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REVIEW | *Control of Movement*

Continuously updating one's predictions underlies successful interception

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Brenner E, Smeets JBJ. Continuously updating one's predictions underlies successful interception. *J Neurophysiol* 120: 3257–3274, 2018. First published October 31, 2018; doi:10.1152/jn.00517.2018.—This paper reviews our understanding of the interception of moving objects. Interception is a demanding task that requires both spatial and temporal precision. The required precision must be achieved on the basis of imprecise and sometimes biased sensory information. We argue that people make precise interceptive movements by continuously adjusting their movements. Initial estimates of how the movement should progress can be quite inaccurate. As the movement evolves, the estimate of how the rest of the movement should progress gradually becomes more reliable as prediction is replaced by sensory information about the progress of the movement. The improvement is particularly important when things do not progress as anticipated. Constantly adjusting one's estimate of how the movement should progress combines the opportunity to move in a way that one anticipates will best meet the task demands with correcting for any errors in such anticipation. The fact that the ongoing movement might have to be adjusted can be considered when determining how to move, and any systematic anticipation errors can be corrected on the basis of the outcome of earlier actions.

catching; hitting; human; motion; prediction

INTRODUCTION

We use the term "interception" to refer to any movement directed toward a moving object. This could be an attempt to catch the object, to hit or kick it away, or to prevent it from continuing on its path in some other manner. Generally, such movements are directed toward a position that the object will only reach some time in the future, which suggests that some form of explicit or implicit prediction of the object's motion is used. In the course of discussing the nature of these predictions, we will present evidence that continuous control of the ongoing movement is fundamental for goal-directed movements. We will subsequently discuss how interceptive movements are regulated to meet various task demands. We will illustrate how the trajectories and velocity profiles in relatively simple interceptive tasks can be explained from a perspective of relying on continuous control to optimize both precision and accuracy.

Studies on interceptive movements have predominantly used target objects that move in a predictable manner: at a constant velocity or accelerated by gravity. A few studies have used targets that move in unpredictable (Mrotek and Soechting 2007a) or somewhat counterintuitive (Dessing and Craig 2010) ways. In daily life, it is not unusual to encounter situations in which we cannot assume that we know how a target will move, such as when stopping an infant from walking onto a busy street. Thinking about such situations can reveal issues that might otherwise be overlooked. If the infant is walking with you and suddenly runs away, the direction in which you should move is obvious so you only need to regulate your speed. You must make sure that you can reach the infant before the infant reaches the street. You should probably consider that the infant might suddenly speed up. It is probably also better not to be moving too much faster than the infant when you reach the infant, to be sure not to frighten him or her or knock him or her over. If the infant is not walking with you but is going to cross your path, you need to regulate both your speed and your direction of motion. In that case you might consider getting between the infant and the street, rather than approaching the infant from behind or from the side. Such strategic aspects of human movements can be studied by examining how the circumstances influence the choices that people make, and by examining how imposed choices influence performance.

One can impose choices that people might not normally make by constraining the movements, for instance by fixing the movement path (Caljouw et al. 2004b; Marinovic et al. 2009; Tresilian and Houseman 2005; Tresilian and Lonergan 2002; Tresilian et al. 2003, 2009; Tresilian and Plooy 2006) or prescribing a certain interception point (Brenner and Smeets

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2011a, 2015b; Marinovic et al. 2009). Comparing performance when the movements are constrained with performance when the movements are not constrained provides the opportunity to systematically investigate why certain strategies are chosen (Brenner and Smeets 2015a). Similarly, much can be learned about the visual information that is used to catch a ball by varying the available information. Studies that have done so have shown how changing angular extent is combined with changing binocular disparity to regulate grip closure when catching (Caljouw et al. 2004a; Rushton and Wann 1999) and have shown how various sources of visual information guide other aspects of interception (Brenner et al. 2014; Tresilian 1999). Comparing studies with various constraints will help us determine how people normally intercept targets.

THE EVIDENCE FOR CONTINUOUS CONTROL

When manipulating static objects in daily life, people generally look at them shortly before reaching out for them (Hayhoe and Ballard 2005, 2014; Land 2006, 2009). They presumably do so to get the best possible information with which to guide the upcoming part of the action (Ballard and Hayhoe 2009; Land et al. 1999). They prefer to gather information immediately before each movement than to rely on memory (Hayhoe et al. 1998), although they do not disregard memory altogether (Brouwer and Knill 2009; Hayhoe et al. 1998, 2003; Hesse et al. 2008). Much of the literature on everyday tasks of the kind that one might encounter when making breakfast has focused on where people fixate at critical moments during the sequence of events (Hayhoe and Ballard 2014; Land 2006, 2009). The emphasis is often on when people switch their gaze between objects, but it is important to realize that people often do not just glimpse at the object of interest and look away, but keep looking at the object until just before the interaction with the object takes place (Land 2009). That it may be particularly important to keep looking at objects if they are moving is supported by the evidence that in games such as baseball, cricket, and tennis the best athletes are the ones who are best at keeping their eyes on the ball at critical moments (Bahill and LaRitz 1970; Lafont 2007; Land and McLeod 2000; Mann et al. 2013).

Making sure not to miss any visual information while an action is unfolding is only useful if such information can be used. We know that such information can be used, because even very fast goal-directed movements to static targets are not ballistic: they are executed less well if access to new information is limited. For instance, performance deteriorates if one cannot see one's hand (Carlton 1981; Elliot et al. 1991; Prablanc et al. 1979; Proteau and Cournoyer 1990) or a cursor guided by one's hand (Elliott et al. 1995) throughout the movement toward the target. Similarly, people sometimes encounter difficulties catching a ball if it is hidden from view for part of its trajectory (Dessing et al. 2009; Elliott et al. 1994; López-Moliner et al. 2010; Whiting and Sharp 1974). They are also less precise at hitting moving objects if the objects are hidden from view (Brenner et al. 2014; De Lucia and Cochran 1985), even if only very briefly (Brenner and Smeets 2011a). Thus, people try not to miss information during the action, and missing information makes them perform less well.

That people try not to miss any information while trying to intercept objects is illustrated by when people blink. People blink every few seconds to protect the surface of their cornea, but the timing of blinks is not arbitrary. It is linked to the flow of information (Drew 1951; Nakano and Kitazawa 2010; Oh et al. 2012). When analyzing the eye movements during interceptive actions, we noticed that there are very few blinks while the hand is moving toward a target that one is trying to intercept. Once participants initiated a trial, their blink rate decreased in anticipation of the target appearing (Fig. 1). After the target appeared, the probability of a blink continued to decline, with blinks being almost completely suppressed during the hand movement. Thus, participants made sure not to miss information that they could use to guide the hand to the target. They even appeared to suppress blinks until they had seen whether and how they hit the target, because the number of blinks only increased ~200 ms after such feedback was provided. After that, the probability of blinking increased very rapidly. Suppressing blinks until after feedback has been acquired is consistent with the findings of an extensive study of blinking while watching a film, where it was shown that blinks are timed to minimize the chance of missing critical information (Nakano et al. 2009).

Acquiring new information is disrupted not only by blinks, but also by saccades. One might therefore expect saccades also to be suppressed during interception. Indeed, when participants had to intercept targets that moved along paths that curved in ways that made them difficult to pursue, the eyes followed the target with a combination of smooth pursuit and corrective saccades until the interceptive movement started, but the corrective saccades were suppressed during the actual interceptive movement (Mrotek and Soechting 2007a).

HOW MOVEMENTS ARE CONTROLLED CONTINUOUSLY

That visual information acquired during a movement is used to adjust the ongoing movement is revealed by studies in which the circumstances change. Movements toward static targets are adjusted when the target is unexpectedly displaced (Paulignan et al. 1991), even if the displacement is irrelevant (Voudouris

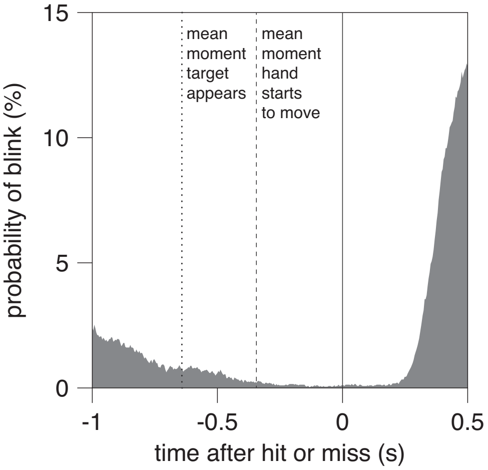

Fig. 1. The percentage of trials during which the eyes were closed as a function of the time relative to the moment the hand passed the target's path (vertical line at zero). The dotted and dashed lines show the average times at which the target appeared and the hand started moving, respectively. People refrain from blinking around the moment of interception, thus at times at which acquiring information may be particularly beneficial. Data from Experiment 1 of the interception task described in Brenner and Smeets (2011a).

et al. Brenner 2013) or is not noticed by the participant (Goodale et al. 1986; Prablanc and Martin 1992). That the displacement does not have to be detected for corrections to be made shows that the adjustments are manifestations of a mechanism that continuously updates the estimate of the target location and guides the movement to that location (Brenner and Smeets 2017; Smeets et al. 2016). The latency of the adjustment depends on how much time it takes to process the relevant sensory information and thus on the properties of the target (Veerman et al. 2008). The magnitude of the adjustment depends on the urgency of the response (how close the hand is to the target; Liu and Todorov 2007; Oostwoud Wijdenes et al. 2011).

