Exp Brain Res (2013) 230:207–218
DOI 10.1007/s00221-013-3645-7

RESEARCH ARTICLE

How the required precision influences the way we intercept a moving object

Eli Brenner · Rouwen Cañal-Bruland · Robert J. van Beers

Received: 16 April 2013 / Accepted: 1 July 2013 / Published online: 16 July 2013
© Springer-Verlag Berlin Heidelberg 2013

Abstract Do people perform a given motor task differently if it is easy than if it is difficult? To find out, we asked subjects to intercept moving virtual targets by tapping on them with their fingers. We examined how their behaviour depended on the required precision. Everything about the task was the same on all trials except the extent to which the fingertip and target had to overlap for the target to be considered hit. The target disappeared with a sound if it was hit and deflected away from the fingertip if it was missed. In separate sessions, the required precision was varied from being quite lenient about the required overlap to being very demanding. Requiring a higher precision obviously decreased the number of targets that were hit, but it did not reduce the variability in where the subjects tapped with respect to the target. Requiring a higher precision reduced the systematic deviations from landing at the target centre and the lag-one autocorrelation in such deviations, presumably because subjects received information about smaller deviations from hitting the target centre. We found no evidence for lasting effects of training with a certain required precision. All the results can be reproduced with a model in which the precision of individual movements is independent of the required precision, and in which feedback associated with missing the target is used to reduce systematic errors. We conclude that people do not approach this motor task differently when it is easy than when it is difficult.

E. Brenner (✉) · R. Cañal-Bruland · R. J. van Beers
Faculty of Human Movement Sciences, MOVE Research Institute Amsterdam, Vrije Universiteit, Van der Boechorststraat 9, 1081 BT Amsterdam, The Netherlands
e-mail: e.brenner@fbw.vu.nl

Keywords Interception · Variability · Feedback · Precision · Knowledge of results

Introduction

Do people perform a given motor task differently if it is easy than if it is difficult? In particular, do they make more precise movements if the task requires a higher precision? Intuitively, one may expect this to be the case, but why would people not always move with the highest possible precision? One possible reason is that people may not only optimize precision. Much has been learnt about why people move in certain ways by evaluating the costs and benefits of various options. From such analyses, we know that people select movements that offer a near-optimal compromise between the likelihoods of obtaining rewards and of incurring losses (Trommershäuser et al. 2006, 2008) and that they select movements that optimally weigh spatial against temporal errors (Brouwer et al. 2000, 2005; Tresilian et al. 2003) and perceptual against motor errors (Battaglia and Schrater 2007; Faisal and Wolpert 2009). The main cost of making spatially precise movements is that they take more time, so people make faster movements if it is less important to be precise (Fitts and Peterson 1964; Harris and Wolpert 1998; Schmidt et al. 1979) or if they are more willing to risk failure (Nagengast et al. 2011). Making more precise movements may also cost more energy, so people may also make more energy-efficient movements if it is less important to be precise (Alexander 1997; Berret et al. 2008, 2011).

There is another reason why changing the required precision might influence how precisely movements are made. Changing the required precision usually changes the feedback that people obtain, because the feedback provided by a hit is usually different from that provided by a miss. Different feedback is likely to result in different movements, for instance, because people use feedback to remove random drifts (de la Malla et al. 2012; Todorov and Jordan 2002; van Beers 2009; van Beers et al. 2013). Changing the circumstances can also change how one responds to feedback (Knill et al. 2011). Moreover, if the task is difficult, people may be more inclined to use strategies that are only advantageous under specific circumstances. It is known that changing the feedback can influence how quickly a task is learnt (Gray 2009; Patton et al. 2013) and even what is learnt (Shmuelof et al. 2012), so that even if changing the required precision does not change the success rate, it may affect how the task is performed, and therefore how people respond when the circumstances change (Diedrichsen et al. 2010; Salmoni et al. 1984; Shmuelof et al. 2012).

We used intercepting (virtual) moving targets by tapping on them with the index finger to study how the required precision influences the way in which movements are made. The feedback provided after each tap varied across sessions from being very strict in terms of hitting the target (the whole fingertip had to be on the target at the moment of the tap for it to be considered hit) to being very lenient (as long as part of the fingertip touched the target it was considered hit). Feedback about the direction of the error with respect to the target was provided whenever the target was missed. The target always looked the same and moved in exactly the same way, to ensure that the precision of visual judgments about the target's position or motion cannot be responsible for any differences between sessions. For a given target speed, the inclination to tap more slowly to increase one's spatial precision is balanced by an inclination to tap faster to increase the precision of the timing of one's tap (Brouwer et al. 2005), so we do not expect substantial changes in tapping speed. We were particularly interested in whether people would have less variability in their movement endpoints when the task required higher precision, and if so, whether such reduced variability would persist when the requirements subsequently became less strict without the participants being told that anything had changed.

Methods

Ten right-handed female subjects who were all between 21 and 26 years old and were unaware of the purpose of the study each took part in five slightly different 200-trial sessions on separate days. Each of the five different sessions was performed first by two of the ten subjects, second by two other subjects, third by yet two others, and so on, while taking care to also vary the order in which successive sessions were presented. The study was part of a research programme that has been approved by the local ethical committee.

The set-up

The experiment was conducted in a normally illuminated room. Images were projected at 120 Hz (InFocus DepthQ Projector; resolution: 1,280 by 768 pixels) from behind onto a 1.00 by 1.25 m (height by width) acrylic rear-projection screen (Techplex 150) that was tilted backwards by 30°. The image was slightly smaller than the physical screen, so image resolution was about 1 mm per pixel. Subjects stood in front of the screen and tapped the screen with their right index finger (Fig. 1a). They were not restrained in any way. An Optotrak 3020 that was placed at about shoulder height to the left of the screen measured the position of an infrared light emitting diode attached to the nail of the right index finger at 500 Hz.

At the beginning of each session, the diode position was measured when the fingertip was at four indicated positions on the screen. This simple four-point calibration was used to relate the position of the fingertip to the projected images, automatically correcting for the fact that the diode was attached to the nail rather than the tip of the finger. The Optotrak also measured the position of a second diode that was attached to the left side of the screen and that stopped emitting infrared light for about 10 ms, 1 ms after light fell on a sensor that was placed in the path of the light directed towards the top left corner of the screen. Flashes were presented at the top left corner of the screen at critical moments during the experiment for temporal calibration. Together, these measurements allowed us to determine the position of the finger with respect to the screen every 2 ms and to determine the moments at which images were presented to within 2 ms (although new images were only presented every 8.3 ms).

