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Comment and Reply

Why eye movements and perceptual factors have to be controlled in studies on "representational momentum"

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In order to study memory of the final position of a smoothly moving target, Hubbard (e.g., Hubbard & Bharucha, 1988) presented smooth stimulus motion and used motor responses. In contrast, Freyd (e.g., Freyd & Finke, 1984) presented implied stimulus motion and used the method of constant stimuli. The same forward error was observed in both paradigms. However, the processes underlying the error may be very different. When smooth stimulus motion is followed by smooth pursuit eye movements, the forward error is associated with asynchronous processing of retinal and extraretinal information. In the absence of eye movements, no forward displacement is observed with smooth motion. In contrast, implied motion produces a forward error even without eye movements, suggesting that observers extrapolate the next target step when successive target presentations are far apart. Finally, motor responses produce errors that are not observed with perceptual judgments, indicating that the motor system may compensate for neuronal latencies.

In his review of the literature on representational momentum, Hubbard (2005) presents two basic paradigms that have been used to investigate the localization of the final position of a moving target and concludes that

> Even though Freyd and Finke (1984) and Hubbard and Bharucha [1988] used different methods of stimulus presentation and response collection, the results from these studies converged on the idea that memory for the final position of a moving target was displaced forward in the direction of target motion. (p. 824)

Contrary to Hubbard's (2005) conclusions, I will show in this comment that the observed convergence is the result of an artifact related to the poor control of eye movements in Hubbard and Bharucha (1988). Furthermore, I will present an alternative view suggesting that forward displacement arises partly from low-level processes, that more than a single process of extrapolation exists, and that each extrapolation process is specific to certain types of motion and responses. To begin with, I will briefly recapitulate the major difference between the work of Jennifer Freyd in the 1980s (e.g., Freyd & Finke, 1984, 1985; Freyd & Johnson, 1987) and that of Timothy Hubbard in the 1990s (e.g., Hubbard, 1995, 1996; Hubbard & Bharucha, 1988).

In Freyd's work (e.g., Freyd & Finke, 1984), observers were shown a succession of rectangles, and each rectangle was shown for about 250 msec at the same position; after a blank interval of 250 msec, it appeared at a new orientation that implied the rotation of the rectangle during the blank interval. After seeing three such stimuli, a fourth stimulus, the probe, was presented at an orientation that differed only slightly from the third, and the observers were asked to report whether the third and the fourth orientations of the stimuli were the same or not. The observers were more prone to accept probe stimuli that had been rotated slightly further as being in the same orientation, indicating a forward error. The stimuli created by Freyd may be referred to as *implied motion* stimuli, and she used the method of constant stimuli that involved a symbolic response, with an arbitrary mapping between response and perceptual content (e.g., pressing one of two buttons). Most of the subsequent work on representational momentum has used Freyd's methodology, even if the stimulus type and the target's trajectory have been changed (for a sample of recent research, see Thornton & Hubbard, 2002).

In Hubbard's work (e.g., Hubbard & Bharucha, 1988), observers were shown a smoothly moving target that resembled real motion. The target moved on a linear trajectory and disappeared suddenly. The observers' task was to adjust a mouse cursor so that it corresponded to the remembered final position, which involved a nonarbitrary relationship between the motor response and the perceptual content.

The results of Hubbard's and Freyd's paradigms converged, in that both studies reported displacement of the final target position in the direction of target motion (forward displacement). However, more recent studies have shown that this convergence is due to the complex interaction between the three factors of motion type (implied vs. smooth), eye movements (smooth pursuit vs. fixation), and response mode (motor response vs. buttonpress). Table 1 presents an overview of the three factors and specifies which conditions produce forward displacement and which do not. Importantly, the smooth motion stimuli used by Hubbard produce forward displacement only when observers track the stimulus with their eyes. The table will be explained in detail in three subsequent sections.

Why Previous Results Obtained With Smooth Stimulus Motion Are Inconclusive: The Role of Eye Movements

In the first section of this comment, I will deal with studies in which smooth stimulus motion on a computer

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monitor that resembled real motion has been used (e.g., Hubbard, 1995, 1996; Hubbard & Bharucha, 1988): In these studies, smooth stimulus motion at a moderate (mostly smaller than 30 deg/sec) velocity was shown, no fixation point was presented, and observers were not given any explicit instructions about where to fixate. This made it highly likely that the observers pursued the target with their eyes. At target velocities below ~30 deg/sec, smooth pursuit eye movements may be used to keep the target in the region of highest acuity, the fovea (Robinson, Gordon, & Gordon, 1986), where it is much easier to see than in the periphery, due to the better spatial resolution. In contrast, implied motion is not sufficient to sustain smooth pursuit eye movements (Churchland & Lisberger, 2000).

