



## Review paper

# Motion-based prediction explains the role of tracking in motion extrapolation



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## ABSTRACT

During normal viewing, the continuous stream of visual input is regularly interrupted, for instance by blinks of the eye. Despite these frequent blanks (that is the transient absence of a raw sensory source), the visual system is most often able to maintain a continuous representation of motion. For instance, it maintains the movement of the eye such as to stabilize the image of an object. This ability suggests the existence of a generic neural mechanism of motion extrapolation to deal with fragmented inputs. In this paper, we have modeled how the visual system may extrapolate the trajectory of an object during a blank using motion-based prediction. This implies that using a prior on the coherency of motion, the system may integrate previous motion information even in the absence of a stimulus. In order to compare with experimental results, we simulated tracking velocity responses. We found that the response of the motion integration process to a blanked trajectory pauses at the onset of the blank, but that it quickly recovers the information on the trajectory after reappearance. This is compatible with behavioral and neural observations on motion extrapolation. To understand these mechanisms, we have recorded the response of the model to a noisy stimulus. Crucially, we found that motion-based prediction acted at the global level as a gain control mechanism and that we could switch from a smooth regime to a binary tracking behavior where the dot is tracked or lost. Our results imply that a local prior implementing motion-based prediction is sufficient to explain a large range of neural and behavioral results at a more global level. We show that the tracking behavior deteriorates for sensory noise levels higher than a certain value, where motion coherency and predictability fail to hold longer. In particular, we found that motion-based prediction leads to the emergence of a tracking behavior only when enough information from the trajectory has been accumulated. Then, during tracking, trajectory estimation is robust to blanks even in the presence of relatively high levels of noise. Moreover, we found that tracking is necessary for motion extrapolation, this calls for further experimental work exploring the role of noise in motion extrapolation.

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## 1. Introduction

### 1.1. Problem statement

The continuous flow of information originating from the visual world is constantly fragmented by different sources of noise, occlusions or blanks. For instance, the path of a moving object can often be transiently blocked from the observer's line of sight. However, one is still able to judge the current position of a moving object during such periods of occlusion as well as estimate its future trajectory at its reappearance. This ability to transform such fragmented sensory inputs into a correct continuous representation has been a major pressure in the evolution of visual systems because it leads to appropriate reactions matched to the physical evidences: It is vital to accurately follow the trajectory of a fleeing prey and stabilize its image onto the retina in order to catch it or, on the contrary, to escape from an approaching predator, despite the fact that it can transiently disappear from the line of sight (Gollisch and Meister, 2010). The problem of motion occlusion is a particular case of a more general problem in neuroscience: *motion extrapolation*. In the absence of sensory input, the visual system can extrapolate the instantaneous position of a moving object from its past trajectory.

An essential clue to solve that problem is the prior knowledge that objects follow smooth, coherent trajectories. Following the first law of newtonian mechanics, the trajectory of an object is only perturbed by external forces. Since we know *a priori* that these forces are more likely to be small compared to the inertia of an object of relevance, the trajectory of objects in the physical world tend to follow smooth, straight trajectories. As such, the projection of these trajectories on the retinotopic space is such that the statistics of natural images also exhibit similar regularities regarding their visual trajectories. Such prior knowledge may be the basis of learning processes based on the prediction of the path of the trajectory. During transient blanking, it is most likely that such processes (along with the knowledge that the sensory input was indeed blanked and not definitively removed) are at the root of the mechanisms underlying motion extrapolation. Their behavioral consequences are well known. For instance, when a moving target disappears, smooth pursuit eye movements continue at the same velocity during the initial period of occlusion (Bennett and Barnes, 2003) and such a feat is only possible when observers have some knowledge on the path of motion (Graf et al., 2003). Therefore, there must be some underlying neural computations but it is yet not clear how this can be done efficiently and where it is implemented in the visual system.

This perceptual phenomenon provides invaluable tools with which we may study the mechanisms of motion detection and draw inferences about the properties of underlying neural populations. First, it is involved in different sensory modalities as sensory fragmentation exists in vision but also for instance in haptic tasks (hence in the somatosensory system). Second, it is a powerful mean to distinguish between the different computational steps of the visual motion system. Object motion information is extracted along a cascade of feedforward cortical areas, where area V1 ex-

tracts local motion information that is integrated in extra-striate middle temporal (MT) and medial superior temporal (MST) areas.

The middle temporal (MT) and medial superior temporal (MST) areas in the superior temporal sulcus (STS) process visual motion and oculomotor signals driving pursuit (see (Ilg, 1997) for a review) and are therefore key elements in motion extrapolation. Early physiological studies in macaque monkey identified area MT as a specialized module for visual motion processing (Allman et al., 1973; Dubner and Zeki, 1971). This involves extracting the speed and direction of the moving object. MT neurons respond selectively to visual motion and tuned for local speed and direction of luminance features moving in their receptive fields (Maunsell and Van Essen, 1983). Pack and Born (2001) have shown that the temporal dynamics of motion integration can be seen from time-varying firing rates. They showed that neuronal responses quickly progress from local to global motion direction in about 100 ms suggesting that such mechanisms are dynamical and progressive. These results pinpoint the key role of MT neurons in local motion analysis as well as global motion integration. However, these neurons respond only when the retinal image motion is present while MST neurons maintain their firing activity when there is no retinal image motion as during a transient image occlusion (Newsome and Paré, 1988) or during tracking imaginary target covering the visual field outside of the receptive field currently recorded (Ilg and Thier, 2003). Similar sustained activity during target occlusion has been found in monkey posterior parietal cortex, and it is linked to an image motion prior to target disappearance (Assad and Maunsell, 1995). In another study (Schwartz and Berry, 2008) have stimulated the retina of tiger salamander with a periodically flashing stimulus and have found various firing patterns when a flash is omitted. This sustained activity is known as "omitted stimulus response" (OSR) and is explained by a model based on tunable oscillators which extrapolate the response to the periodic stimulation even at times matched to the missing stimulus. OSR has also been reported in the flicker electroretinogram (ERG) of the human cone system (McAnany and Alexander, 2009).

What is the link between behavioral and neuronal signatures of motion extrapolation? Visual motion information is primarily used for gaze stabilization (Ilg, 1997; Kawano, 1999; Masson et al., 2010) and sensorimotor transformation underlying smooth pursuit eye movements (Lisberger et al., 1987). The fact that sustained activity in area MST was seen during transient occlusion of a moving target supports the notion that the two phenomena are closely related (Newsome and Paré, 1988). On the other hand, since motion extrapolation is also seen in lower level neuronal structures, such as the retina, this calls for a more generic computational framework. Since motion extrapolation is implemented at the scale of a single cortical area, this would suggest that such a mechanism would be implemented by a finely structured set of diffusive mechanisms. A potential candidate is naturally the dense network of lateral interactions as found in sub-cortical and cortical structures involved in sensory processing as well as sensorimotor control. However, direct evidence for such neural mechanisms is still lacking. Before proposing a solution using motion-based prediction, we

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