Stimulus and procedure

After the calibration, subjects started each trial by placing their index finger at the starting point (a 15-mm-diameter grey disc) that was 5 cm to the right of the screen centre (slightly below shoulder height; as shown in Fig. 1a). Subjects could rest whenever they wanted by not placing their finger at the starting point. Between 2.0 and 2.5 s after the finger was placed at the starting point, the target appeared 20 cm to the left of and 15 cm above the screen centre. The target was a white, 15-mm-diameter disc that moved to the right across the screen at 40 cm/s. If the finger left the starting point before the target appeared nothing happened until it was placed back at the starting point and remained there for the required time. Once the target appeared, subjects were expected to lift their finger off the screen and

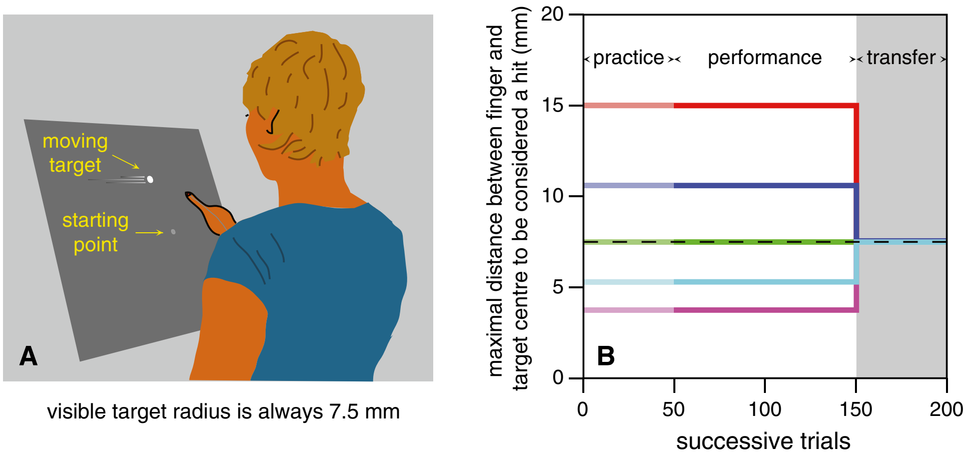

Fig. 1 **a** Illustration of the set-up. The subject started a trial by placing her right index finger on a *grey* starting point. Shortly after the trial started, a 15-mm-diameter target appeared on the screen. The target was always moving to the right at 40 cm/s, 15 cm above the starting point. The subject's task was to lift her finger off the screen and tap on the moving target. **b** Each of the five sessions consisted of 200 trials. During the first 150 trials, the centre of the subject's finger had to be within 15, 10.6, 7.5, 5.3 or 3.75 mm of the target centre at the moment that it hit the screen for the trial to be classified as a hit. The only difference between the sessions (indicated by *different colours* in this and all subsequent figures) was this maximal distance. During the final 50 trials of all sessions, the required distance was 7.5 mm, which meant that the centre of the finger had to be within the visible target radius (*dashed line*)

tap on the target. They were free to choose when exactly to try to intercept the target, but they were warned that they had to hit it at the first attempt. Once a tap was detected (acceleration of more than 30 m/s^2 while the finger was less than 5 mm above the screen and within 2.25 cm of the target's path), the performance was evaluated (in a manner that depended on the session as explained below) and feedback was provided for 500 ms. The extent to which the criteria for detecting the tap were adequate is discussed in the *analysis* section.

Feedback

To determine whether the target had been hit, we compared the position of the fingertip at the moment of the tap with the (interpolated) target position at that moment. All the delays in our equipment were considered when doing so. If the target was hit, it disappeared and a sound indicated that it had been hit. If the target was missed, it deflected away from the finger at 1 m/s (for example, if the finger tapped above and to the left of the target, the target moved down and to the right). It took about 20 ms to adjust the images to the subjects' actions. Subjects did not notice that this meant that the target continued to move for up to 1 cm after the tap before feedback was provided, because at that time the hand was occluding the target. If the finger had missed the target, the target then jumped to the appropriate place on the line through the position at which the fingertip hit the screen and the position at which the target had been at the moment that it had done so. Subjects did not notice this jump either. Subjects could see their finger and the target throughout, but without the explicit feedback provided by the deflected target it was extremely difficult to tell whether or not one had hit the target.

The five sessions

Each session consisted of 200 trials and lasted about 20 min. The only difference between the five sessions is in when taps were designated to be hits or misses. This varied between the centre of the fingertip having to be within 3.75 mm of the target centre for the tap to be considered a hit (requiring almost complete overlap between the fingertip and the target at the moment of the tap) to the centre of the fingertip having to be within 15 mm of the target centre for the tap to be considered a hit (in which case the fingertip barely had to touch the target at the moment of the tap). Within each session, we distinguish between three stages: *practice*, *performance* and *transfer* (Fig. 1b). In the *practice* and *performance* stages, the maximal distance between fingertip and target for a tap to be considered a hit was 3.75, 5.3, 7.5, 10.6 or 15 mm. This maximal distance remained the same for 150 trials, so these two stages were completely identical, but we considered the first 50 trials as practice because people tend to perform poorly on the first few trials. The *performance* stage was followed by a *transfer* stage in which the maximal distance between finger and target for a tap to be considered a hit was 7.5 mm. Subjects were not aware that the required precision had changed, and this was not indicated in any way except for the fact that their taps were more or less likely to be successful. The transfer stage consisted of 50 trials that were completely identical in all five sessions. These trials were included to examine to what extent differences between the required precisions in the preceding 150 trials (and the associated differences in feedback) had lasting influences on performance. Subjects were not aware of there being different stages.

Analysis

For the analysis, we determined the moment of the tap on the basis of the acceleration of the fingertip in the direction orthogonal to the screen. Acceleration was determined from three consecutive measurements of the distance from the screen, by subtracting the difference between the last two distances from the difference between the first two distances. We assigned the outcome to the moment of the central measurement. The acceleration was highest at the moment of impact with the screen. This method of determining the moment of the tap is more reliable than the one we used for providing the feedback, but it cannot be used online because doing so would introduce additional delays in providing the feedback. In total, 4 trials (out of 5,000) during the *performance* stage and 3 (out of 2,500) during the *transfer* stage could not be used for the analysis because the subject did not move in time to intercept the target or did not clearly tap the screen. For 3,923 of the remaining 7,493 trials, the moment that the tap was considered to have occurred during the experiment was precisely at the peak acceleration. For another 2,947 trials, the peak acceleration was one measurement (2 ms) later. This difference arises because the true moments of impact are usually between two samples, and whereas the peak acceleration is at the sample closest to the true moment of impact, the acceleration often reaches the threshold for providing feedback at the first of these samples even if it is not closest to the moment of impact. For 223 trials, the peak acceleration was one measurement earlier, and for 186 trials, it was two measurements later. These are probably cases in which the online sampling of the Optotrak data missed a measurement during the experiment (such data are available for our analysis but were not available during the experiment). For 50 trials (about 0.7 %), the error was larger, reflecting true errors in determining the moment of the tap during the experiment. On 164 trials, the finger tapped the screen too gently, so the target simply continued on its path (and no explicit feedback was provided). All trials except the 7 in which no tap was detected were included in the analysis.