Besides continuously using visual information to update the estimated position of the target when the external circumstances change, people also adjust movements on the basis of new visual information about the position of their moving hand. This can be a cursor indicating the position of the hand (Franklin and Wolpert 2008; Franklin et al. 2012; Sarlegna et al. 2003; Saunders and Knill 2003, 2005). It is even effective if the cursor is considerably delayed (de la Malla et al. 2012, 2014) or at an arbitrary position with respect to the hand (Brenner and Smeets 2003, 2006). People also respond to unanticipated changes in obstacles' positions (Aivar et al. 2008, 2015). Moreover, people do not only adjust their movements to changes in position. They also readily adjust their movements to changes in other attributes such speed (Brenner et al. 1998), orientation (Desmurget et al. 1996; Brenner and Smeets 2009a; Voudouris et al. 2013), and shape (Eloka and Franz 2011).

Thus, it is evident that movements are continuously adjusted on the basis of the latest information. This is not only true for arm movements, because stepping movements are also adjusted very quickly, despite the potential risk of losing balance by doing so (Hoogkamer et al. 2015; Reynolds and Day 2005). Continuous control is most obviously useful when the circumstances change unpredictably, and especially for movements that take a long time. Unpredictable changes are not unusual in daily life, especially when interacting with other people or animals. However, the benefits of continuous control extend beyond being able to deal with unexpected changes in the environment. Even when the circumstances do not change, new options may be revealed as one's head or eyes move. More importantly, feedback about one's own ongoing movement may reveal that one initially activated one's muscles inappropriately for reaching a target. This must occur, at least to some extent, because our sensory and motor systems are not perfect. Moreover, the precision with which we can judge an object's position and motion is limited (Brenner and Smeets 2018), as is the precision with which we can execute a desired movement (e.g., Fitts 1954; Harris and Wolpert 1998). As the movement progresses, impending errors as a result of such sensorimotor imperfections will gradually be revealed. Constantly using the latest information about how the movement is progressing as well as about all relevant objects to guide one's movement could help reduce such errors. There is an abundance of evidence that movements are continuously adjusted, including evidence from interception studies in which virtual balls' trajectories unexpectedly change (Fink et al. 2009).

HOW MUCH OF AN INTERCEPTIVE MOVEMENT IS PLANNED IN ADVANCE?

Numerous attempts have been made to account for interceptive movements on the basis of continuous control alone, without any anticipation or planning (Chapman 1968; Lee 1998; Lee et al. 1999, 2001a; Shaffer et al. 2008; Smith et al. 2014; Zhao and Warren 2015). People could make sure to be at the right place when trying to catch balls that follow a high parabolic path (fly balls) by adjusting their running trajectories to how the visual information changes as a result of the combination of them running and the gravitational acceleration of the ball (Brouwer et al. 2002; Chapman 1968; McBeath et al. 1995; McLeod et al. 2006; Michaels and Oudejans 1992; Postma et al. 2014). They could make sure to close their grip at the right moment by relating their grip to the ratio between angular extent and the rate of change of angular extent (the optical variable tau), which specifies the time to contact for an object approaching the vantage point at a constant velocity (Chieffi et al. 1992; López-Moliner et al. 2010; van de Kamp et al. 2012; Savelsbergh et al. 1991). By attributing the kinematics of interceptive movements to task-dependent "couplings" between instantaneous sensory input and motor output, various authors have been able to reproduce selected regularities of interceptive movements. For stopping the infant from walking onto the street this could involve moving in a manner that keeps the bearing angle with respect to the infant constant as one runs toward it by adjusting one's running speed (Cutting et al. 1995) or adjusting the direction in which one runs (Diaz et al. 2009). An attractive feature of strategies that do not require any planning is that they are based exclusively on continuous control and therefore automatically adjust to changes in the environment, such as any changes in the infant's actions or a flying ball not moving as initially anticipated because it is spinning or there is a lot of wind (Craig et al. 2011; Dessing and Craig 2010).

One finding that has been considered to support the idea that actions are coupled to sensory information rather than arising from predictions of how one can best move is the apparently superfluous movement of the hand when trying to catch a target that is moving toward the hand from the onset (Montagne et al. 1999). Participants had to intercept a target that approached them at a constant velocity. Their hand could only move laterally. In a subset of the conditions, the targets were moving toward the initial position of the hand, so there was no need to move the hand. Nevertheless, the hand moved. Depending on the direction from which the target was approaching, the hand gradually moved laterally, in the direction of the target, and then returned to its initial position (Fig. 2).

Although later studies question the generality of the findings of Montagne et al. (1999) (Arzamarski et al. 2007; Dessing et al. 2005), we will use them to illustrate that there are various ways to interpret superfluous movements of the kind that are shown in Fig. 2. Following earlier reasoning by Peper et al. (1994), Montagne et al. (1999) concluded that the hand's movement is coupled to the target in a way that gives rise to the superfluous initial movements. One might alternatively be tempted to interpret the superfluous initial movements as an error in prediction instead, because systematically misjudging how a target will move in the future can give rise to errors at motion onset that are corrected later during the movement

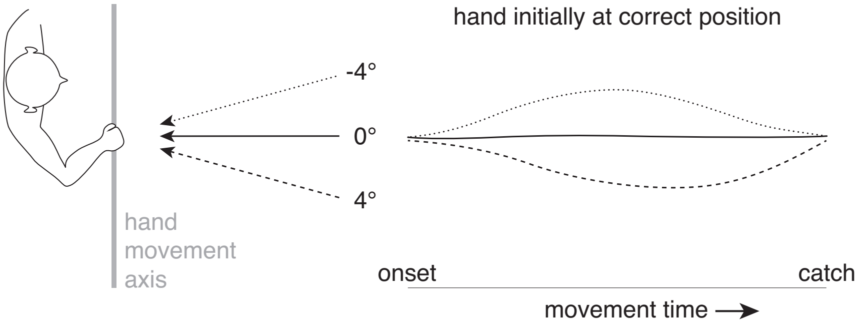

Fig. 2. When intercepting targets that are moving toward the hand from the onset, the hand sometimes moves away from its initial position and then returns (selected conditions from Montagne et al. 1999). *Left*: setup with the three target trajectories. *Right*: lateral position of the hand as a function of time.

(Arzamarski et al. 2007). People certainly make many kinds of systematic perceptual errors, as will become apparent when we discuss dealing with acceleration. However, apparently superfluous lateral movements of the kind shown in Fig. 2 are also found when the trajectories are tailored to avoid visual errors in anticipating the interception position (Ledouit et al. 2013). Another possibility is that the initial error arises from people partly relying on motion information from the previous trial (de Lussanet et al. 2001). A fundamentally different possibility is that the lateral movements are not superfluous at all. Before discussing the possibility that the lateral movements are intentional, we will briefly discuss two reasons to question whether interception could be controlled without making any predictions.

The first reason is that the coupling that is proposed in most prediction-free models of interception is instantaneous, which obviously cannot be true. In some of the successful examples of models of interception that avoid predicting the interception point, such as running to catch fly balls, where performance is evaluated across several seconds, the delay might not be a problem (Kistemaker et al. 2009), but for batting a ball, with movement times of as little as 240 ms (Brenner et al. 2014), a sensorimotor delay of at least 100 ms (Brenner and Smeets 1997) cannot be ignored. The inevitability of delays implies that one must make some kind of prediction. If one were to simply ignore the delay one would always be too late. The prediction might only compensate for the neuromuscular delays (Nijhawan 1994; Rotman et al. 2005), rather than considering how the whole motion will proceed. It does not need to be very precise, because even a prediction that is not very precise is better than none at all. However, considering the incredible temporal precision with which people can perform interceptive actions (a standard deviation of ~7 ms: Brenner et al. 2012; Brenner and Smeets 2015a; McLeod and Jenkins 1991), the prediction cannot be very imprecise.