Neuronal latencies and the *sensation time*. The study of localization errors associated with smooth pursuit eye movements has a long history. The earliest studies were concerned with the mislocalization of a flash during smooth pursuit eye movements. In the 1920s, Hazelhoff and Wiersma (1924) developed a paradigm based on smooth pursuit to measure the sensation time of a stimulus. They argued that there is a minimal time for the perception of a stimulus (*sensation time*) and that the distance covered by the eyes during this time interval may be used to estimate the duration of the sensation time. In their experiments, Hazelhoff and Wiersma asked observers to follow a smoothly moving target with the eyes. At an unpredictable moment, they presented a flash while the smooth pursuit eye movement continued. It was noted that the perceived position of the flash was displaced in the direction of motion by a distance x. Because the eye moved at a velocity v while traversing the distance x, the authors reasoned that the signal representing the flash arrived in the brain at the time $t = x/v$, which turned out to be on the order of 100 msec, regardless of target velocity. A large number of more recent studies have confirmed Hazelhoff and Wiersma's observations (Brenner, Smeets, & van den Berg, 2001; Metzger, 1932; Mita, Hironaka, & Koike, 1959; Mitrani & Dimitrov, 1982; Rotman, Brenner, & Smeets, 2004; van Beers, Wolpert, & Haggard, 2001) and have refined his argument in terms of sensation time (overview in Schlag & Schlag-Rey, 2002).

Table 1
Overview of Three Factors That Influence the Occurrence of Forward Displacement (FD)

		Motion Type	
Eye Movement	Response	Smooth	Implied
Smooth pursuit		FD	n/a
Eye fixation	Verbal	No FD	FD
	Motor	FD	FD

Note—Smooth pursuit eye movements may be sustained only by smooth stimulus motion, not by implied motion. Smooth motion looks real, whereas implied motion shows a target separated by large spatiotemporal gaps. A verbal response mode involves a symbolic response that indicates the content of perception (*left of*, *right of*), whereas a motor response involves a nonarbitrary relation between response (e.g., pointing) and the content of perception.

Although most of the studies of perception time have been concerned with the localization of flashes, the concept may easily be applied to the localization of the endpoint of a moving target. It is known that smooth pursuit eye movements may not be stopped instantaneously but that the eye continues to move for about 300 msec after target disappearance (Mitrani & Dimitrov, 1978). The continuation of smooth pursuit after target offset will be referred to as *oculomotor overshoot*. Because the eye continues to move after a discrete event (i.e., target disappearance), Hazelhoff and Wiersma's (1924) logic may be applied to endpoint localization: The distance covered by the eyes during the time it takes to consciously notice the disappearance of the target results in a localization error, because when the sudden event is registered, it will be associated with the current position of the eyes, and not with the eye position at physical target offset (see Figure 1). In accord with this idea, it has been observed that the size of the oculomotor overshoot and the mislocalization of the endpoint are closely coupled. The oculomotor overshoot decreases when the target disappearance is more probable, because the target reaches the end of a trajectory (Mitrani & Dimitrov, 1978) or because target disappearance can be voluntarily controlled (Stork, Neggers, & Müsseler, 2002). Similarly, the mislocalization decreases toward the end of the trajectory (Mitrani & Dimitrov, 1978) and when the target disappearance can be voluntarily controlled (Stork & Müsseler, 2004).

In addition to the timing error between retinal (target disappearance) and extraretinal (perceived eye position, oculomotor commands) signals, purely retinal factors may contribute to the mislocalization of the target endpoint. As is shown in Figure 1, the current gaze position after oculomotor overshoot is displaced in the direction of motion. That is, the fovea is directed at a position beyond the final position of the moving target. Because there is a tendency to mislocalize objects toward the fovea (Kerzel, 2002b; Sheth & Shimojo, 2001), the final target position will be displaced in the direction of motion. Finally, the possibility cannot be ruled out that the target is subjectively perceived beyond the physical disappearance point, due to visible persistence of the target (Kerzel, 2000).

In sum, there are a number of reasons for the displacement of the final position with a smoothly moving target that is pursued with the eyes. Although the argument from neuronal latencies (sensation time) definitely precludes high-level factors, high-level factors such as expectations about the future trajectory of the target may influence smooth pursuit eye movements (Krauzlis & Stone, 1999). As was illustrated above, there is a close coupling between smooth pursuit and mislocalization of the final target position. When the eye velocity, v, during the period of oculomotor overshoot is reduced, the displacement of the final position will be reduced, under the assumption that the neuronal latency, t, is constant: $x = t * v$. Thus, any factor that will reduce eye velocity will also reduce displacement. For instance, smooth pursuit eye movements will slow down before a predictable reversal of target di-