For each trial, we determined whether the target was considered to have been hit, the initiation time (from target onset until the finger moved 1 mm), the movement time (from when the finger moved 5 mm until the moment of tap), the finger's horizontal position on the screen and relative to the target at the moment of the tap, the finger's vertical position relative to the target at the moment of the tap (note that we refer to the distance along the screen as 'vertical' despite it actually being slanted backwards), and 101 equally spaced positions along the finger's path from the starting point to the position of the tap. The 100 equal distances between the 101 positions were determined in three-dimensional space using linear interpolation between the measurements. For each subject, stage (*performance* and *transfer*) and session we then determined the fraction of targets that were hit and the mean values of all of the other measures. We also determined the horizontal and vertical standard deviations of the tapping positions and the lag-one autocorrelations of both the horizontal and vertical tapping errors. The tapping error is the position of the finger relative to the centre of the target at the moment of the tap. Lag-one autocorrelations (A) were determined (both for the errors and for the tapped positions on the screen) with the equation

$$A = \frac{\sum_{i=1}^{N-1} (x_i - \bar{x})(x_{i+1} - \bar{x})}{\sum_{i=1}^{N-1} (x_i - \bar{x})^2}$$

where N is the number of trials involved, x_i is the position tapped on trial i, and $\bar{\mathbf{x}}$ is the mean tapped position (considering all N trials). The mean, standard deviation and lag-one autocorrelation of the tapping errors provide information about systematic biases, the precision with which the target is hit and the serial dependence between errors, respectively. Unless mentioned otherwise, all the values that we report are averages across the 10 subjects' mean values, with the standard errors associated with this averaging. For several variables, the results were evaluated with 2×5 repeated measures analyses of variance with factors stage and session. Whenever such analyses are mentioned, all significant effects ($\alpha = 5$ %) are reported.

Results

Subjects moved their finger upwards along the screen until it was above the target's path and tapped on the target (Fig. 2a, b). They tended to move to the right near the moment of the tap, possibly in order to reduce the relative motion between the finger and the target (Brenner and Smeets 2005). There was no clear relationship between the trajectories and the differences between the sessions.

Subjects initially systematically tapped to the right of the target centre (or equivalently, hit the screen too early; Fig. 2c). After several practice trials, during which this tendency gradually decreased, performance stabilized at a level that depended on the session, but that was on average always to the right of the target centre. The larger the tolerance for deviations of the finger from the target, the larger was the residual systematic error. During *transfer* trials,

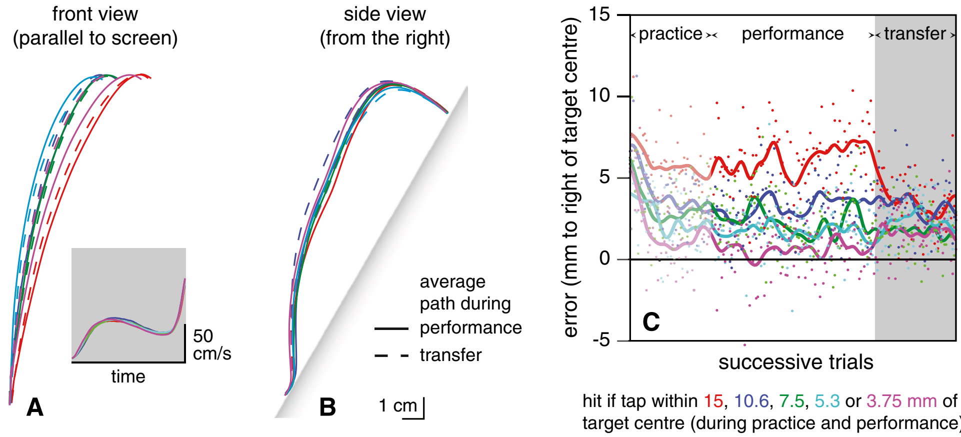

Fig. 2 **a** Average path in the *performance* and *transfer* stage of each session. The component parallel to the screen shows that subjects curved to the right, in pursuit of the target, near the end of the movement. **b** A side view of the same movements shows that the finger's height above the screen increased until it was above the target's path, after which the finger moved down to tap the screen. There were no evident systematic differences that could be related to the different requirements in the five sessions. The *inset* shows the average tangential velocity profiles from motion onset until the screen is hit (during the performance stage). **c** Average systematic error on successive trials. Each point is the average of the ten subjects' errors, where an error is defined as how much further to the right than the centre of the target the centre of the finger hit the screen. The curves are moving averages of these points weighted by a Gaussian with a standard deviation of 3 trials

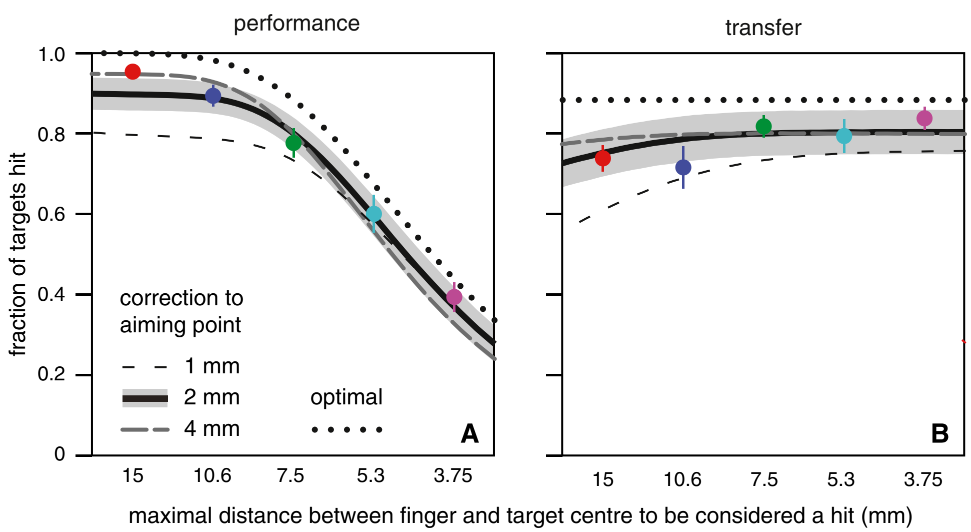

Fig. 3 Success in performing the task. Average fractions of targets that the ten subjects hit during the *performance* (**a**) and *transfer* (**b**) stages of each session, with standard errors. The *solid curves* and *grey* areas show the mean and standard deviation of the outcome of simulations with a model that is described in the text. The *dashed curves* show means of model simulations with larger and smaller corrections after each error. The *dotted curves* show the best possible (average) performance for the assumed variability in movement execution (i.e. assuming that subjects always aimed for the target centre)

performance rapidly converged to the value that was appropriate for the level of tolerance used in that stage (centre of finger within the visible target; hit if tap within 7.5 mm of target centre). Surprisingly, the systematic error did not only decrease when more precise tapping was required (transition from *performance* to *transfer* stage; red curve) but it also increased when less precise tapping was tolerated (same transition; purple curve).

