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RESEARCH ARTICLE

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Limits to human movement planning with delayed and unpredictable onset of needed information

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Abstract In motor tasks with explicit rewards and penalties, humans choose movement strategies that nearly maximize expected gain (Trommershäuser et al. in J Opt Soc Am A 20:1419–1433, 2003). Here, we examine whether performance is still close to optimal when information about payoffs is not available prior to movement onset. Subjects rapidly touched a target region while trying to avoid hitting an overlapping penalty region placed randomly to the left or right of the target. Subjects received rewards and incurred penalties for hitting the corresponding regions. Late responses (>700 ms) were heavily penalized. The penalty region was displayed 0, 200 or 400 ms after the reward region and the subject could not know where it would be until then. Reaction times to begin the movement after stimulus appearance were constant across conditions. Median reaction times were approximately 200 ms, i.e., the time the penalty was first displayed in the 200 ms delay condition. Performance was compared to that of an optimal movement planner that chooses mean end points to maximize expected gain despite movement variability. In the 0 and 200 ms delay conditions, subjects selected strategies that did not differ significantly from optimal, indicating that humans are able to plan their movements well despite delayed and unpredictable onset of information. Performance dropped below optimal in the 400 ms delay condition, with mean movement end points closer to the penalty region than predicted by the optimal strategy (in the high-penalty condition). We conclude that relevant information concerning the reward structure is required between 200 and 400 ms prior to the end of the movement, but can still be integrated into the movement plan after movement initiation.

Keywords Visuo-motor control · Movement planning · Movement under risk · Statistical decision theory

Introduction

Successful movement requires both planning and improvisation. Movement planning may involve processing of stored information about the final arm position (Rosenbaum et al. 1995; Sabes and Jordan 1997) as well as information about the target position (Desmurget et al. 1998; Diedrichsen et al. 2004). After the movement is initiated, however, the target and its environment may change unexpectedly. Several groups of researchers have demonstrated that the motor system can update a planned movement in response to unanticipated changes in position, velocity and visual properties of the target (Brenner and Smeets 2004; Elliot et al. 1999; Saunders and Knill 2004; Schmidt 2002). These and other researchers have examined the relative importance of planning prior to movement initiation and corrective processes based on feedback during the movement (Brenner and Smeets 2004; Castiello 2001; Connolly and Goodale 1999; Desmurget et al. 1998; Diedrichsen et al. 2004; Elliot et al. 1999; Glover and Dixon 2002; Goodale and Westwood 2004; Hamilton and Wolpert 2002; Howard and Tipper 1997; Jeannerod 1988; Keele and Posner 1968; Rosenbaum et al. 1995; Sabes and Jordan 1997; Saunders and Knill 2004; Woodworth 1899).

Typically the time of target display is varied with respect to the time of movement initiation to study how visual information about the movement goal is

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integrated into the movement plan (see e.g., Desmurget et al. 1998). To study corrective processes of online control, the target is suddenly displaced during the movement and the delays are estimated until the motor response follows the shift in target position (Brenner and Smeets 2004; Saunders and Knill 2004).

However movement planning involves more than directing a movement at a visual target. Failures to reach the movement goal or deviations from the intended trajectory may lead to drastic consequences (e.g., by accidentally hitting an obstacle). We therefore studied movement planning in a task in which the goal of the movement was not defined by a visual stimulus alone. Instead two visual stimuli differing in color were presented on the screen. While a green region always indicated the goal of the movement, a second, red penalty region was presented close to the target region. Hits within the target region gained a monetary reward; accidental hits within the penalty region incurred a monetary cost. In some of the trials, the penalty region was displayed after the target region, forcing subjects to direct their movements away from the center of the target region during the movement. The penalty region was displayed either roughly 200 ms before, at the time of, or 200 ms after movement onset. The current study was performed to test whether information about the configuration of monetary payoffs can be integrated into the movement plan after the movement is initiated.