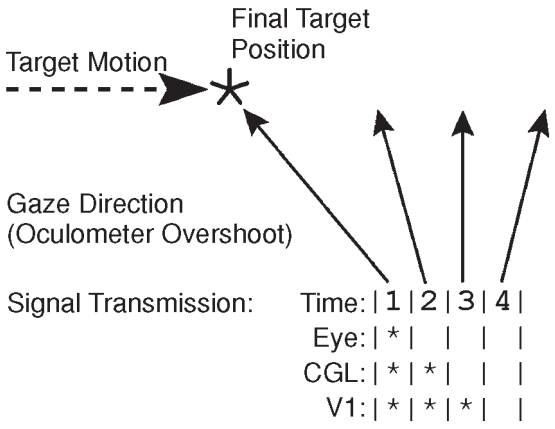

Figure 1. Asynchronous processing of retinal and extraretinal input. Gaze direction is indicated by upward pointing arrows. Initially, the eye pursues the target (an asterisk) by smooth pursuit eye movements. Unpredictably, the target disappears at Time 1. While the target continues to move (oculomotor overshoot), the signal indicating that the target has disappeared is transmitted. Three important stages—the eye, the corpus geniculatum laterale (CGL) in the thalamus, and the primary visual cortex (V1)—are shown. At Time 2, the eyes receive the signal that the target is no longer present; at Time 3, this signal has reached the CGL; and at Time 4, the signal arrives in the cortex. During Times 1–4, the target has moved the distance x at the velocity v, so that the transmission time equals $t = x/v$. Note that gaze (i.e., the foveated position) is directed at a position ahead of the final target location, so that a bias to localize the target toward the fovea will also result in a forward bias.

rection, and therefore, forward displacement will also be reduced (Kerzel, 2002a). Or, when the eye velocity is zero during eye fixation, forward displacement is entirely suppressed (see, e.g., Baldo, Kihara, Namba, & Klein, 2002; Kerzel, 2000; Kerzel, Jordan, & Müsseler, 2001; Whitney & Cavanagh, 2002; Whitney, Murakami, & Cavanagh, 2000).

Let us consider the relation between internalized physics,[1] eye movements, and displacement more formally. We have two premises (A and B) and one conclusion (C):

A. High-level processes, such as internalized physics or expectations about stimulus motion (for a complete listing of high-level factors, see Hubbard, 2005).

B. Smooth pursuit eye movements.

C. Forward displacement of the final position of a smoothly moving target.

Hubbard's (2005) argument is that high-level factors produce forward displacement with smooth stimulus motion—that is, A→C (i.e., when A, then C)—but he did not control for smooth pursuit eye movements (= B), and one may assume that in all of his experiments, B was simultaneously present. Therefore, B→C is also possible. When smooth pursuit eye movements were suppressed (no B) in some of my studies (Kerzel, 2000; Kerzel et al., 2001), the first real test of A→C was performed with smooth stimulus motion: Suppressing smooth pursuit does not affect internalized physical laws and expectations about future target motion. However, displacement (C) was not obtained under these conditions. Thus, it has to be concluded that high-level processes (= A) are *not sufficient* to produce forward displacement of a smoothly moving target (= C). Rather, the actual causal chain is more likely to be B→C.

However, it is not easy to dismiss the hypothesis that high-level processes (= A) are necessary for smooth pursuit eye movement (= B), because smooth pursuit eye movements are always predictive in nature and prediction is a high-level process (Krauzlis & Stone, 1999). Therefore, eye movements (= B) cannot be completely separated from expectations and predictions (= A). Given the prominent role of prediction in motor control, one may try to save Hubbard's (2005) argument by claiming that A→B→C, so that a high-level process (= A) would be ultimately responsible for the displacement. The problem with this idea is that it is unclear where to stop the causal chain of nonsufficient but necessary factors. For instance, the subject would have never localized the target if he or she had not been motivated to do so. Obviously, motivation is necessary to obtain displacement, but not sufficient. Thus, one may conclude that the subject's motivation (= M) is the ultimate cause of the displacement: M→A→B→C. It is obvious that this reasoning does not advance our understanding of the processes underlying displacement. Therefore, it may be best to restrict the causal chain to necessary *and* sufficient factors. Extending the causal chain to factors that are necessary but not sufficient makes the argument arbitrary.

Effects of velocity, friction, and centripetal force with smooth motion. Basically, all the studies in which localization of the endpoint of a smoothly moving target during eye fixation and with smooth pursuit eye movements has been compared have reported differences between these conditions. In the most basic version, Kerzel (2000; Kerzel et al., 2001) found that the final position of a target moving smoothly on a linear trajectory was displaced in the direction of motion during smooth pursuit eye movements and that forward displacement increased with increasing velocity. During fixation, there was no forward displacement and no increase of displacement with increasing velocity. Effects of velocity are typically considered to be a robust piece of evidence in favor of *representational momentum* (Freyd & Finke, 1985), because the momentum of an object is jointly determined by its mass and velocity.[2] The absence of effects of velocity during fixation poses a major challenge for an account in terms of internalized physics because the "physical" content of the scene remains unaltered. In contrast, an eye-movement-based explanation may easily explain effects of velocity during smooth pursuit with reference to the equation given above: displacement = constant delay ∗ velocity. When the eye does not move during fixation, no displacement is expected with smooth motion, because the eye velocity equals zero.

Furthermore, Hubbard reported that forward displacement decreased when the moving target made contact with an adjacent surface and that forward displacement decreased even further when the moving object made con-

tact with two objects (Hubbard, 1997, 1998). The interpretation of this effect was that the contact between the moving object and the surface implied friction and that the mental representation of friction reduced forward displacement. However, the presence of more than one object may have distracted the observers' eye movements, so that they either did not follow the target or did so at a lower eye velocity. It is well known that a structured background reduces the velocity of smooth pursuit (Collewijn & Tamminga, 1984). In accord with such an interpretation, the observers could easily have switched between a strategy of following the target and one of looking at the friction surface. A reduction of forward displacement was found in the latter, but not in the former, condition (Kerzel, 2002a). Thus, it may be that effects of a cluttered visual display on eye movements, and not the associated physical implications, reduced forward displacement.