Not surprisingly, more targets were hit when larger errors were tolerated (Fig. 3a). Slightly fewer targets were hit during the transfer stage if larger errors had just been tolerated (Fig. 3b), presumably because subjects made larger systematic errors during the first few trials (Fig. 2c). To determine whether tolerating larger errors, or the associated success in hitting targets, affected the precision with which subjects made their movements, we compared the

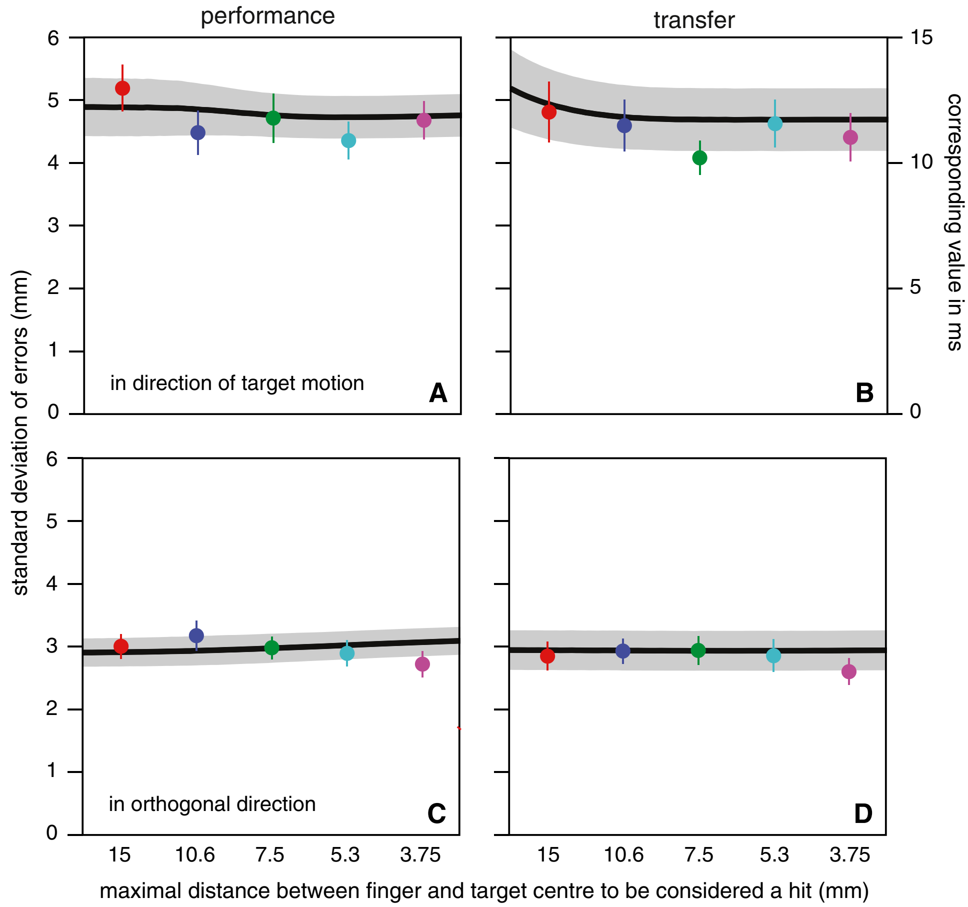

Fig. 4 Variable errors. Average standard deviations of the horizontal (**a**, **b**) and vertical (**c**, **d**) errors that the ten subjects made during the *performance* (**a**, **c**) and *transfer* (**b**, **d**) stages of each session, with standard errors. The values in ms for the horizontal errors (right axis in **b**) are obtained by dividing the values in mm by the target's speed (40 cm/s). The *curves* and *grey* areas show the mean and standard deviation of the outcome of simulations with a model that is described in the text

variability in the errors across sessions (Fig. 4). Separate repeated measures analyses of variance for the horizontal and vertical variability in the errors (standard deviations), with factors session (errors tolerated of up to 15, 10.6, 7.5, 5.3 or 3.75 mm) and stage (*performance* or *transfer*), did not reveal any significant main effects or interactions. Thus, the variability in the movements did not depend on how difficult it was to perform the task successfully.

Similar analyses of variance for the mean horizontal error (Fig. 5a, b) did reveal significant differences between sessions ($F_{4,36} = 15.9$; $p < 0.0001$) and a significant interaction between session and stage ($F_{4,36} = 19.7$; $p < 0.0001$). There were no significant effects for the vertical error (Fig. 5c, d). The significant effects are consistent with what we saw in Fig. 2c: a bias to tap to the right of the target centre that decreases as the required precision increases.

The lag-one autocorrelation in the horizontal errors differed significantly between sessions ($F_{4,36} = 3.05$; $p = 0.029$), and there was a significant interaction between session and stage ($F_{4,36} = 3.69$; $p = 0.013$). These two effects can be summarized as the autocorrelation differing systematically across sessions, but only for the *performance* stage (Fig. 6a, b). There was also a significant interaction between session and stage for the autocorrelation in the vertical errors ($F_{4,36} = 4.13$; $p = 0.007$), presumably for the same reason (Fig. 6c, d).

A near-zero lag-one autocorrelation is an indication of adequate corrections. This can be understood by considering the average performance after errors. If one corrects too little, on average the next error will be in the same direction, so there will be a positive lag-one autocorrelation. If one corrects too much, on average the next error will be in the opposite direction, so there will be a negative lag-one autocorrelation. If one corrects by exactly the right amount, the lag-one autocorrelation will be zero, and the overall variability will be minimized (van Beers 2009). In our experiment, we only provided explicit feedback about the direction of the error. An indication that subjects responded to this feedback in a similar manner in the different sessions is that they often responded too much (leading to negative autocorrelations) when the required precision was high (so that feedback was provided when the finger was close to the centre of the target) and too little (leading to positive autocorrelations) when the required precision was low (so that feedback was only provided when the finger tapped the screen quite far from the target centre).

On average, our subjects' fingers started moving 251 ms after the target appeared. There were no