The second reason to question whether prediction-free coupling between sensory input and motor output is the underlying principle of interception is that not predicting how a movement will progress will necessarily make one neglect potentially useful options. For instance, without predicting the outcome of the movement, it is not clear how one could tell whether it is worth trying to catch a ball or worth trying to run to prevent an infant from running onto the street. Neither is it clear how one could tell how best to circumvent obstacles. Making predictions allows you to optimize the aspects of the movement that are most relevant for the action. In interception, this is likely to be end point accuracy (Harris and Wolpert 1998), although in some circumstances the velocity with which you hit the target may be important too. For dancing, the trajectory may be more important than the end point. One may want to move smoothly (Flash and Hogan 1985) or to minimize energy expenditure.

Although some authors have portrayed prediction and continuous control as alternatives (Zhao and Warren 2017), there is no reason to dismiss the option that people combine the best of both approaches by making predictions that they continuously update (Brenner and Smeets 2017). Even if an initial prediction is quite inaccurate, it can be very useful because initially moving in about the correct direction makes it easier to adjust the movement as the prediction improves during the course of the movement. In the next sections we will illustrate how considering the whole movement might allow people to choose the best trajectory for intercepting the target. Besides planning the trajectory, one might also plan the extent to which one should allow the movement to be guided by new information at each moment (Todorov 2004). This may be necessary to ensure that corrections in response to changing task demands and to deviations from the planned trajectory are adequate (Dimitriou et al. 2013; Franklin and Wolpert 2011; Keyser et al. 2017; Liu and Todorov 2007; Scott 2012, 2016).

HOW INTERCEPTIVE MOVEMENTS ARE ADJUSTED TO THE TASK DEMANDS

In daily life people have to deal with a large variety of task demands besides reaching targets. For instance, returning to the example of the infant running toward the street, one must obviously reach the infant before the infant reaches the street. Football players usually do not only want to make sure that their foot touches the ball, but also that the kick propels the ball to their teammate or into the goal. When reaching out to grasp a pen that someone is giving you, your fingers need to reach appropriate positions precisely and at the right time, and not to hit other objects such as the other person's hand. In such cases one must consider the task demands, but also one's own limitations. One must ensure that one does not at some time need to move or accelerate faster than one is actually capable of, or more precisely. To what extent are all these issues considered when planning and controlling interceptive movements?

It is evident that to plan a movement that one can actually execute, one must consider one's limitations in terms of movement speed and acceleration. It is also evident that specified additional task demands have to be considered when planning interceptive movements. For instance, if the task is not to hit a target, but to accelerate it in a certain direction (Fig. 3*A*, Brenner and Smeets 2009b), people obviously approach the target accordingly, irrespective of how doing so might reduce the chance of hitting the target. They do so because they want

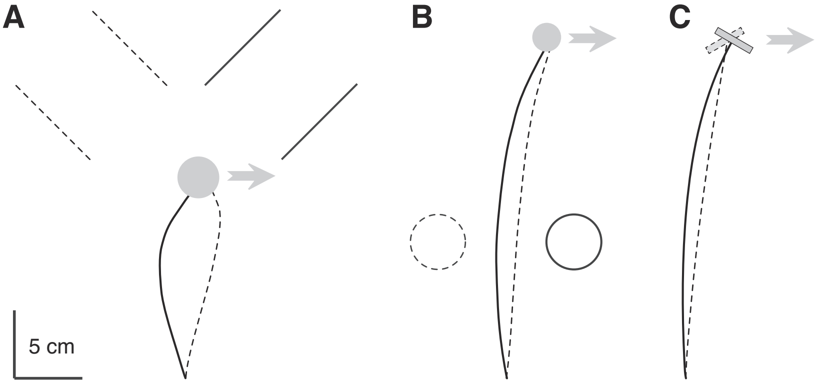

Fig. 3. How additional task demands affect the curvature of interceptive movements. The gray disk or bar is the target. It is moving to the right. The solid and dashed curves are average trajectories across participants for selected conditions when the task was to hit the target between two lines that were placed as indicated (*A*; Brenner and Smeets 2009b), when obstacles were present at the positions indicated by the circles with the same line style (*B*; Brenner and Smeets 2007), and when the target was oriented as indicated by the line style of the outline of the bar (*C*; Brenner and Smeets 2007). Participants followed a curved path to hit the target in a certain direction (*A*), to decrease the chance of colliding with the obstacle (*B*), or to increase the chance of hitting the target (*C*).

to achieve the actual goal of accelerating the target in a specific manner, rather than only managing to hit the target at all (Brenner and Smeets 2009b; Caljouw et al. 2004b). It is slightly less obvious that it is also beneficial to consider limitations in sensory and motor precision, but there are some simple examples that show that it is. After presenting two simple examples of this we will turn to more elaborate considerations.

The first example is that trajectories toward moving targets veer away from obstacles (Brenner and Smeets 2007). In Fig. 3*B*, the two mean paths are clearly different. The point at which the target is hit does not differ for the two obstacle positions, so the difference in curvature does not arise from selecting to hit the target at different positions. The mean paths presumably curve to maintain a safe distance from the obstacle to ensure that even movements that deviate to some extent from the intended path will not hit the obstacle. In the study from which these data were taken (Brenner and Smeets 2007) participants only hit the obstacles on 2 of the 1,350 trials.

The second example is that the trajectory toward a moving elongated target depends on the target's orientation (Brenner and Smeets 2007; Fig. 3*C*). Presumably the different paths were chosen because approaching the target orthogonally to its longest extent increases the likelihood of hitting the target even if one makes small judgment or movement errors. The likelihood is increased for purely geometric reasons (Smeets and Brenner 1999). That the approach is not completely orthogonal to the longest extent is probably because doing so would require moving along a longer, more curved path, which would introduce additional variability (Brenner and Smeets 2007).

Since moving in a certain way can be advantageous in a certain respect but disadvantageous in another respect, one might wonder whether people always move in the way that optimizes task performance considering all constraints. Unfortunately, determining the optimal trajectory can be a challenge for the investigator, and it is not evident that the person doing the movement can have access to all the relevant parameters. That is why some of the more successful attempts to show that people perform optimally use specially designed tasks in which the investigator can judge the optimal performance and the participants can figure out the relevant parameters. Faisal and Wolpert (2009) did so by limiting continuous control. They conducted an interception study in which the target disappeared as soon as the participant started to move. They then separately determined how precisely the target's motion could be extrapolated if it disappeared at various moments and how precisely the movement could be made within various amounts of time. They combined the two to see whether people started moving near the optimal time in the original interception study. They found performance that was close to optimal.

Does such a finding of near-optimal performance imply that we know our variability when planning a movement? An elegantly simple study in which near-optimal performance has been found is a hitting task with explicit, sometimes overlapping, target and penalty regions (Trommershäuser et al. 2003, 2008). The movement end points suggested that participants knew their movement variability and used this knowledge to determine the optimal position to aim for given the gains and losses. For that case, we have demonstrated that simple responses to feedback could give the kind of near-optimal performance that is observed (Brenner and Smeets 2011b). Here, we will therefore not try to argue that performance in interception is optimal, or how optimality could be achieved, but will only try to explain differences between the movement paths under various circumstances by how selecting certain paths could increase precision. We hope hereby to illustrate some of the more complicated considerations that arise under natural circumstances.

One example of how following a curved path could be beneficial is that it might be advantageous to move along with the target as one comes close to it (Brenner and Smeets 2005, 2015a). The reasoning is that moving along with the target as it approaches the hand reduces the relative motion between the hand and the target. This might decrease spatial judgment errors as well as decreasing the error that one makes if one gets the timing wrong. There are many reasons why the timing is unlikely to be perfect, including misjudging the target's motion, but also misjudging the distance to the target and any imperfections in motor planning or execution. The extent to which a timing error makes one hit the wrong part of the target, or even miss it altogether, depends on how far the target moves relative to the hand within this time. It therefore depends on the relative motion. In the extreme, when the hand moves along with the target so that there is no relative lateral motion, misjudging the moment at which the target will cross the hand's path has no influence on the error. Thus, following a curved path need not indicate that one initially made an incorrect judgment but could serve a purpose: initially moving in the "wrong" direction to enable one to later move back and therefore perform better in the face of sensory and motor uncertainty. This presupposes that the final approach is already considered when starting to move.