In addition to representational momentum and representational friction, Hubbard (1996) reported displacement consistent with centripetal force: When a target moving on a circular trajectory suddenly disappeared, displacement was in the direction of motion and toward the center of the circular trajectory (inward displacement). Again, the stimulus was appropriate for smooth pursuit eye movements. In a close replication of Hubbard's (1996) study, eye movements were recorded while observers pursued the target on a circular trajectory (Kerzel, 2003b). It was observed that the eyes continued on the circular trajectory after target disappearance; that is, the final eye position was displaced forward and toward the center of the circular trajectory (inward), thereby mirroring the localization error.

Overall, there is ample evidence that studies reporting effects of internalized analogues of momentum, friction, and centripetal force with smooth stimulus motion may rather reflect modulations of smooth pursuit eye movements induced by the displays. In fact, there is no recent evidence that would suggest the opposite. Furthermore, I do not think that oculomotor effects add to or modulate displacement arising from higher level effects, such as internalized physics, expectations, landmark attraction, or motion source. Hubbard (2005) suggests that all of these factors may jointly determine the pattern of displacement. For instance, displacement may be larger when the target moves toward a landmark, because landmark attraction and representational momentum add up, and smaller when it moves away from the landmark, because landmark attraction and representational momentum cancel out (Hubbard & Ruppel, 1999). Data from my own lab do not support the view that the effects of eye movements will add up with any of the hypothesized mechanisms (internalized momentum, friction, centripetal force) observed with smooth stimulus motion. Rather, the data suggest that these mechanisms simply do not exist. This may explain why the effects of friction and centripetal force have not yet been replicated with implied motion, where smooth pursuit eye movements are not possible. In contrast to smooth motion, implied motion produces forward displacement even during fixation.

Forward Displacement Occurs With Implied Motion: The Role of Apparent Motion Perception

In the studies of Freyd and co-workers, there were large spatial and temporal gaps between successive presentations of the target that made smooth pursuit eye movements impossible. To vary the velocity of target motion, the time interval between successive presentations was reduced from 900 to 100 msec (Freyd & Finke, 1985). An increase in forward displacement was observed when the time interval was reduced, and the interpretation was that the increased velocity of the stimulus increased representational momentum, because momentum equals the product of mass and velocity. As was pointed out earlier, forward displacement and the effects of velocity with implied motion do not depend on eye movements. In contrast, the effects of velocity on forward displacement and forward displacement itself are absent with smooth motion during eye fixation (Kerzel, 2003b; Kerzel et al., 2001).

Internalized physics can explain neither the difference between smooth and implied motion nor the difference between fixation and pursuit, because the underlying physical properties (i.e., target velocity) are unchanged. Furthermore, the effects of velocity with implied motion may exemplify a fundamental problem associated with the idea of internalized physics in dynamic events. As is shown in Figure 2, the idea summarized in Hubbard's (2005) review is that properties of the stimulus are represented mentally after an initial perceptual analysis and that the represented properties of the stimulus influence the remembered target position at a late stage of processing. For instance, the velocity or the identity of an object (e.g., a fast-moving rocket or a stationary church) is represented mentally and influences the representation of the final target position. However, one may also put forth the alternative view that all the effects of the stimulus influence only motion perception and that the displacement of the final target position depends solely on the goodness of the perceived motion. For instance, the effect of velocity reported by Freyd and Finke (1985) may reflect the fact that apparent motion is best perceived at shorter intervals between successive presentations of the target (~100 msec) and degrades when the interval is prolonged (Graham, 1965; Neuhaus, 1930). In other words, target velocity and the goodness of apparent motion perception were completely confounded in Freyd and Finke (1985), so that improved goodness of apparent motion, and not increased speed, may have produced stronger forward displacement at high velocities (i.e., shorter intervals).

Similarly, in studies that have reported the effects of the typical motion associated with an object on memory displacement (larger displacement for a more dynamic object; Reed & Vinson, 1996), the effects may have been mediated by apparent motion perception. Nagai and Yagi (2001) demonstrated that this effect was due to the different shapes of objects: Pointed objects elicited larger forward displacement, regardless of the associated dynamics (but see Cooper & Munger, 1993; Vinson & Reed, 2002). The underlying source of the effect of pointedness may be that the perception of apparent motion is stronger when