Under conditions in which target and penalty region are presented roughly 200 ms prior to movement onset, humans have been shown to choose movement strategies that nearly maximize expected gain (Trommershäuser et al. 2003b). In selecting an optimal movement strategy, a subject has to shift the mean movement end point away from the center of the green target region to minimize the risk of accidental hits into the penalty region. This shift is larger for closer penalty regions and higher penalty values. In shifting their mean movement end point away from the target center (and from the penalty region), subjects adopt a motor strategy that is defined not simply by the spatial position of both circles on the screen, but also depends on the subject's motor variability and the rewards and penalties assigned to target and penalty region. Delayed presentation of the penalty region therefore forces subjects to update this motor strategy in response to a change in visual, spatial and monetary information. The delays in presenting the penalty region were chosen to include presentation of information about the penalty position prior to movement onset (Delay = 0 ms), with movement onset (Delay = 200 ms) or after (Delay = 400 ms). In addition, we compared performance to a model of optimal movement planning (Trommershäuser et al. 2003a, b) to explore the limits of movement planning with delayed onset of information about the movement goal.

Materials and methods

Apparatus

The experimental apparatus was similar to that used previously (Trommershäuser et al. 2003a, b). Each subject was seated in front of a touch screen (AccuTouch from Elo TouchSystems, accuracy < ±2 mm standard deviation, resolution of 15,500 touch points/cm^2) which registered the movement end point. A chin rest was used to control the viewing distance, which was 44 cm in front of the touch screen. The computer keyboard was mounted on the table and centered in front of the monitor. A small notch on the keyboard marked the starting position for the movement. The experimental room was dimly lit. The experiment was run using the Psychophysics Toolbox (Brainard 1997; Pelli 1997) on a Pentium III Dell Precision workstation. Motor trajectories were measured using an Optotrak 3020 Motion Tracking Device. A rigid configuration of three sensors mounted on a light piece of metal was attached to the subject's right index finger near the finger tip, but not so near as to interfere with the subject's touching movements. At the beginning of every experimental session, a calibration procedure was performed to ensure that the center of the subject's right index finger pad, estimated from sensor measurements, was aligned with the touchscreen measurements.

Stimuli

The stimuli consisted of one green target region and possibly one red penalty region. The target region was an open green circle and the penalty region was a filled red disk. Overlap of the target and penalty was readily visible. The target and penalty regions had radii of 8 mm/32 pixel. The center of the penalty region was 8 ("Near") or 12 mm ("Far"), left or right of the center of the target region (Fig. 1a). The penalty region was either presented at trial start together with the target region (Delay = 0 ms), 200 ms after presentation of the target region (Delay = 200 ms) or 400 ms into the trial (Delay = 400 ms) (Fig. 1b).

The target position was chosen randomly from a uniform distribution on a square with a range of ±22 mm (vertically and horizontally) relative to screen center. The penalty position was chosen randomly relative to the target center.

Procedure

The procedure in a single trial was similar to that employed by Trommershäuser et al. (2003a, b). Subjects were instructed to rapidly touch a green target region while trying to avoid hitting an overlapping red penalty region placed randomly to the left or right of the target.