ACCELERATION

There is evidence that we neglect the acceleration of a falling ball when jumping to intercept it (Lee et al. 1983). The idea that acceleration is ignored raises issues that could shed some light on how strategic decisions and continuous control are combined. We will illustrate this with the results of an experiment in which we examined how precisely people could tap on interleaved accelerating and decelerating targets (Brenner and Smeets 2015a). We adjusted the targets' initial velocities to their accelerations so that the targets could appear at a fixed position and would be at about the same place by the anticipated time of the tap (Fig. 4*B*; participants tapped slightly later than we had anticipated). Thus, the target's starting point was the same, and its mean velocity and the end point of the interception movement were about the same, for all values of acceleration. Targets always moved to the right. If participants had only been interested in reaching the correct position, and had correctly considered the velocity and acceleration, we would expect them to move straight toward a single interception point within a fixed time, irrespective of the acceleration. This is clearly not what they do (Fig. 4*A*). We see that the trajectories start in different directions and that the trajectories are far from straight, all ending with rightward motion. What determines the shapes of the trajectories?

If acceleration is neglected, an obvious contribution to the differences between the trajectories is the target's position when the hand starts to move. The hand started to move ~300 ms after the targets appeared. At that moment, all targets were moving at about the same speed, but accelerating targets had moved less far to the right than decelerating ones (Fig. 4*B*). If people base their predictions about where they can hit the target on the target's speed and position, one expects movements to initially be directed further to the right for decelerating targets in this study (thin curves in Fig. 4*A*) simply because such targets are further to the right as a result of having moved faster until then. The fingers' paths later converge due to continuous updating on the basis of the latest estimate of the target's position and velocity. However, continuously adjusting the movement to the latest estimates of the target's position and velocity cannot explain the conspicuous rightward movements toward the ends of the paths in Fig. 4. Moreover, largely ignoring the acceleration would result in systematic errors because the latest estimate of the target's position and velocity that can be used to update the movement is necessarily made some time before the tap, so acceleration during the remaining time will be ignored.

It might seem strange to consider so many factors but to ignore acceleration, so we will next discuss the evidence that acceleration is really ignored, because maybe the differences between the early parts of the paths for the various target accelerations in Fig. 4*A* have some other origin than misjudging how the target will move. The fact that the paths toward decelerating targets (thin lines) initially moved too far to the right, curving leftward when about halfway and then rightward again, suggests that something was initially misjudged, but it need not be that the acceleration was ignored and there is always the possibility that there is some other reason for moving in this way.

The initial reason to suspect that acceleration might be ignored is that people are very poor at visually judging acceleration, probably actually relying on detecting that the velocity is different at different moments rather than actually judging the acceleration (Brouwer et al. 2002; Calderone and Kaiser 1989; Gottsdanker et al. 1961; Werkhoven et al. 1992). Judging acceleration from changes in velocity might be very imprecise, but does interception improve by ignoring the unreliable acceleration altogether? One difference between ignoring acceleration and using an unreliable estimate of acceleration is that ignoring acceleration will give rise to the same error on repeated attempts under identical circumstances, whereas using an unreliable estimate will give rise to different errors on different movements. If one knows the circumstances, it might be better to use a reasonable value of acceleration for those circumstances, rather than simply ignoring acceleration or using a very unreliable instantaneous visual estimate. We will first review the evidence for ignoring the visually perceived acceleration and then turn to the possible use of reasonable, nonzero acceleration values for the prevailing circumstances, in particular assuming gravitational acceleration for objects flying through the air.

SYSTEMATIC EFFECTS OF IGNORING ACCELERATION

The data in Fig. 4 are from a study in which different rates of acceleration were presented in random order (Brenner and

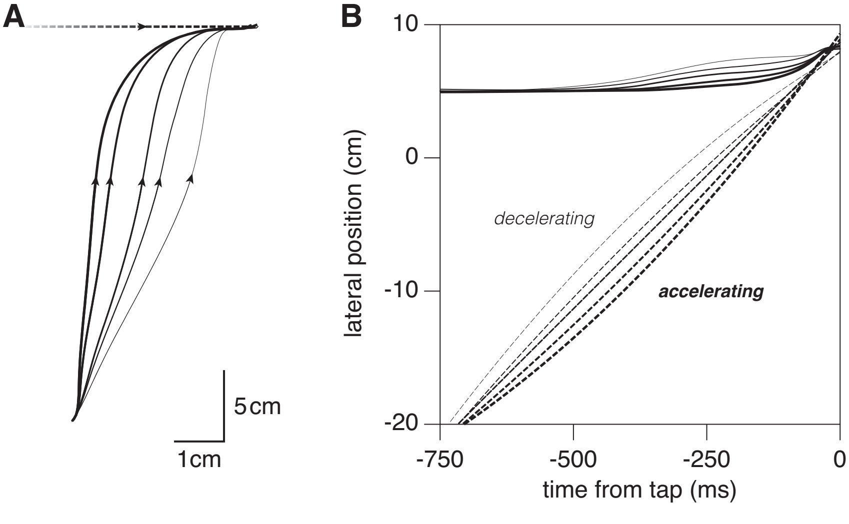

Fig. 4. Influence of target acceleration on path curvature when trying to tap on moving targets. *A*: average finger paths parallel to the screen (solid lines) and target path (dashed line). Participants started each trial by placing their finger at an indicated starting position, 25 cm below the target's path. When the target appeared, they lifted their finger and tried to tap on the target. *B*: lateral positions of target and finger (zero is the screen center) as a function of the time before the tap. The targets either moved to the right at a constant velocity of 40 cm/s or accelerated or decelerated at 20 or 40 cm/s^2. The targets' initial velocities differed so that all targets would have traveled the same distance after 625 ms. For details of the experiment, see Brenner and Smeets (2015a). The data shown here are from session 4 of that paper.

Smeets 2015a). If it is true that the acceleration is ignored, the initial differences between the paths in Fig. 4*A* should reflect the error in predicting the end points at that moment as a result of ignoring the acceleration. Averaging the displacements that were made during the first 100 ms after the average reaction time (between 300 and 400 ms after the target appeared) across all participants and trials with the same value of acceleration provides an estimate of the initial direction of motion for each acceleration. With respect to targets moving at a constant velocity, the directions deviated by −4.1, −2.7, 0.9, and 3.4° for targets accelerating at 40, 20, −20, and −40 cm/s, respectively. Rough estimates of what we would predict at motion onset if acceleration were ignored are −4.9, −2.5, 2.5, and 4.9° for the same accelerations, assuming that the movement during this time is determined by the target's position and velocity after 300 ms. Given that these values are all rough approximations, the correspondence suggests that acceleration is indeed totally neglected.

Later during the movement, errors due to ignoring the acceleration are gradually corrected by the position and velocity of the target constantly being updated (Benguigui and Bennett 2010; Benguigui et al. 2003; Brenner and Smeets 2015a; Lee et al. 1983; Senot et al. 2003; Soechting et al. 2009). The final error therefore only reflects the displacement due to the acceleration during the last 100 ms or so of the movement in which one can no longer respond to new visual information about the target's position (Brenner and Smeets 2015a). The findings from studies in which different rates of acceleration were presented in random order are consistent with constantly relying on instantaneous judgments of position and velocity rather than relying on an unreliable judgment of acceleration. However, it is not always that simple because various regularities can be used to improve performance if the circumstances allow them to.

The total neglect of acceleration that we found in the experiment portrayed in Fig. 4 is only observed under specific circumstances. If the same acceleration is repeated, people quickly adjust their behavior to the errors that they observe (Brenner et al. 2016; Fialho and Tresilian 2017; Gray 2009; Mrotek and Soechting 2007b). We know that the adjustment is a response to the feedback rather than to repeated exposure to the same acceleration, because just watching the target accelerate without trying to intercept it does not help remove such errors (Brenner et al. 2016). That people might rely on feedback to improve their performance rather than on gradually acquiring knowledge about the circumstances is also consistent with batters needing several attempts at hitting a ball to adjusting their swing to a heavier or lighter bat, even if they are allowed to perform a similar number of practice swings with the bat (but no ball) when given the heavier or lighter bat (Scott and Gray 2010). Learning to deal with a consistent acceleration may therefore be no different than learning to deal with a new tool (Scott and Gray 2010), a consistent delay (de la Malla et al. 2012), or a consistent visuoproprioceptive mismatch (Smeets et al. 2006; van der Kooij et al. 2013).

Movements that appear to unfold suboptimally because acceleration is ignored have also been found for goalkeepers attempting to stop an approaching ball that accelerates laterally (Dessing and Craig 2010). People also fail to anticipate the consequence of a constant acceleration orthogonal to a target's motion direction in the frontal plane (ones following a curved path; Reid and Dessing 2018a; Soechting and Flanders 2008). These studies involved rather unusual accelerations and expected participants to realize that the acceleration would remain constant. In some everyday circumstances one could rely on experience to anticipate the acceleration rather than trying to judge it visually. There is ample evidence that people combine sensory information with prior experience when making all sorts of judgments (Mamassian and Goutcher 2001; Stocker and Simoncelli 2006; van Beers et al. 2011). One might therefore expect people to readily learn to associate certain circumstances with certain accelerations. Alternatively, they might learn to move slightly differently under different circumstances to compensate for reproducible errors that would otherwise arise by ignoring acceleration. However, presenting different background images for different interleaved deceleration values did not help people deal with the different decelerations, even when participants were fully aware of the association between the image and the deceleration (Brenner et al. 2016). Possibly, associating a certain environment with a certain acceleration requires prolonged experience. The acceleration we are most experienced with is gravity.