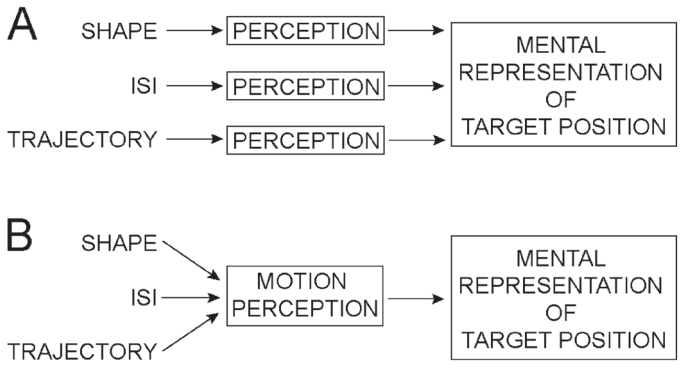

Figure 2. Two possible routes by which the effects of shape, interstimulus interval (ISI), and trajectory may influence the mental representation of target position. (A) In the classical conception, these attributes are perceived, and the representation of these attributes influences the mental representation of target position. (B) Alternatively, it may be that the three stimulus attributes exert an influence on motion perception and that motion perception determines the mental representation of target position. For instance, shortening the ISI of an implied motion stimulus may not influence the perceived velocity of the target but may influence the quality of the perceived apparent motion.

the object points in the direction of apparent motion than when the direction of the point and the direction of motion are in conflict (McBeath, Morikawa, & Kaiser, 1992). Similarly, the reduction of forward displacement observed when the shape of an object was changed in a sequence of apparent motion stimuli (Kelly & Freyd, 1987) may have been due to the reduced impression of apparent motion, rather than to higher level factors, such as object continuity.

Thus, for any manipulation for which a modulation of forward displacement with implied motion is reported, there is a risk that the effects were mediated—and potentially, caused—by effects on motion perception. Strong support for such an idea was provided in a study in which the step size between successive target presentations was manipulated, whereas target velocity was held constant (Kerzel, 2003c): When the spatiotemporal steps between successive target presentations were small and smooth motion resulted, forward displacement was absent. When the size of the spatiotemporal steps was increased and apparent motion resulted, forward displacement increased and was maximal with the implied motion used by Freyd. Because step size is related to motion perception (real vs. apparent motion), but not to any physical principle, the internalized physics approach has difficulty explaining this result. Rather, this result suggests that forward displacement occurs only with apparent motion. The reason may be that observers automatically extrapolate the next step in a sequence of target steps and that attention moves to this next step (Kerzel, 2003a). If an implied motion stimulus is presented, the next logical target step after target offset is large, so that observers will end up far beyond the true final position. This may result in a larger error than is shown when observers extrapolate a small step with smooth stimulus motion.

Support for this idea comes from a study showing that the ease of extrapolation and the size of the forward error are related: The more difficult it was to extrapolate the next step in an implied motion sequence, the smaller was the forward error (Munger & Minchew, 2002). It should also be noted that previous studies in which the error during an explicit extrapolation task has been looked at (Finke & Freyd, 1985; Finke & Shyi, 1988) are irrelevant for the above-mentioned hypothesis: When asked to extrapolate the next logical position in a sequence of implied motion, observers made an error opposite to the direction of motion (i.e., the extrapolated distance was too short). Because of the conflicting sign of the error in extrapolation and endpoint localization, it was concluded that two different processes were at work. However, my hypothesis has been that observers automatically extrapolate and that the (attentional) overshoot causes a bias in endpoint localization. The hypothesis is not that observers mistake the extrapolated position for the final target position. The confusion of the final target position and the extrapolated next position is highly unlikely, because the large separation between successive steps (typically about 2º) is easy to discriminate. Therefore, errors in motion extrapolation are completely irrelevant for endpoint localization, since the assumption is that observers' memory for the final target position is biased toward the extrapolated position, and not that they confound the two positions.

From a functional point of view, it may be that extrapolation with implied motion reflects the necessity to predict where an object that is temporarily hidden from view will reappear. For instance, prey in the forest may be temporarily hidden from view by trees or bushes. This results in apparent motion of the prey. To intercept the prey, the predator will have to move to positions beyond the presently available stimulation, so that being able to extrapolate the next position is an advantage, even if it results in erroneous localization of the last-seen position. In contrast, prey that is continuously visible and suddenly disappears

may "freeze," whereby it tries to visually fuse with the background. Therefore, it may be important to reliably estimate the final target position, rather than to extrapolate the next position with smoothly moving objects. In sum, the localization errors observed with perceptual measures may reflect different environmental constraints associated with these motion types.

Forward Displacement Depends on the Response Mode and Is Larger With Motor Responses

So far, I have examined effects of eye movements and motion type that clearly distinguish the effects observed in the paradigms developed by Freyd (e.g., Freyd & Finke, 1984) and Hubbard (e.g., Hubbard & Bharucha, 1988). One final difference between the two paradigms is the nature of the response mode: Freyd used symbolic judgments about what observers remembered, whereas Hubbard used mouse pointing to the final target position. In an influential neurophysiological theory, Goodale and Milner (1992) have claimed that visual information for perception is treated in a different cortical pathway than is visual information for action. This idea predicts differences between psychophysical methods that do not involve motor action, such as the method of constant stimuli, and methods that use motor responses, such as pointing or grasping.

