopped by another signal, for instance, the offset of the motor outflow. In fact, we have proposed a field model for motor preparation in which action plans for reaches or saccadic eye movements are self-stabilized by cooperative interactions (Erlhagen & Schöner, 2002; Schöner et al., 1997). Moreover, we have recently shown that recurrent network models similar to the one used in this paper may exhibit a self-stabilized wave in parametric space, which travels with a velocity defined by the interaction parameters (Erlhagen, 2003). The learning of an association between a neuronal population representing a motor command such as a velocity signal for a certain direction and a neuronal population with the appropriate spatial interaction structure would automatically trigger the corresponding predictive representation for position.

Assad and Maunsell (1995) and Eskandar and Assad (1999) described firing patterns of neurons in PPC that are consistent with the idea of a predictive signal about the direction of a moving object which is to some extent independent of sensory input and motor output. These neurons fired during occluded trials without hand or eye movements whenever the monkey could infer the movement direction because of the direction-blocked organization of the experiments. Assad and Maunsell suggested that this type of signal might act as an additional contribution to the extra retinal responses, which converge during smooth pursuit on the medial superior temporal area (MST) and allow the maintenance of pursuit eye movements. Moreover, these neurons might explain why in a ''motion area'' such as MST the activity of some cells persists when the target is transiently occluded (Newsome, Wurtz, & Komuatsu, 1988).

The fact that we are able to simultaneously track several moving targets despite brief periods of occlusion (Scholl & Pylyshyn, 1999) has been used as an argument against an eye movement account as a sole explanation for representational momentum (Finke & Freyd, 1985). Kanwisher and colleagues called this attentive tracking ''attentional pursuit'' to stress the fact that like for smooth eye movements the attentional focus can be maintained on moving targets. They reported fMRI activation pattern for attentive tracking, saccades, and smooth pursuit with a ‘‘surprising amount of neuroanatomic overlap’’ (Culham, Brandt, Cavanagh, Kanwisher, Dale, & Tootell, 1998). One possible explanation could be that the proposed predictive modelling process, which is first triggered by oculomotor outflow, becomes during learning directly associated with the visual input (for the learning aspect, see Erlhagen, 2003).

It may be hypothesized that also the spatial perception of stimuli that are not changing in real time is directly influenced by some kind of motor plan. In fact, several authors have argued that implicit knowledge of motor rules for the production of static images may affect their perception (for a recent review see Decety & Grèzes, 2001). On this view, the priming signal applied to model the representational momentum for implied displays (Figure 10) would represent a simulated action that may ‘‘explain’’ the coherent rotation of the object. The only difference to the integration of an actual motor plan might be a reduced relative strength of the subthreshold priming signal. The discovery of the ‘‘mirror system’’ by Rizzolatti and colleagues (for a review see Rizzolatti, Fogassi, & Gallese, 2001) provides physiological evidence in support of such a simulation theory. It was shown that the mere observation of visual cues associated with a particular motor action might automatically trigger the neuronal representation of that action in the motor repertoire of the observer. The notion of such a direct mapping from perception to action might be of particular importance when attempting to explain movement prediction observed with more natural displays including biological motion (see Thornton & Hayes, 2004).

In conclusion, we have shown that the intrinsic dynamics of our network model triggered during the target’s seen motion may cause a ‘‘momentum’’ of the dynamic trajectory representation. However, the experimental and theoretical results convincingly reveal that whenever overt or covert action plans are integrated into the processing these plans decide to a large degree the extent to which motion is extrapolated.

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