IS GRAVITY A SPECIAL CASE?

When objects are falling, one could assume that they are accelerating at slightly less than 9.8 m/s^2 due to gravity, even if one cannot actually judge the acceleration visually. Some such assumption must be made, because people can catch a ball even when it is hidden from view for most of its path, although they obviously do better when they can see the ball (Lacquaniti and Maioli 1989; La Scaleia et al. 2015; Zago et al. 2004). They can even catch a ball that they have only seen moving upward, in which case they anticipate that it will come back down for them to catch (López-Moliner et al. 2010). There is ample evidence that people consider that falling objects will be accelerated by gravity (reviewed in Jörges and López-Moliner 2017; Zago et al. 2009). Astronauts even appear to anticipate the effects of gravity when gravity is absent (McIntyre et al. 2001), although vestibular signals also appear to contribute to objects' anticipated motion (Senot et al. 2012).

It is easy to manipulate the gravitational acceleration in virtual environments. When asked to intercept virtual targets that moved upward or downward (Senot et al. 2005), participants performed best when the targets moved at a constant velocity but performed better when targets approaching from below decelerated than when they accelerated, whereas they performed better when targets approaching from above accelerated rather than decelerated. Thus, they performed best when there was no acceleration, but when there was a nonzero acceleration they performed better when the acceleration was consistent with gravity than when it was not. In that study all the different possibilities were interleaved. When trying to hit simulated balls that were flying toward them, rather than only moving upward or downward, people hit in a manner that suggests that they expected the balls to be accelerated downward by gravity, even when no gravitational acceleration was present (Russo et al. 2017).

As already mentioned, people do not have to constantly see falling targets to intercept them. They can account for gravitational acceleration that takes place while the target is hidden from view (Katsumata and Russell 2012), so they cannot only be responding to the changing position and velocity. When asked to press a button when they thought that a briefly occluded descending virtual target reached an indicated position (Zago et al. 2010), people made smaller systematic errors for targets that accelerated in accordance with gravity than for targets that decelerated at the same rate, and even than for targets that moved at a constant velocity. When the target was not occluded they usually made the smallest systematic errors when the targets moved at a constant velocity. In both cases, the way in which different kinds of acceleration were interleaved clearly made a difference, so the assumed acceleration depends not only on lifelong experience with gravity, but also on recent experience (Brenner et al. 2016).

One might think that lifelong experience makes people know the exact acceleration due to gravity, but their estimate cannot be very precise because real objects accelerate differently since drag differs considerably between objects as it depends on many factors (Baurès et al. 2007). Thus, although one can evidently estimate how a falling object will accelerate in the near future more reliably than one can how an infant running toward a street will proceed, in both cases it could be advantageous to continuously update one's predictions. That continuous control can and does help deal with acceleration by gravity is illustrated by the results of an unpublished study in which ten participants were asked to hit falling tennis balls and foam balls with a bat (using the same methods as in Brenner et al. 2012, 2014). The two types of balls accelerated at different rates due to air resistance. For each type of ball, we used the time they took to reach the height at which they were hit to determine the deceleration due to drag using a simplified equation for falling in the presence of drag (acceleration = $g - c\, v^2$). Using the calculated values of c we could estimate the balls' positions and velocities at every moment, so we could determine the error that would be made by ignoring differences in acceleration.

When the participants hit tennis balls and foam balls in separate blocks of trials, their timing with respect to the ball was similar for both kinds of balls. When the balls were interleaved, there was a 2.2-ms time difference between the mean error when hitting tennis balls and foam balls, which corresponds to ignoring the difference in acceleration for 147 ms (the difference between the mean errors may sound negligible, but the mean standard deviation in individual participants' timing errors was only 7.4 ms). Presumably they anticipated some gravitational acceleration on the basis of years of experience (Jörges and López-Moliner 2017; Zago et al. 2009) but also adjusted their anticipation on the basis of the instantaneous information (limiting the impact of drag) and on the basis of feedback from recent trials (removing the influence of drag altogether when repeatedly presented with the same kind of ball). Thus, although gravitational acceleration is probably special in that one anticipates that even static unsupported objects will accelerate downward, we see no reason to assume that completely different mechanisms are involved in dealing with gravity than in dealing with other kinds of acceleration.

THE FINAL APPROACH OF THE TARGET

We have observed that the hand tends to move along with the target near the moment of contact. A clear example is the movement to the right just before the tap that is shown in Fig. 4. Moving along with the target just before the tap could be the result of not predicting where the target will be hit but coupling the movement of the hand to the instantaneous position and motion of the target in such a way that the hand systematically lags behind the target. It could also result from participants systematically underestimating the target's velocity or the remaining time until the tap. However, it seems strange that such systematic errors would not be corrected across multiple trials. Moreover, such explanations cannot account for the movements toward the most strongly decelerating targets (thinnest curve in Fig. 4). For such targets the finger appears to start almost in the correct direction and then to make a superfluous correction to the left when it is about halfway to the target. Our interpretation of such observations is that the final curvature is intentional (Brenner and Smeets 2005, 2015a).

The task in the study of which the data are shown in Fig. 4 was simply to tap on the target, so the direction in which the hand was moving at the time of the tap may seem to be irrelevant. However, this is not necessarily true, as we explained briefly when discussing curvature in movement paths. Any error that one makes in timing the moment at which one taps gives rise to a spatial error. The magnitude of the error increases with the target's speed because the target moves further or less far in the same time if it is moving faster. Moving along with the target can reduce the spatial error that arises from a given temporal error in judging the time of the tap, as might happen if one misjudges the distance to the screen, because as the target moves further or less far in the misjudged time, so does the hand. In the extreme case of the hand following the target perfectly just before the tap, misjudging when the tap will take place is irrelevant. Timing errors might also be reduced when following the target with one's hand because one can better judge the relative positions of target and hand when their relative motion is reduced. Of course, one can only move along with the target near the moment of contact if one has anticipated that it would be beneficial to move along with the target early in the movement, because one must initially move accordingly. Moreover, it need not always be beneficial to follow a clearly curved path, because moving along a curved path is likely to decrease precision (see Fig. 5), so the best performance is presumably usually achieved when the hand is not moving quite as fast as the target at the moment of the tap.

The advantage of intentionally moving in a certain way near the moment of contact may be even more intuitive in one-handed catching. To catch a ball, grip must close late enough to let the ball reach the palm of the hand, but not so late that the ball will have bounced out of the hand. Moving one's hand ahead of the ball, along its path, near the moment of contact will increase the time available for closing one's grip, because the relative speed between hand and ball is reduced. Moving along with the ball also decreases the force at impact, making catching less painful. It is therefore somewhat surprising that not all catchers do this (Cesqui et al. 2012). Maybe the additional displacement that is needed to be able to move along with the ball when catching it sometimes does not make it worthwhile. Or maybe timing is not the problem when moving along the ball's path, perhaps because impact with the ball can help close the hand, as has been proposed for the release of the ball in throwing (Hore and Watts 2011).

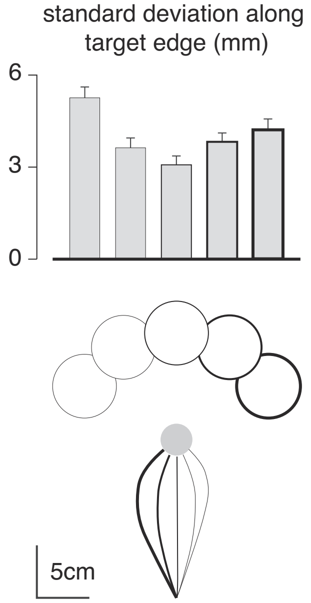

Fig. 5. To hit a static target (the gray disk) in a certain direction (toward one of the white circles) one's movement path (the curves) must curve to ensure that one makes contact with the correct part of the target. Having to move along a curved path increases the variability in the position that is hit (along the target's edge; gray bars above the corresponding white circles). The standard deviation in the hit position probably increases with path curvature as a result of the path length increasing, of the distance to the target becoming relevant for reaching the correct position along its edge, and of the curvature itself requiring additional planning. Data from the static target conditions of Experiment 3 of Brenner and Smeets (2007).