Consistent with such a notion, Kerzel and Gegenfurtner (2003) found forward displacement of the final position of a smoothly moving target when observers had to point to the final target position, but not when the observers judged its position relative to a probe stimulus (for similar results, see Ashida, 2004). The latter condition replicates the results presented in the section on eye movements. Thus, the results obtained with Hubbard's paradigm confounded two different localization errors: one due to eye movement, and the other due to forward extrapolation in the motor system. This multitude of processes responsible for one and the same observable error pattern is difficult to explain from the point of view of internalized physics: Why should the motor system, the system for the perception of apparent motion, and the eye movement system have internalized physical principles, but not the system responsible for the perception of smooth motion? After all, smooth motion is the dominant motion type in the environment, given that each movement of the eyes or the head is accompanied by continuous motion.

It appears much more plausible that the isolatable sources of errors subserve different functions. Extrapolation with apparent motion may be helpful when obstacles block the view, and extrapolation in the motor system may overcome the problem of neuronal latencies. As has been pointed out by Nijhawan (1994), the visual system does not have access to real-time information about the environment. In order not to lag behind, which is particularly problematical with moving objects, the visual system has to compensate for neuronal processing delays. Nijhawan later suggested that neuronal delays are compensated for at an early stage: The perceived position of smoothly moving objects is extrapolated into the direction of motion at the perceptual level; that is, observers *see* the target ahead of the currently transmitted position (Nijhawan, 2002). This explains why a briefly flashed stationary object is seen to lag behind a moving object (Nijhawan, 1994) but fails to explain why there is no perceptual overshoot of the moving object at the end of the trajectory (Eagleman & Sejnowski, 2000; Nijhawan, 1992). In contrast to the early-compensation hypothesis, extrapolation in the motor system (Ashida, 2004; Kerzel, 2003c; Kerzel & Gegenfurtner, 2003) suggests that neuronal latencies may be compensated for at a late stage of visual processing: Observers may point or reach too far into the direction of motion in order not to be late, even if the position information available to conscious perception is not distorted.

Is Auditory Representational Momentum a Problem for the Current Account?

In two recent reports, it was observed that the final position of a smoothly moving auditory target was mislocalized in the direction of motion (Getzmann, 2005; Getzmann, Lewald, & Guski, 2004). One of these reports compared localization of the final position of an auditory target after observers pursued the target with their eyes and its localization during eye fixation (Getzmann, 2005). In contrast to the above-cited studies on the localization of visual targets, no difference between the smooth pursuit and the fixation condition emerged. Forward displacement was of equal magnitude, regardless of eye movement condition. However, a motor task was used to localize the auditory targets, which may explain why forward displacement was observed with fixation (see above). Otherwise, these results are in strong contrast to visual localization, where the forward error was found to disappear with eye fixation and smooth motion. The question is whether this supports the notion that higher level and, presumably, supramodal processes, such as representational momentum, are responsible for the forward error. In my view, the answer is no, because a supramodal process should produce the same error patterns in different modalities, but this is obviously not the case. Therefore, specialized and modality-dependent processes are much more likely to cause the forward error than is a unifying, high-level process at the cognitive level.

Concluding Remarks

In sum, recent research suggests that results obtained with smooth motion have to be reexamined, because the observed displacement pattern may reflect more than one process and partly low-level processes: the asynchronous processing of retinal and extraretinal information during smooth pursuit, or a tendency to extrapolate the next position of a moving object in the motor system. With implied motion, eye movements do not play a role, but the previously reported effects of interstimulus interval or object identity may be caused by the goodness of apparent motion, and not by a cognitive representation of stimulus characteristics. Taken together, more than one process of extrapolation exists, and future studies should try to neatly separate between these different processes. For instance, researchers should avoid measuring the effects of eye

movements and motor responses in an uncontrolled fashion, because the results cannot be attributed unequivocally to any of the processes involved. Nonetheless, future research may reveal that the different processes identified in this article may obey the same computational principles or feed into a common representation (see, e.g., Erlhagen & Jancke, 2004); however, it appears unlikely that physical principles will play a major role.

REFERENCES

Ashida, H. (2004). Action-specific extrapolation of target motion in human visual system. *Neuropsychologia*, **42**, 1515-1524.

Baldo, M. V., Kihara, A. H., Namba, J., & Klein, S. A. (2002). Evidence for an attentional component of the perceptual misalignment between moving and flashing stimuli. *Perception*, **31**, 17-30.

Brenner, E., Smeets, J. B. J., & van den Berg, A. V. (2001). Smooth eye movements and spatial localisation. *Vision Research*, **41**, 2253-2259.

Churchland, M. M., & Lisberger, S. G. (2000). Apparent motion produces multiple deficits in visually guided smooth pursuit eye movements of monkeys. *Journal of Neurophysiology*, **84**, 216-235.

Collewijn, H., & Tamminga, E. P. (1984). Human smooth and saccadic eye movements during voluntary pursuit of different target motions on different backgrounds. *Journal of Physiology*, **351**, 217-250.

Cooper, L. A., & Munger, M. P. (1993). Extrapolating and remembering positions along cognitive trajectories: Use and limitations of analogies to physical motion. In N. Eilan, R. A. McCarthy, & B. Brewer (Eds.), *Spatial representation: Problems in philosophy and psychology* (pp. 112-131). Oxford: Blackwell.