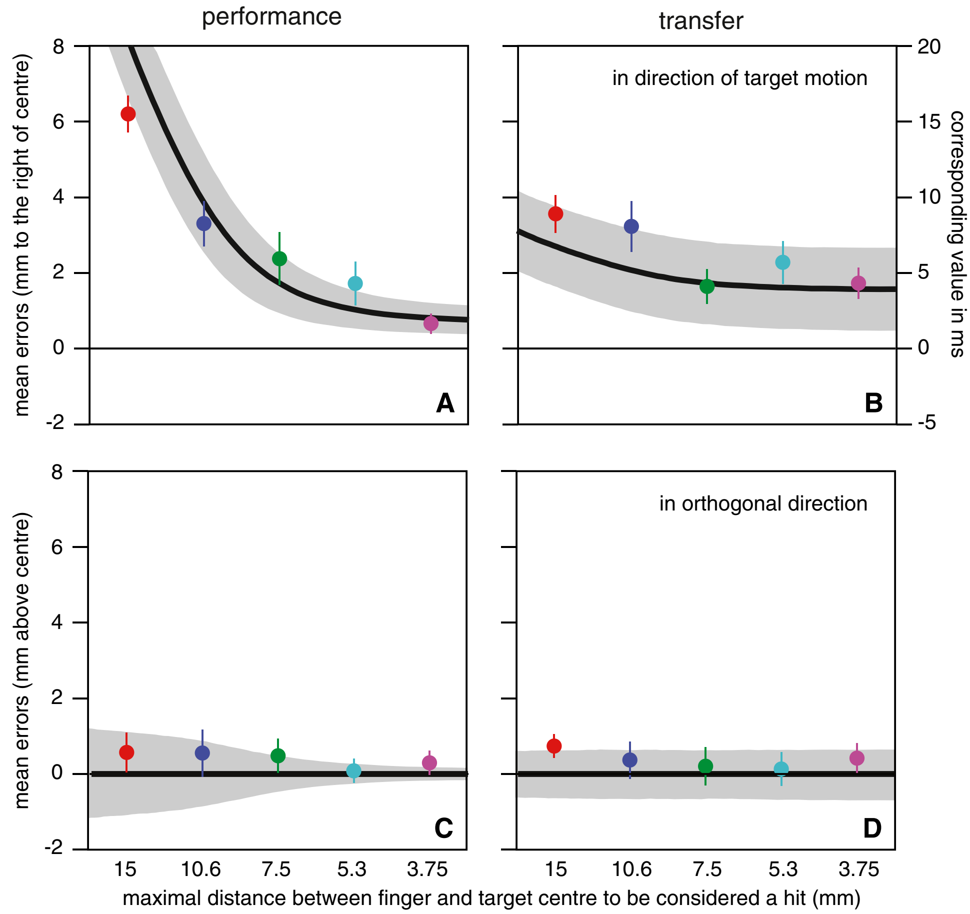

Fig. 5 Systematic errors. The tendency to hit to the right of (**a**, **b**) and above (**c**, **d**) the target centre during the *performance* (**a**, **c**) and *transfer* (**b**, **d**) stages of each session; means and standard errors across the ten subjects. The values in ms for the horizontal errors (right axis in **b**) are obtained by dividing the values in mm by the target's speed (40 cm/s). The *curves* and *grey* areas show the mean and standard deviation of the outcome of simulations with a model that is described in the text

significant differences across sessions or stages. The average movement time was 499 ms and did not differ significantly across sessions or stages either, but there was a significant interaction between stage and session ($F_{4,36} = 4.62$; $p = 0.004$). This interaction mainly arose from a shortening of movement times after the trials with the highest required precision (by about 30 ms; a consequence of this change in movement time is the visible difference in endpoints between the two purple curves in Fig. 2a) and a lengthening of movement times after the trials with the lowest and second highest required precision (by about 17 and 20 ms, respectively). The velocity profiles were also very similar across sessions (shown for the *performance* stages in the inset of Fig. 2). Our subjects did not hit the targets at a fixed position on the screen: the horizontal position at which they tapped the screen was quite variable (the average standard deviation was about 41 mm; averaged across the values for each participant, session and stage) and changed during the course of each stage (the average lag-one autocorrelation was 0.19). Neither the mean position on the screen nor the variability in this position differed systematically between sessions or stages.

Modelling our data

Finding similar variable errors in all the sessions of our study (Fig. 4) suggests that the precision of individual movements does not depend on the precision that is required to hit the target. However, there were systematic differences between the sessions in other measures (Figs. 5, 6), so we decided to ascertain that such differences could arise without the movements being controlled differently. The origin of the differences in systematic errors and in the serial dependence in the errors between the sessions is presumably that the feedback is different. To evaluate whether differences in feedback could account for all the differences between the sessions, we extended a model that was proposed by van Beers (2009) from a purely spatial to a spatio-temporal domain. As in the original model, feedback serves to change the *aim point* on the next trial. This *aim point* can be considered as a set of motor commands that might result in a certain movement endpoint. The original model is summarized by two equations:

$$\mathbf{p}_i = \mathbf{p}_{i-1} - B\mathbf{e}_{i-1} + \mathbf{r}_{\mathrm{pl},i}$$

$$\mathbf{x}_i = \mathbf{p}_i + \mathbf{r}_{\mathrm{ex},i}$$

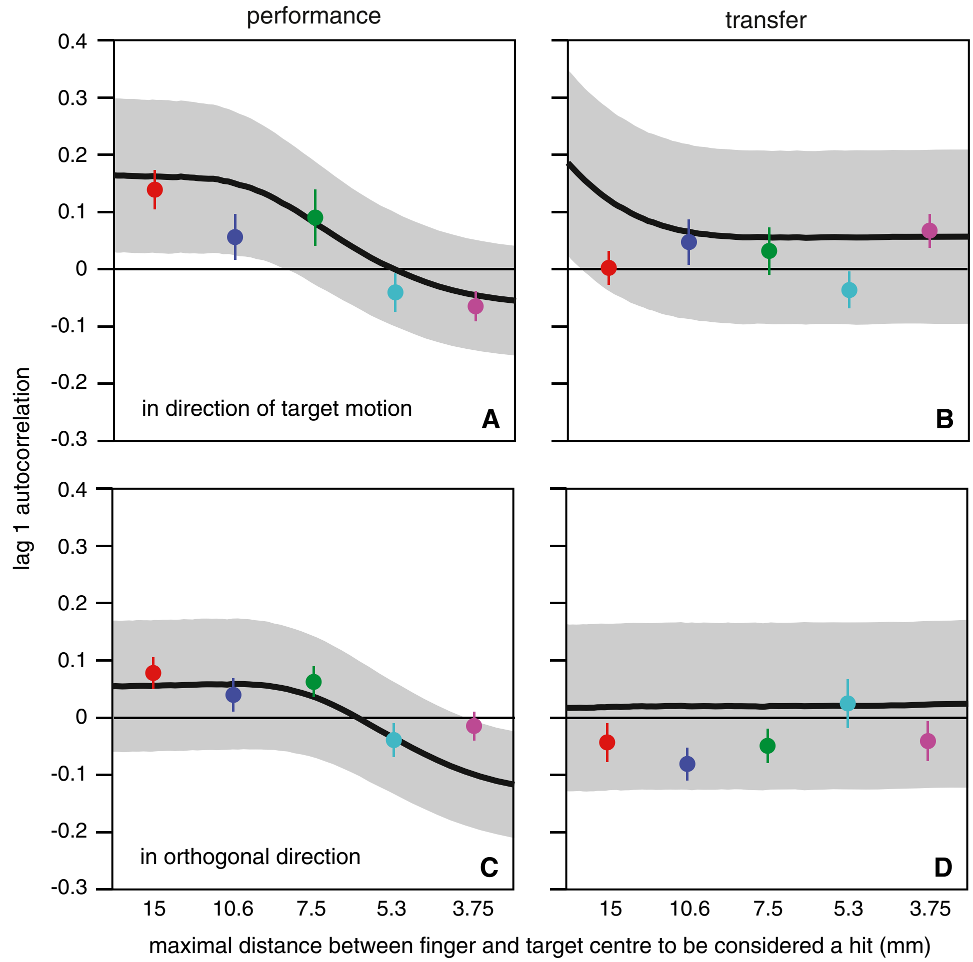

Fig. 6 Serial dependence in the errors. Lag-one autocorrelations in the horizontal (**a**, **b**) and vertical (**c**, **d**) errors during the performance (**a**, **c**) and transfer (**b**, **d**) stages of each session; means and standard errors across the ten subjects. The *curves* and *grey* areas show the mean and standard deviation of the outcome of simulations with a model that is described in the text