If not only where the target is to be intercepted but also how the hand is to be moving at that moment is planned in advance, path curvature can be difficult to interpret because one needs to know all the relevant factors and to what extent they are taken into consideration. Moreover, if one relies on the plan continuously being adjusted on the basis of the latest information about the target's motion and probably also about one's own motion (Brenner and Smeets 2003, 2006; de la Malla et al. 2012, 2014; Franklin and Wolpert 2008; Franklin et al. 2012; Sarlegna et al. 2003; Saunders and Knill 2003, 2005) to be able to deal with factors that cannot be judged reliably in advance (such as target acceleration), one cannot assume that all curvature is intentional, making interpreting it even more difficult.

MOVEMENT SPEED

In the preceding section, when discussing the paths that the hand takes to intercept moving targets, we already hinted at a way in which movement speed could be relevant: moving along with the target. There can be many more reasons for choosing a particular velocity profile. A well-established strategy when moving toward static targets is to slow down near the end of the movement to make sure to see the hand close to the target when there is still enough time to adjust the movement (Elliott et al. 2010, 2017; Woodworth, 1899). We already mentioned that moving along with a moving target just before contact could help people to see the hand close to the target. That the movement speed when catching balls is adjusted to be able to make use of such information is supported by the fact that it depends on the expected feedback (Tijtgat et al. 2011). Moreover, movement speed can be adjusted during the movement if one suddenly realizes that one is going to arrive too early or too late (Brenner and Smeets 2015a), although people more readily modify where than when they hit the target if they can. This has been shown to be the case both when the target is displaced and when a delay is introduced between arm movements and movements of a cursor representing the hand (Brenner and Smeets 2015a; de la Malla et al. 2014).

In the preceding section we proposed that people might decrease the sensitivity to misjudging the moment of contact by moving along with a moving target near that moment. This is probably especially useful if the target is moving fast, although doing so could come at the expense of having to move along a curved and therefore longer path, which is likely to decrease the spatial precision (Brenner and Smeets 2007; Fig. 5). Another way to decrease the sensitivity to misjudging the moment of impact is by moving fast. This is especially useful if the moment of impact is misjudged because one misestimates the distance along the movement path between oneself and the anticipated point of impact, or because one misestimates how long it will take to cover that distance. Moving fast does not improve the estimate, but it reduces the spatial error that arises from misestimating the distance because it reduces the difference between the time taken to travel the estimated and true distance, so that the target will (or would) have moved less far during that time (Brenner et al. 2012; Brenner and Smeets 2015a; Schmidt 1969). How much less far depends on the target's speed, making it more beneficial to move quickly when hitting faster targets (Smeets and Brenner 1995; Brouwer et al. 2000; Tresilian et al. 2003; Tresilian and Houseman 2005). Thus, approaching the target fast can be an advantage. Of course, moving fast for dealing with uncertainty in timing will decrease the spatial precision (Fitts 1954; Harris and Wolpert 1998; Schmidt et al. 1979), so there is an optimal speed to deal with both temporal and spatial uncertainties (Brouwer et al. 2005).

Some studies report multiple velocity peaks in interceptive movements. Caljouw et al. (2005) had participants move their hand laterally to hit an approaching ball, starting with their hand on the ball's future trajectory, so the hand had to move away from the trajectory and then return, giving rise to multiple peaks. The participants in a study by Port, Lee, Dassonville and Georgopoulos (Port et al. 1997; Lee et al. 1997) could in principle move with a single-peaked velocity profile, but they did not. The authors interpreted finding multiple peaks as indicative of discrete corrections of errors, with an initial misjudgment of the interception point. This is, however, not necessarily the case, as multiple velocity peaks might be optimal given the task constraints (Flash and Hogan 1985; Viviani and Cenzato 1985). We already mentioned the advantages of moving fast near the moment of impact (Brenner and Smeets 2015a). If one tries to move fast at the end of a task that specifically prescribes moving slowly toward a specified position of impact (Port et al. 1997), the only solution is to slow down at some time during the movement.

DO PEOPLE'S EYE MOVEMENTS REVEAL HOW INTERCEPTIVE MOVEMENTS ARE CONTROLLED?

We started this review by pointing out that people generally look where they are likely to find important information for guiding the current action. People often follow targets that they are trying to intercept with their eyes (Brenner and Smeets 2007, 2009b; Cámara et al. 2018; Postma et al. 2014; Soechting et al. 2009). There is clear evidence that doing so improves one's ability to intercept the target (Brenner and Smeets 2011a; de la Malla et al. 2017; Sharp and Whiting 1975). Presumably, pursuing the target increases the precision of the constantly updated judgment of the target's position and velocity (Brenner and Smeets 2015a). Missing small parts of the trajectory can make a difference (Brenner and Smeets 2011a) and blinks are presumably suppressed to prevent such loss (Fig. 1), but one does not have to pursue the target smoothly and precisely to successfully intercept it (Cesqui et al. 2015; de la Malla et al. 2017; Sharp and Whiting 1975).

Pursuing a target might improve judgements of its position because of the high spatial resolution of the fovea, but a high spatial resolution does not seem to be essential for hitting targets (Mann et al. 2010). Pursuing a target might improve judgements of its motion because one can rely on extraretinal signals related to the rotation of the eyes. The rotation of the eyes can be fine-tuned using feedback from the target's retinal slip (explaining why pursuing the target is not advantageous if the target is only presented very briefly; Montagne et al. 1993). Relying on extraretinal signals in this manner has the additional advantage that it prevents factors that are known to influence judged retinal motion from influencing interception. For example, the motion of the pattern on the top of a rolling ball can make the ball appear to move faster than it really is if one is looking elsewhere. This makes people systematically hit ahead of the ball unless they are pursuing it with their eyes (de la Malla et al. 2017). A second reason to pursue the target is that one can probably judge the velocity at which the large image of the static background moves across the retina more precisely than one can the velocity at which the small image of the target does so.

During the last part of the target's motion, seeing the target can no longer aid the current action, but the feedback provided by seeing how one hit the target can influence subsequent movements (de la Malla et al. 2012). However, if how one hit the target is best judged by looking elsewhere, for instance because the task is not just to hit the target but to hit it toward a goal, people stop pursuing the target once they can no longer adjust their movement due to neuromuscular delays, making fast eye movements to where the critical feedback is provided (Brenner and Smeets 2007, 2009b). When there is a second relevant object, such as a goal or a region within which the target is to be hit, pursuit is also sometimes briefly interrupted by saccades toward such structures, presumably to help localize them. In the case of hitting a target toward a goal, pursuit is interspersed with brief glimpses to the goal. Such glimpses occur well before the target is hit (Brenner and Smeets 2009b). In the case of hitting a target within a specified region, gaze often shifts toward the region just before the hit (de la Malla et al. 2017).

In some sports, pursuing the ball at certain times appears to be particularly important. If it is evident that a ball is going to bounce, as is the case in sports such as cricket, table tennis, and racquetball, people make saccades to the bouncing point (Land and Furneaux 1997; Land and Mcleod 2000; Mann et al. 2013) or to a position that the ball will pass sometime after the bounce (Diaz et al. 2013) before the bounce takes place. This probably helps judge the ball's direction of motion after the bounce and improves pursuit after the bounce, which might be particularly important if the ball changes direction when it bounces (due to the surface being uneven or due to spin; McLeod and Jenkins 1991). There are also reports of saccades to the interception point (Mann et al. 2013), possibly to receive better feedback about the way the ball was hit. Such feedback could be used to improve performance on the next attempt (Brenner et al. 2013, 2016; Gray 2009). Thus, although people naturally pursue the target, they are not just automatically following the moving object with their eyes but are presumably doing so to obtain the most relevant information. In all the preceding examples people try to pursue the target most of the time. However, there may also be situations in which it is important to look elsewhere.

When deciding which (static) object to intercept is more complicated than actually intercepting the selected object, people regularly look away from the object that they are going to intercept to gather information for the next step in the task (Ballard et al. 1992). When playing ball games, hitting the target is usually not the only goal. To hit a ball toward a teammate, or so that an opponent cannot reach it, you might need additional information. In a study that was designed to make people look away from the target as they might under such circumstances, subjects had to read a height off a screen while catching a ball. They then had to throw the ball back with the ball reaching the peak height that they had just read. They could not read the height without directing their gaze at the screen. During the 800 ms that the ball was in the air subjects directed their gaze consecutively at the screen and then the ball, or the ball and then the screen (López-Moliner and Brenner 2016). People never seem to look directly at their hand during interception tasks. Even when a target is to be hit with a cursor, and the cursor's movement is delayed in an unpredictable manner, people do not look at the cursor. They keep looking at the target and adjust their movements to the imposed delay using peripheral vision (Cámara et al. 2018). Thus, eye movements do often reveal when certain information is used, but information can sometimes be used without directing gaze toward its source.