Eagleman, D. M., & Sejnowski, T. J. (2000). Motion integration and postdiction in visual awareness. *Science*, **287**, 2036-2038.

Erlhagen, W., & Jancke, D. (2004). The role of action plans and other cognitive factors in motion extrapolation: A modelling study. *Visual Cognition*, **11**, 315-340.

Finke, R. A., & Freyd, J. J. (1985). Transformations of visual memory induced by implied motions of pattern elements. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, **11**, 780-794.

Finke, R. A., & Shyi, G. C. (1988). Mental extrapolation and representational momentum for complex implied motions. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, **14**, 112-120.

Freyd, J. J., & Finke, R. A. (1984). Representational momentum. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, **10**, 126-132.

Freyd, J. J., & Finke, R. A. (1985). A velocity effect for representational momentum. *Bulletin of the Psychonomic Society*, **23**, 443-446.

Freyd, J. J., & Johnson, J. Q. (1987). Probing the time course of representational momentum. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, **13**, 259-268.

Getzmann, S. (2005). Representational momentum in spatial hearing does not depend on eye movements. *Experimental Brain Research*, **165**, 229-238.

Getzmann, S., Lewald, J., & Guski, R. (2004). Representational momentum in spatial hearing. *Perception*, **33**, 591-599.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, **15**, 20-25.

Graham, C. H. (1965). Perception of movement. In C. H. Graham (Ed.), *Vision and visual perception* (pp. 575-588). New York: Wiley.

Hazelhoff, F. F., & Wiersma, H. (1924). Die Wahrnehmungszeit: Erster Artikel. Die Bestimmung der Schnelligkeit der Wahrnehmung von Lichtreizen nach der Lokalisationsmethode [The time to perception: First article. The determination of the speed of perception of light stimuli with the localization method]. *Zeitschrift für Psychologie*, **96**, 171-188.

Hubbard, T. L. (1995). Cognitive representation of motion: Evidence for friction and gravity analogues. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, **21**, 241-254.

Hubbard, T. L. (1996). Representational momentum, centripetal force, and curvilinear impetus. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, **22**, 1049-1060.

Hubbard, T. L. (1997). Target size and displacement along the axis of implied gravitational attraction: Effects of implied weight and evidence of representational gravity. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, **23**, 1484-1493.

Hubbard, T. L. (1998). Some effects of representational friction, target size, and memory averaging on memory for vertically moving targets. *Canadian Journal of Experimental Psychology*, **52**, 44-49.

Hubbard, T. L. (2005). Representational momentum and related displacements in spatial memory: A review of the findings. *Psychonomic Bulletin & Review*, **12**, 822-851.

Hubbard, T. L., & Bharucha, J. J. (1988). Judged displacement in apparent vertical and horizontal motion. *Perception & Psychophysics*, **44**, 211-221.

Hubbard, T. L., & Ruppel, S. E. (1999). Representational momentum and the landmark attraction effect. *Canadian Journal of Experimental Psychology*, **53**, 242-256.

Jordan, J. S. (2000a). The role of "control" in an embodied cognition. *Philosophical Psychology*, **13**, 233-237.

Jordan, J. S. (2000b). The world in the organism: Living systems are knowledge. *Psycoloquy*, **11**(113).

Kelly, M. H., & Freyd, J. J. (1987). Explorations of representational momentum. *Cognitive Psychology*, **19**, 369-401.

Kerzel, D. (2000). Eye movements and visible persistence explain the mislocalization of the final position of a moving target. *Vision Research*, **40**, 3703-3715.

Kerzel, D. (2002a). The locus of "memory displacement" is at least partially perceptual: Effects of velocity, expectation, friction, memory averaging, and weight. *Perception & Psychophysics*, **64**, 680-692.

Kerzel, D. (2002b). Memory for the position of stationary objects: Disentangling foveal bias and memory averaging. *Vision Research*, **42**, 159-167.

Kerzel, D. (2003a). Attention maintains mental extrapolation of target position: Irrelevant distractors eliminate forward displacement after implied motion. *Cognition*, **88**, 109-131.

Kerzel, D. (2003b). Centripetal force draws the eyes, not memory for the target, toward the center. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, **29**, 458-466.

Kerzel, D. (2003c). Mental extrapolation of target position is strongest with weak motion signals and motor responses. *Vision Research*, **43**, 2623-2635.

Kerzel, D. (2005). Representational momentum beyond internalized physics: Embodied mechanisms of anticipation cause errors in visual short-term memory. *Current Directions in Psychological Science*, **14**, 180-184.

Kerzel, D., & Gegenfurtner, K. R. (2003). Neuronal processing delays are compensated in the sensorimotor branch of the visual system. *Current Biology*, **13**, 1975-1978.

Kerzel, D., Jordan, J. S., & Müsseler, J. (2001). The role of perception in the mislocalization of the final position of a moving target. *Journal of Experimental Psychology: Human Perception & Performance*, **27**, 829-840.