In these equations, $\mathbf{p}_i$ is the planned *aim point* on trial i, $\mathbf{x}_i$ is the actual position tapped on trial i, $\mathbf{r}_{\mathrm{pl},i}$ and $\mathbf{r}_{\mathrm{ex},i}$ represent the random independent deviations in planning and execution on trial i, $\mathbf{e}_i$ is the observed error on trial i, and B is the extent to which one corrects for observed errors on the next trial. Considering our evidence that subjects did not always aim for the same position on the screen, we will consider adjustments to the planned *aim point* to be made relative to the target. Van Beers showed that the optimal value of B depends on the relative magnitudes of the variances in planning and execution and that for the optimal value of B the lag-one autocorrelation of the errors is zero.

For the moving targets of the present task, we modify the equations in three ways. The first modification is very straightforward: since the target is now moving, the task is no longer only spatial, so we include terms that result from variability in timing ($\mathbf{r}_{\mathrm{pl}',i}$ and $\mathbf{r}_{\mathrm{ex}',i}$). Such variability influences performance in a velocity-dependent manner, thereby introducing anisotropic spatial effects (as can be seen in the data in Figs. 4 and 5).

The fast motion of the target makes it very difficult to perceptually judge its position at the moment of the tap. The second modification is therefore to assume that subjects relied exclusively on the explicit feedback that we provided to adjust the *aim point*. This feedback provides information about the direction of errors, but not about their amplitudes. Moreover, information is only provided after errors. Thus, subjects modify the *aim point* by a constant amount (C) in the appropriate direction after every miss, and do not modify the *aim point* at all after a hit (as proposed in Brenner and Smeets 2011a). Note that we assume that subjects rely exclusively on the explicit feedback, rather than for instance on deviations of the actual movement from the intended movement (Miall and Wolpert 1996). This assumption is consistent with the finding that for hand movements towards elongated targets, fluctuations that influence the extent to which the goal is achieved are corrected, while similar fluctuations that are irrelevant to succeeding in the task are not (van Beers et al. 2013).

The third modification is a post hoc adjustment to the perceived tendency to tap too far to the right (or equivalently, too early; Figs. 2c, 5a, b). To introduce such behaviour in the model, we added a constant drift term ($\mathbf{d}$) that shifted the *aim point* further to the right after each trial.

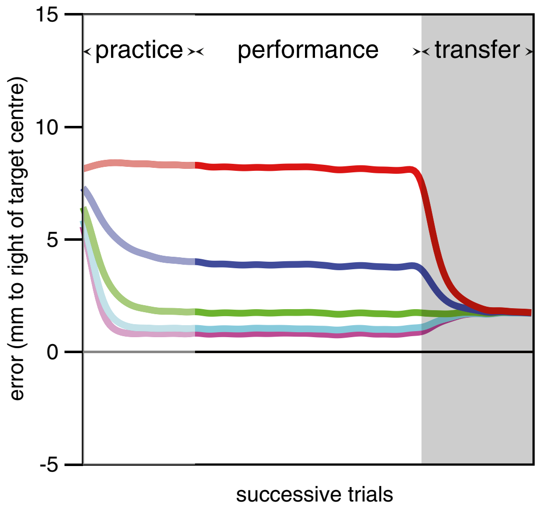

Fig. 7 Simulations of average systematic lateral errors on successive trials. Each curve is based on 5,000 simulated sessions that were analysed as was done for the real data in Fig. 2c. For details see text

These modifications give us the following set of equations:

$$\mathbf{p}_i = \mathbf{p}_{i-1} + C\,\mathbf{f} + \mathbf{r}_{\mathrm{pl},i} + V\,\mathbf{r}_{\mathrm{pl}',i} + \mathbf{d}$$

$$\mathbf{x}_i = \mathbf{p}_i + \mathbf{r}_{\mathrm{ex},i} + V\,\mathbf{r}_{\mathrm{ex}',i}$$

In these equations, V is the velocity of the target (40 cm/s to the right) and $\mathbf{f}$ is a vector representing the direction of the feedback (a zero vector for a hit; a unit vector in the opposite direction than the error for a miss). The aim point $\mathbf{p}_i$ and position of the tap $\mathbf{x}_i$ are described here in spatial terms, but since they are defined relative to the target all adjustments and errors in the lateral direction could also be described in temporal terms.

Figure 7 shows the mean time course of the horizontal component of $\mathbf{x}_i$ as determined by running 5,000 simulations for each required precision. We determined values for the six parameters of our model for which the simulations match the data. Four of the six parameters are magnitudes of variability: random variability was drawn from zero-mean, normal distributions with standard deviations of 0.2 mm and 2 ms for noise that influences the plan ($\mathbf{r}_{\mathrm{pl},i}$ and $\mathbf{r}_{\mathrm{pl}',i}$) and of 2.8 mm and 8 ms for noise that only influences execution ($\mathbf{r}_{\mathrm{ex},i}$ and $\mathbf{r}_{\mathrm{ex}',i}$). Apart from these random effects, the plan also changed by 2 mm after each miss (C) and drifted in the direction of target motion by 0.2 mm per trial ($\mathbf{d}$). We based the initial value of $\mathbf{p}_i$ on the first points in Fig. 2c ($\mathbf{p}_0$ is 8 mm to the right of the target), but this choice is not critical because its influence decreases rapidly during the practice stage.

Simulations were conducted for a large range of required precision values, including the five that were used in the experiment. For each required precision, we determined the means and standard deviations of the values of each experimental measure. The means and standard deviations (black curves and shaded areas in Figs. 3, 4, 5, 6) were determined separately for the performance and transfer stages. Overall, the simulations produce similar values to the experimental data (compare points and curves in all panels of Figs. 3, 4, 5 and 6 and compare Fig. 2c with Fig. 7). There are some minor differences, such as that the model does not reproduce the observed tendency for subjects to tap above the target (Fig. 5c, d), but the modelling shows that controlling movements in a manner that does not depend on the required precision can reproduce all the data very well.

Discussion

Our main question was whether people would have less variability in their movement errors when the task required higher precision. Analysis of the variability in the position of the tap with respect to the target's position at the moment of the tap shows that they did not (Fig. 4). Consequently, requiring more precise taps led to fewer targets being hit (Fig. 3). Missing more targets meant that there were more trials in which subjects received feedback about the direction of their deviations from hitting the target centre. This additional feedback decreased the systematic tendency to hit to the right of the target centre (Figs. 2c, 5a, b). The lag-one autocorrelation also depended on the required precision, with a tendency to overcorrect for errors when one had to be very precise (negative values) and correct too little when one did not have to be precise (positive values). At least qualitatively, this is what one would expect if the response to feedback did not depend on the required precision. This is also consistent with the lag-one autocorrelation being similar for all sessions in the transfer stages. An intriguing finding is that for the highest required precision, the bias to hit too far to the right (or too early) increased as soon as the feedback changed. This finding suggests that there is something driving subjects to hit further to the right (or to hit earlier) and that this tendency is continuously counteracted by responding to feedback.