SUMMARY OF THE PROPOSED MECHANISMS

We propose that interceptive movements are planned in advance and then continuously controlled on the basis of the latest available information. The continuous control is not limited to compensating for deviations from the plan, but also involves adjusting the plan to the most recent information. We assume that where people look and how they move is tuned to using information to optimize performance. Many aspects of a movement must be planned in advance, because most movements could be performed in many different ways. Even such a simple matter as when to start moving requires planning, because when one starts moving must match how fast one intends to move and where one intends to intercept the target. Similarly, how one starts moving determines how one will circumvent any obstacles on the way and may be necessary to make it possible to be moving in a particular way as one reaches the target. However, the plan is unlikely to be perfect, and its execution certainly will not be, making it advantageous to continuously adjust the movement.

Both the plan and the predictions underlying continuous control can be wrong due to errors in acquiring or interpreting sensory information, due to relevant sensory information not being considered, or due to changes in the circumstances. When predictions are only incorrect due to errors in judging the position and velocity of the target (left panel of Fig. 6), updating predictions primarily reduces the magnitude of variable errors. When predictions are also incorrect because incorrect assumptions are made, such as assuming that the target is moving at a constant velocity when it is actually decelerating (right panel of Fig. 6), updating predictions also reduces the magnitude of systematic errors. Similar reasoning can be applied to other sources of error, such as motor errors.

The values used in the simulations of Fig. 6 are quite realistic. A coefficient of variation of ~5% for judging velocity (Snowden and Braddick 1991), a minimal sensorimotor delay of 100 ms (Brenner and Smeets 1997) and movement times of ~400 ms (Brenner and Smeets 2015a) are reasonable. The standard deviation of 3 mm for position is a reasonable estimate of the combination of perceptual and motor errors when moving the arm to a planned position within ~400 ms (Brenner and Smeets 2015a). The pattern of results that the figure illustrates corresponds to what has been found in experiments: Briefly removing vision of the target before the moment of interception reduces precision (Brenner and Smeets 2011a), corresponding to the effect of forcing people to rely on earlier information in the manner illustrated in the left panel of Fig. 6. Interleaving various accelerations gives rise to small systematic errors (Brenner and Smeets 2015a), corresponding to the small difference between the peak of the pink distribution and the blue target position portrayed in the right panel.

Dealing with acceleration by a combination of continuously adjusting one's current movements on the basis of the latest information and avoiding repeated systematic errors by rapidly adjusting one's movement plan to the feedback on previous trials might seem very complicated. However, there is no real alternative if one considers that predictions based on the current acceleration are not good enough, both because of limitations of the visual system and because the target may not always behave as one expects. Thus, it should come as no surprise that there are many circumstances in which people use some expectation of how the target will move, based on recent or more general experience, when trying to intercept moving targets (de Azevedo Neto and Teixeira 2009, 2011; de Lussanet et al. 2001, 2002; de Rugy et al. 2012; Marinovic et al. 2010; van Donkelaar et al. 1992; Zago et al. 2004, 2009).

THE NEURONAL SUBSTRATE

Until now we have only discussed how movements are controlled from the perspective of the information that is used and the constraints of the task. We considered one constraint that is imposed by the underlying neural substrate: the sensorimotor delay. Implicitly, we also considered the neuromuscular properties that constrain human movements to be smooth and that introduce noise in the sensorimotor transformation. We do not present details about how the human nervous system actually uses sensory information to activate the muscles that guide the hand to intercept a target, or about how such neuronal transformations constrain our actions, because we know very little about this.

Several studies have shown that disrupting the normal activity in particular brain areas at specific times by applying localized transcranial magnetic stimulation can influence interceptive movements. Such studies confirm that the interception of visual targets is guided by processing within the temporal and posterior parietal areas of the dorsal visual pathway (Bosco et al. 2008; Delle Monache et al. 2017; Schenk et al. 2005),

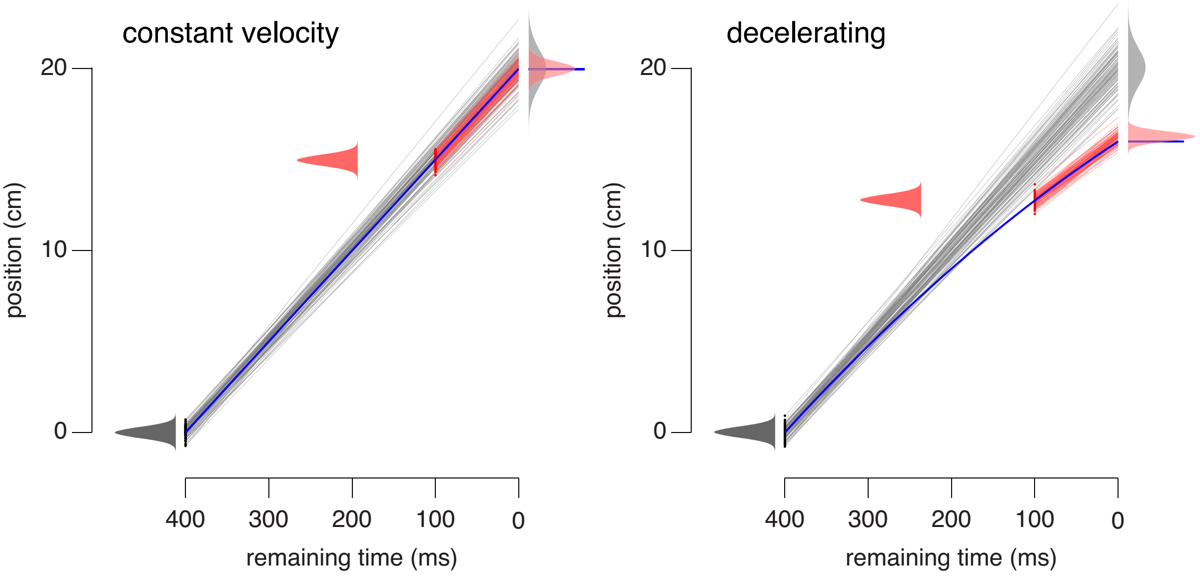

Fig. 6. Illustration of why continuous control improves both precision and accuracy of interception. The thick, blue curves show the change in target position across time for a target moving at a constant velocity of 50 cm/s (*left*) or initially moving at the same speed but decelerating at 50 cm/s^2 (*right*). The thin lines represent simulations of anticipated target trajectories, either long before the end of the interceptive movement (gray lines; 400 ms before contact) or at the last moment at which adjustments can be made (red lines; 100 ms before contact). The anticipation is based on unbiased sensory estimates with a standard deviation of 3 mm for position (black and red distributions to the left of the thin lines) and 5% of the velocity (variability in slopes of thin lines). The resulting distribution of errors in where the target will be at the time at which one attempts to intercept it (*time zero*) is shown by the distributions to the right of the lines. The pink distributions on the right are narrower than the gray ones, indicating a higher precision. The one in the right panel is also closer to the blue line, indicating a higher accuracy. The equations underlying this figure are given in the APPENDIX.

where retinal information about object and self-motion is combined with information about posture and the orientation of the eyes to guide human movements. Differences between the activity of individual cells or groups of cells in the parietal and motor cortical areas of rhesus monkeys during interception reveal that processing continues throughout these pathways (Lee et al. 2001b; Merchant and Georgopoulos 2006; Port et al. 2001). However, little is known about the way in which these brain areas control interception.

The posterior parietal cortex probably plays a particularly important role in the continuous control of interception (as it does in other reaching movements; Caminiti et al. 1998; Battaglia-Mayer et al. 2014) because disrupting activity in the posterior parietal cortex primarily disrupts adjustments to ongoing movements (Desmurget et al. 1999). This is consistent with the reported increase in spatial variance in movement end points following such disruption (Dessing et al. 2013). A role in guiding the action on the basis of new visual information is also supported by the finding that interception performance is disrupted by stimulation of regions that correspond with the current target position rather than of regions that correspond with the interception point (Reid and Dessing 2018b). The fact that a patient with damage to the posterior parietal cortex did not make quick adjustments to compensate for small target shifts but could make deliberate adjustments also supports this view (Pisella et al. 2000). The posterior parietal cortex appears to have neurons that anticipate how an object that is hidden from view will continue to move (Assad and Maunsell 1995) and ones that respond differently when intercepting a target than when making the same movement to a static target (Merchant et al. 2004). However, the short latency that is characteristic of continuous control has also been taken to suggest that subcortical pathways are involved (Day and Brown 2001; Reynolds and Day 2012). Adjustments to movements based on the outcome of recent similar movements appear to rely on processing within the cerebellum (Bastian 2006; Fautrelle et al. 2011; Tseng et al. 2007), so aspects of the movement that are planned before the movement starts might rely on processing within the cerebellum.