Krauzlis, R. J., & Stone, L. S. (1999). Tracking with the mind's eye. *Trends in Neurosciences*, **22**, 544-550.

McBeath, M. K., Morikawa, K., & Kaiser, M. K. (1992). Perceptual bias for forward-facing motion. *Psychological Science*, **3**, 362-367.

Metzger, W. (1932). Versuch einer gemeinsamen Theorie der Phänomene Fröhlichs und Hazelhoffs und Kritik ihrer Verfahren zur Messung der Empfindungszeit [An attempt at a common theory of Fröhlich's and Hazelhoff's phenomena and a critique of their procedure for measuring sensation time]. *Psychologische Forschung*, **16**, 176-200.

Mita, T., Hironaka, K., & Koike, I. (1959). The influence of retinal adaptation and location on the "Empfindungszeit." *Tohoku Journal of Experimental Medicine*, **52**, 397-405.

Mitrani, L., & Dimitrov, G. (1978). Pursuit eye movements of a disappearing moving target. *Vision Research*, **18**, 537-539.

Mitrani, L., & Dimitrov, G. (1982). Retinal location and visual localization during pursuit eye movement. *Vision Research*, **22**, 1047-1051.

Munger, M. P., & Minchew, J. H. (2002). Parallels between remembering and predicting an object's location. *Visual Cognition*, **9**, 177-194.

Nagai, M., & Yagi, A. (2001). The pointedness effect on representational momentum. *Memory & Cognition*, **29**, 91-99.

Neuhaus, W. (1930). Experimentelle Untersuchung der Scheinbewegung [Experimental investigations of apparent motion]. *Archiv für die gesamte Psychologie*, **775**, 315-458.
Nijhawan, R. (1992). Misalignment of contours through the interaction of apparent and real motion systems [Abstract]. *Investigative Ophthalmology & Visual Science*, **33**, 1415.
Nijhawan, R. (1994). Motion extrapolation in catching. *Nature*, **370**, 256-257.
Nijhawan, R. (2002). Neural delays, visual motion and the flash-lag effect. *Trends in Cognitive Sciences*, **6**, 387-393.
Reed, C. L., & Vinson, N. G. (1996). Conceptual effects on representational momentum. *Journal of Experimental Psychology: Human Perception & Performance*, **22**, 839-850.
Robinson, D. A., Gordon, J. L., & Gordon, S. E. (1986). A model of the smooth pursuit eye movement system. *Biological Cybernetics*, **55**, 43-57.
Rotman, G., Brenner, E., & Smeets, J. B. J. (2004). Mislocalization of targets flashed during smooth pursuit depends on the change in gaze direction after the flash. *Journal of Vision*, **4**, 564-574.
Schlag, J., & Schlag-Rey, M. (2002). Through the eye, slowly: Delays and localization errors in the visual system. *Nature Reviews Neuroscience*, **3**, 191-215.
Sheth, B. R., & Shimojo, S. (2001). Compression of space in visual memory. *Vision Research*, **41**, 329-341.
Stork, S., & Müsseler, J. (2004). Perceived locations and eye movements with action-generated and computer-generated vanishing points of moving stimuli. *Visual Cognition*, **11**, 299-314.
Stork, S., Neggers, S. F., & Müsseler, J. (2002). Intentionally-evoked modulations of smooth pursuit eye movements. *Human Movement Science*, **21**, 335-348.
Thornton, I. M., & Hubbard, T. L. (Eds.) (2002). *Representational momentum: New findings, new directions*. New York: Psychology Press/Taylor & Francis.
van Beers, R. J., Wolpert, D. M., & Haggard, P. (2001). Sensorimotor integration compensates for visual localization errors during smooth pursuit eye movements. *Journal of Neurophysiology*, **85**, 1914-1922.
Vinson, N. G., & Reed, C. L. (2002). Sources of object-specific effects in representational momentum. *Visual Cognition*, **9**, 41-65.
Whitney, D., & Cavanagh, P. (2002). Surrounding motion affects the perceived locations of moving stimuli. *Visual Cognition*, **9**, 139-152.
Whitney, D., Murakami, I., & Cavanagh, P. (2000). Illusory spatial offset of a flash relative to a moving stimulus is caused by differential latencies for moving and flashed stimuli. *Vision Research*, **40**, 137-149.

NOTES

1. In Hubbard's notion of internalization, physical principles or naive physics have become part of our cognitive architecture. The level of cognition is referred to as *high level*. This is different from the idea that the dynamics of our visual world have been incorporated into that architecture or our motor system, which is sometimes referred to as *embodied cognition* (Jordan, 2000a, 2000b). The errors incurred during smooth pursuit and pointing tasks may actually be considered a case of embodied cognition (Kerzel, 2005).

2. Effects of mass have been notoriously difficult to obtain with smooth (Hubbard, 1997) and implied (Cooper & Munger, 1993) motion. This has led researchers to abandon the literal metaphor of representational momentum. Rather, representational momentum and other internalized regularities may combine with other high-level factors, such as expectations. Also, the internalized regularities may not be physical laws but naive conceptions about the physical world (Hubbard, 2005).

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