We focused on the position of the tap with respect to the target because this is the value that determines whether the target is hit. However, we also determined the variability in the position of the tap on the screen. Such variability did not depend on the required precision either. The positive lag-one autocorrelation in the positions of the taps on the screen, together with the much larger variability in this position than in the errors, suggests that this position drifted during the course of the experiment (van Beers et al. 2013). Such drifts could not have differed systematically between the sessions, because systematically drifting towards hitting the target at different positions on the screen, and therefore at different times, in the different sessions would give rise to differences in initiation or movement times. We did not find such differences. The absence of systematic differences in movement time across sessions is also consistent with the idea that the speed of the finger movements was primarily determined by the target's speed (Brouwer et al. 2005). Note that decreasing the maximal distance between the fingertip and target centre for which the target is considered to have been hit increases the required temporal precision as well as the required spatial precision, so the overall precision does not necessarily increase if one moves more slowly.

In order to better understand the whole combination of results, we simulated performance on our task with a model that combines variability from various sources with responding to feedback. In this model, the variability does not depend on the difficulty of the task, and the difficulty of the task is not considered when responding to feedback. The model simulations were generally very similar to our subjects' data. It is therefore worth considering the underlying assumptions and the parameter values. The assumption that there is both spatial and temporal variability and that there is variability both in movement planning and execution, is hardly controversial (Churchland et al. 2006; Faisal et al. 2008). Neither is the assumption that people shift their aim point in response to feedback (Baddeley et al. 2003; van Beers 2009; van Beers et al. 2013). The idea of a fixed magnitude of adjustments to the aim point is not new (Brenner and Smeets 2011a), but it is certainly not generally accepted (Cheng and Sabes 2007; Faisal and Wolpert 2009; Trommershäuser et al. 2008; Marko et al. 2012; van Beers 2009; Wei and Körding 2009, 2010). A justification for adjustments having a fixed magnitude in our model is that our virtual targets' high speed made it impossible for subjects to reliably judge the magnitude of their errors (despite being able to see their finger approach the target). Relying exclusively on the explicit feedback that we provided would give rise to adjustments that do not scale with the magnitude of the error, other than that there will be an adjustment whenever the deviation from hitting the target centre is beyond the precision limit for that session, and no adjustment if it is within the limit. We obviously cannot be certain that our subjects never supplemented the explicit feedback that we provided with information from seeing how the finger hit (or missed) the target. We also cannot be sure that the magnitude of adjustments is completely independent of the success on previous trials. However, the magnitude of adjustments to the plan does not have to depend on the magnitude or number of errors, or to differ between the sessions, for the simulations to fit the data.

The final assumption in our model is that there is a steady rightward shift in the *aim point*. This assumption is based on our own data, and its origin remains to be determined, as does the extent to which it is specific to our task or set-up. We have no explanation for the systematic tendency to hit to the right of the target centre (or equivalently, to hit too early). A similar overall tendency to hit too early appears to be present in some previous studies (e.g. Tresilian and Plooy 2006), but an overall tendency to hit too late is also sometimes found (e.g. de Azevedo Neto and Teixeira 2011). The systematic bias is largely responsible for the characteristic pattern of systematic errors (Figs. 2c, 5, 7), because the *aim point* appears to drift to the right until it is constrained by the target's right edge. For a larger target, the right edge is further to the right of the target centre, so the aim point can shift further to the right. Consequently, on average, subjects hit further to the right. Considered as a bias to hit too early, an explanation could be that people are used to having to deal with delays when interacting with computer-generated images (and are very good at dealing with them if given sufficient feedback; de la Malla et al. 2012).

How about the values of the parameters? The spatial standard deviation of 2.8 mm is similar to the values found in some earlier studies (Brenner and Smeets 2007, 2011b) but poorer performance has also been reported (Brenner and Smeets 2009). The temporal standard deviation of 8 ms (corresponding to 3.2 mm of target motion) is also better than many estimates of human temporal precision (Brenner and Smeets 2009, 2011b), although slightly more precise performance has also been reported (Brenner et al. 2012; McLeod and Jenkins 1991). In our simulations, about 7 % of the spatial variability and 25 % of the temporal variability are in the plan. Previous studies have estimated that variability in the plan is responsible for 21 % of the variability in movements towards static targets (van Beers 2009) and about 15 % of the variability in movements towards moving targets (de la Malla et al. 2012; combining spatial and temporal variability). It is not evident that these fractions can be compared across studies, because the extent to which variability is present in the plan rather than arising during execution undoubtedly depends on details of the task. We obviously also have no way to judge whether a rightward shift of 0.2 mm per trial is reasonable, but the shift is small enough to be credible. The magnitude of the adjustment (2 mm) is also difficult to evaluate directly, but we can determine whether this is a suitable magnitude given the other parameters and task constraints.

To determine whether 2 mm is a suitable adjustment magnitude, we examined whether making larger or smaller adjustments would have led to better performance. The dashed curves in Fig. 3 show the anticipated success in performing the task for adjustments with half and with twice the magnitude (keeping all other parameters the same). Making smaller (1 mm) adjustments would have clearly resulted in poorer performance. Making larger (4 mm) adjustments would have improved performance slightly when it was relatively easy to hit the targets, but would have resulted in poorer performance when it was relatively hard to do so. Thus, 2-mm adjustments are quite suitable for this task. The dotted curves in Fig. 3 show what the performance would be like if subjects always aimed at the centre of the target (with no drift and no corrections). This can be considered to be the best possible performance for the assumed variability. The actual performance is obviously poorer than this, but the difference is not very large. This confirms that near-optimal performance can be achieved through adjustments that are primarily based on recent experience (Brenner and Smeets 2011a; Narain et al. 2013; Trommershäuser et al. 2005; van Beers 2009, 2012).

The changes in performance that we found may seem disappointing in that all influences of experience on performance were transient, rather than giving rise to persistent improvements (Salmoni et al. 1984). Moreover, our analysis suggests that the influences were restricted to subtle adjustments based on the feedback on preceding trials, while maintaining the overall spatio-temporal movement profile (Fig. 2a, b). An advantage of adjusting one's movements according to the principles underlying our model is that this does not require detailed long-term recollection of past performance, for instance in the form of knowledge about the precision of all possible movements (to select the best one) or about the origins of the variability in the chosen movement (to tune the magnitude of adjustments to the relative contributions of fluctuations in planning and in execution). This strategy is well suited to cope with tiring muscles, additional forces associated with lifting objects, offsets introduced by using a tool to perform a task, visual distortions produced by wearing spectacles, and so on. It remains to be seen whether extensive training on a task would result in permanent improvements in performance, and in particular whether the individual movements can become more precise after extensive training.