We are still far from understanding how the activity within all these pathways gives rise to adequate movements. We do not know how the trajectory is optimized or how movement plans are converted into the responses of the many muscles involved, including ones that are needed to maintain posture. Neither do we know how the brain deals with muscle fatigue or the mechanical interactions between moving segments, or how the current posture and the use of tools is dealt with. We do not even know to what extent the brain really considers such issues (building forward models; Desmurget and Grafton 2000; Flanagan and Wing 1997; Ishikawa et al. 2016; Mehta and Schaal 2002; Wolpert and Flanagan 2001; Miall and Wolpert 1996; Wolpert et al. 1998) and to what extent near-optimal movements arise from small adjustments based on recent feedback (Brenner and Smeets 2011b; Todorov and Jordan 2002; van Beers 2009; van Beers et al. 2013). Whereas the former would appear to be necessary to quickly find optimal solutions in ever changing circumstances, the latter is necessary to readily adjust movements to arbitrary changes when using tools, such as occur when shifting the computer mouse to a different position on a cluttered table (or when an experimenter unexpectedly shifts the cursor; Brenner and Smeets 2003), changing the relationship between arm postures and cursor positions on the screen.

ADDITIONAL CONSIDERATIONS

In the present review we have concentrated on laboratory studies that were performed under controlled conditions, but many of the findings are consistent with the sports literature, where the performance of experts who have made their living from optimizing interception in various sports has been examined (Bootsma and van Wieringen 1990; Mann et al. 2013; McLeod and Jenkins 1991; Regan 1992). Aspects that we have ignored altogether are strategic choices such as whether to intercept a target with a forehand or backhand drive in table tennis (Sørensen et al. 2001), how to deal with mechanical perturbations of a moving hand (Button et al. 2000), or how to deal with intentional attempts to deceive a batsman (Müller and Abernethy 2006) or goalkeeper (Dessing and Craig 2010) by spinning the ball, or expert batsmen's ability to detect this before the ball is even released (Müller et al. 2006). We have also ignored the benefits of having auditory and tactile feedback (Gray 2009).

We have not dwelled extensively on how judgments of position and velocity are made. We mentioned that there is some evidence that binocular disparity is considered when judging when to close one's hand to catch an approaching ball (Rushton and Wann 1999; Savelsbergh and Whiting 1992; von Hofsten et al. 1992), but there are also studies that find no evidence for a role of binocular disparities when catching (Servos and Goodale 1998) or batting (Brenner et al. 2014) a ball. Studies that directly compared monocular with binocular performance (Savelsbergh and Whiting 1992; von Hofsten et al. 1992) have sometimes ignored the benefit of having two estimates of the relevant monocular cues (Brenner et al. 2014), but there are probably circumstances in which binocular disparities are useful (Rushton and Wann 1999). It also appears that interception does not require very high acuity, because blurring the image of the approaching ball hardly influences batting performance (Mann et al. 2010).

We have also only briefly mentioned the issue of deciding when to start moving to intercept an approaching ball. An early suggestion was that interceptive movements are initiated when a measure of time to contact based on the relative rate of expansion of the ball's retinal image passes a certain threshold value (Lee et al. 1983). Later studies questioned the exclusive use of this measure of time to contact by examining whether this threshold value remained constant under various circumstances (Michaels et al. 2001; Tresilian 1994; Watson and Jakobson 1997). A problem with assuming that movements are initiated when some measure reaches a fixed value is that the circumstances may make it advantageous to change the value (Tresilian 2005), for instance to be moving faster when hitting faster targets (Brouwer et al. 2000; Tresilian et al. 2009). If interceptive movements are optimized in accordance with the task constraints, the moment of movement onset is probably determined by factors such as when one plans to hit the target and at what speed, rather than being controlled directly.

There are many studies that argue for a fundamentally different use of sensory information at different moments before and during an action, for instance on the basis of evidence that the moment at which visual information about the moving hand is provided matters (Kennedy et al. 2015; Tremblay et al. 2017), as does the time at which vision of the target is occluded (Brenner and Smeets 2011a; Sharp and Whiting 1974; Whiting and Sharp 1974). According to our proposal, providing information late during the movement is advantageous because as the hand approaches that target it is easier to anticipate errors. However, if information is presented too late there may not be enough time to make the required adjustments, so anticipating errors correctly is no longer of any use. Similarly, some strategic adjustments such as starting by moving in the opposite direction than the target's motion to later move along with the target can only be considered if one can anticipate the target's motion well in advance. The precise moment at which information is most useful, or even useful at all, should therefore depend on the kind and magnitude of the required adjustments as well as on the sensorimotor delay for using that kind of information. Consequently, we do not discuss possible fundamental distinctions between different moments.

Future studies are likely to expand on our analysis of exactly what information is used to make predictions and what information is ignored. Do people ignore all information that takes relatively long to obtain, or is such information considered later in the movement? Do people ignore all information that cannot be obtained very precisely, or is such information used but to a lesser extent? Is control really completely continuous or are there some intermittent components? Can all aspects of a movement be updated at any moment, or are there aspects that cannot be changed once the movement starts? Future studies may also show whether what we have learned from studies using rather simplified conditions with quite predictable target motion and constraints on the movements also apply in daily life, including sports situations, where the circumstances are usually less predictable.

CONCLUSIONS

We conclude that interception is primarily guided by a continuously updated prediction of where one will be able to reach the target, based on the latest judgments of its current position and velocity. The trajectory that one will take to the target and the velocity profile are planned in accordance with the circumstances and task demands. They will therefore depend on the goal of the interception, constraints imposed by obstacles, the extent to which one will be able to use feedback, and so on. This combination provides people with the flexibility to deal with unpredictable and changing circumstances when trying to optimize the movement in relation to the task demands, as one must when faced with tasks such as preventing an infant from running onto the street.

APPENDIX

The predictions presented in Fig. 6 are based on an extremely simplified model of interception: the hand moves to where the target is expected to be at some time in the future (x) given its current position (x_O) and velocity (v):

$$x = x_0 + vR \tag{1}$$

where R is the remaining time until the moment of interception. Assuming that judgments of remaining time and velocity are independent, the variance in the target's expected position (and therefore in the errors) can be given by

$$\sigma_x^2 = \sigma_{x_0}^2 + v^2R^2\left(\frac{\sigma_v^2}{v^2} + \frac{\sigma_R^2}{R^2}\right) \tag{2}$$

Fig. 6 only illustrates the influences of errors in judging the position and velocity, which we assume to be normally distributed with $\sigma_{x_0} =$ 3 mm and $\sigma_v = 0.05v$ (a Weber fraction of 5%). It shows simulations of individual trials for values of the remaining time R of 400 and 100 ms, assuming perfect judgments of R ($\sigma_R = 0$) and that the planned movements are executed perfectly.

From *Eq. 2* it is clear that the uncertainty in the prediction decreases when R (the remaining time) does so, especially if one considers that the precision of judging R is more or less proportional to its value (Westheimer 1999) so that $\sigma_v^2/v^2 + \sigma_R^2/R^2$ is approximately constant. Thus, even if the quality of the judgments themselves does not change, updating the judgments improves the prediction and thereby potentially performance. For targets that do not move at a constant velocity, ignoring acceleration (a) means that the variance in the expected position depends on the judged velocity when the prediction is made. For decelerating targets, this decreases the variance in the expected position as the remaining time decreases, but for accelerating targets it increases the variance. Importantly, ignoring acceleration also gives rise to a systematic bias (B) that decreases as the remaining time becomes smaller (i.e., when the prediction is updated), because

$$B = \frac{1}{2}aR^2 \tag{3}$$

Of course, selecting a time and predicting where the target will be at that time is only one possible way in which movements might be controlled. One could also select a position and predict when the target will reach that position. Doing so involves dividing the separation (S) between the current and selected position by the current velocity. The remaining time for the target to reach the selected position can be given by

$$R = \frac{S}{v} \tag{4}$$

in which case:

$$\sigma_R^2 = \frac{S^2}{v^2}\left(\frac{\sigma_v^2}{v^2} + \frac{\sigma_S^2}{S^2}\right) \tag{5}$$

So, assuming that the precision of S is also proportional to the value itself, the variability in the estimate of time will decrease with the decreasing separation in a similar way as the estimate of position did with decreasing remaining time. Of course, in real movements one might use a strategy that involves continuously estimating both the time and the place of the hit from the incoming information. The same reasoning applies if we replace judgements of separation and velocity by optical measures of gap size and rate of change of gap size (Lee 1998).

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

E.B. analyzed data; E.B. and J.B.J.S. interpreted results of experiments; E.B. prepared figures; E.B. drafted manuscript; E.B. and J.B.J.S. edited and revised manuscript; E.B. and J.B.J.S. approved final version of manuscript.

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