Acknowledgments We wish to thank Jenny Edner for collecting the data.

References

Alexander RM (1997) A minimum energy cost hypothesis for human arm trajectories. Biol Cybern 76:97–105

Baddeley RJ, Ingram HA, Miall RC (2003) System identification applied to a visuomotor task: near-optimal human performance in a noisy changing task. J Neurosci 23:3066–3075

Battaglia PW, Schrater PR (2007) Humans trade off viewing time and movement duration to improve visuomotor accuracy in a fast reaching task. J Neurosci 27:6984–6994

Berret B, Darlot C, Jean F, Pozzo T, Papaxanthis C, Gauthier JP (2008) The inactivation principle: mathematical solutions minimizing the absolute work and biological implications for the planning of arm movements. PLoS Comput Biol 4:e1000194

Berret B, Chiovetto E, Nori F, Pozzo T (2011) Evidence for composite cost functions in arm movement planning: an inverse optimal control approach. PLoS Comput Biol 7:e1002183

Brenner E, Smeets JBJ (2005) Intercepting moving targets: why the hand's path depends on the target's velocity. In Rogowitz BE, Pappas TN, Daly SJ (eds) Proceedings of SPIE-IS&T electronic imaging on human vision and electronic imaging X, vol 5666. SPIE, pp 374–384

Brenner E, Smeets JBJ (2007) Flexibility in intercepting moving objects. J Vis 7:14

Brenner E, Smeets JBJ (2009) Sources of variability in interceptive movements. Exp Brain Res 195:117–133

Brenner E, Smeets JBJ (2011a) Quickly 'learning' to move optimally. Exp Brain Res 213:153–161

Brenner E, Smeets JBJ (2011b) Continuous visual control of interception. Hum Mov Sci 30:475–494

Brenner E, van Dam M, Berkhout S, Smeets JBJ (2012) Timing the moment of impact in fast human movements. Acta Psychol 141:104–111

Brouwer AM, Brenner E, Smeets JBJ (2000) Hitting moving objects. The dependency of hand velocity on the speed of the target. Exp Brain Res 133:242–248

Brouwer AM, Smeets JBJ, Brenner E (2005) Hitting moving targets: effects of target speed and dimensions on movement time. Exp Brain Res 165:28–36

Cheng S, Sabes PN (2007) Calibration of visually guided reaching is driven by error-corrective learning and internal dynamics. J Neurophysiol 97:3057–3069

Churchland MM, Afshar A, Shenoy KV (2006) A central source of movement variability. Neuron 52:1085–1096

de Azevedo Neto RM, Teixeira LA (2011) Intercepting moving targets: does memory from practice in a specific condition of target displacement affect movement timing? Exp Brain Res 211:109–117

de la Malla C, López-Moliner J, Brenner E (2012) Seeing the last part of a hitting movement is enough to adapt to a temporal delay. J Vis 12(10):1–15

Diedrichsen J, White O, Newman D, Lally N (2010) Use-dependent and error-based learning of motor behaviors. J Neurosci 30:5159–5166

Faisal AA, Wolpert DM (2009) Near optimal combination of sensory and motor uncertainty in time during a naturalistic perception-action task. J Neurophysiol 101:1901–1912

Faisal AA, Selen LP, Wolpert DM (2008) Noise in the nervous system. Nat Rev Neurosci 9:292–303

Fitts PM, Peterson JR (1964) Information capacity and discrete motor responses. J Exp Psychol 67:103–112

Gray R (2009) How do batters use visual, auditory, and tactile information about the success of a baseball swing? Res Q Exerc Sport 80:491–501

Harris CM, Wolpert DM (1998) Signal-dependent noise determines motor planning. Nature 394:780–784

Knill DC, Bondada A, Chhabra M (2011) Flexible, task-dependent use of sensory feedback to control hand movements. J Neurosci 31:1219–1237

Marko MK, Haith AM, Harran MD, Shadmehr R (2012) Sensitivity to prediction error in reach adaptation. J Neurophysiol 108:1752–1763

McLeod P, Jenkins S (1991) Timing accuracy and decision time in high-speed ball games. Int J Sport Psychol 22:279–295

Miall RC, Wolpert DM (1996) Forward models for physiological motor control. Neural Netw 9:1265–1279

Nagengast AJ, Braun DA, Wolpert DM (2011) Risk sensitivity in a motor task with speed-accuracy trade-off. J Neurophysiol 105:2668–2674

Narain D, van Beers RJ, Smeets JB, Brenner E (2013) Sensorimotor priors in nonstationary environments. J Neurophysiol 109:1259–1267

Patton JL, Wei YJ, Bajaj P, Scheidt RA (2013) Visuomotor learning enhanced by augmenting instantaneous trajectory error feedback during reaching. PLoS ONE 8:e46466

Salmoni AW, Schmidt RA, Walter CB (1984) Knowledge of results and motor learning: a review and critical reappraisal. Psychol Bull 95:355–386

Schmidt RA, Zelaznik H, Hawkins B, Frank JS, Quinn JT Jr (1979) Motor-output variability: a theory for the accuracy of rapid motor acts. Psychol Rev 86:415–451

Shmuelof L, Huang VS, Haith AM, Delnicki RJ, Mazzoni P, Krakauer JW (2012) Overcoming motor "forgetting" through reinforcement of learned actions. J Neurosci 32:14617–14621

Todorov E, Jordan MI (2002) Optimal feedback control as a theory of motor coordination. Nat Neurosci 5:1226–1235

Tresilian JR, Plooy A (2006) Systematic changes in the duration and precision of interception in response to variation of amplitude and effector size. Exp Brain Res 171:421–435

Tresilian R, Oliver J, Carroll J (2003) Temporal precision of interceptive action: differential effects of target size and speed. Exp Brain Res 148:425–438

Trommershäuser J, Gepshtein S, Maloney LT, Landy MS, Banks MS (2005) Optimal compensation for changes in task-relevant movement variability. J Neurosci 25:7169–7178

Trommershäuser J, Landy MS, Maloney LT (2006) Humans rapidly estimate expected gain in movement planning. Psychol Sci 17:981–988

Trommershäuser J, Maloney LT, Landy MS (2008) Decision making, movement planning and statistical decision theory. Trends Cogn Sci 12:291–297

van Beers RJ (2009) Motor learning is optimally tuned to the properties of motor noise. Neuron 63:406–417

van Beers RJ (2012) How does our motor system determine its learning rate? PLoS ONE 7(11):e49373

van Beers RJ, Brenner E, Smeets JBJ (2013) Random walk of motor planning in task-irrelevant dimensions. J Neurophysiol 109:969–977

Wei K, Körding K (2009) Relevance of error: what drives motor adaptation? J Neurophysiol 101:655–664

Wei K, Körding K (2010) Uncertainty of feedback and state estimation determines the speed of motor adaptation. Front Comput Neurosci 4:11