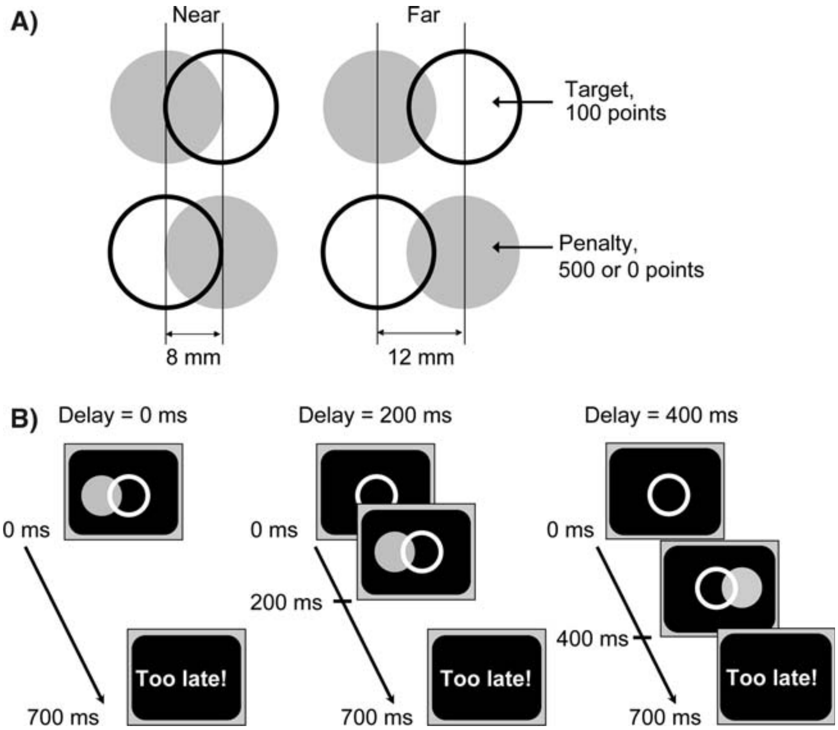

Fig. 1 Stimulus configurations and basic experimental design. **a** Subjects pointed at a green target and a red penalty region (here displayed in gray). The target and penalty areas were circular with radius 8 mm/32 pixel. The target was displaced leftward or rightward of the penalty region. The distance between the centers of the target and penalty regions was either 8 mm/32 pixel ("Near") or 12 mm/40 pixel ("Far"). **b** Basic experimental design. First, the target was presented, at which point the subject could begin the movement. The penalty region could either be presented simultaneously with the target region (Delay = 0 ms), 200 ms after presentation of the target region (Delay = 200 ms) or 400 ms after presentation of the target region (Delay = 400 ms). The overall time limit for the subjects' response was 700 ms

A target hit was always worth 100 points. A penalty hit cost zero or 500 points, and the penalty value was constant during a block of trials. If the subject touched the region where the target and penalty overlapped, both the reward and penalty were incurred. If a subject moved from the starting position before or within 100 ms after stimulus presentation, the trial was abandoned and repeated later during that block. Subjects were instructed to earn as many points as possible. Subjects were required to complete the finger movement within 700 ms of the presentation of the stimulus; if they did not, they incurred a timeout penalty of 1,000 points.

Subjects first underwent a training session with no penalty to learn the speeded pointing task including its time constraints. The training session consisted of 270 trials in which the target region was always presented together with the penalty region (Delay = 0 ms). The time constraint of completing the response was slowly decreased across the 270 trials. The first 30 trials were run without a time limit for the response (and penalty values of zero points), followed by four blocks of 20 trials each with a time limit of 850 ms and penalty values alternating between zero and 200 points, followed by eight blocks of 20 trials each with a time limit of 700 ms and penalty values alternating between zero and 200 points. After the training session, the time limit for the response was held constant at 700 ms throughout the experiment and data collection began. Data were collected in two sessions of 60 min duration, run on two consecutive days. Each session consisted of a total of 444 trials: 12 warm-up trials (with penalty values of zero) followed by 12 blocks of 36 trials of data recording. Penalty values alternated between zero and 500 points across blocks. Within a single block, each of the four spatial configurations was presented three times for each of the three delay conditions in random order. Thus, subjects did not know whether the penalty region would be presented at target onset or delayed.

Subjects and instructions

Five subjects participated. All subjects were male and ranged in age from 24 to 36 years. All were unaware of the experimental purpose and were paid for their participation; they also received bonus payments determined by their cumulative score (25 cents per 1,000 points). All subjects had normal or corrected-to-normal vision. All but one were right handed. Subjects used their right index finger for the pointing movement. Subjects were told the payoffs and penalties before each block of trials. Subjects gave informed consent before testing.

Model of optimal movement planning

Subjects' performance in the task was compared to an optimal movement strategy based on statistical decision theory (Trommershäuser et al. 2003a, b). Here, we summarize the key elements of the model as applied to the task. In this model the optimal movement strategy is the one that maximizes expected gain.

In our experiment, the scene is divided into three regions: a circular target region (R_1) with a positive gain, a circular penalty region (R_2) with no or negative gain, and the background (no gain). An optimal visuo-motor strategy S on any trial is one that maximizes the subject's expected gain

$$\Gamma(S) = \sum_{i=1}^{2} G_i P(R_i \mid S) + G_{\text{timeout}} P(\text{timeout} \mid S). \tag{1}$$

$P(R_i|S)$ is the probability, given a particular choice of strategy S, of reaching region R_i before the time limit (t = timeout) has expired; G_i is the gain the subject receives if region R_i is reached on time ($G_1 = 100$ points; $G_2 = 0$ or -500 points). The last term in Eq. 1 deals with timeout penalties.

In our experiments, subjects win and lose points by touching the reward and penalty regions before the timeout. Penalties and rewards depend only on the position of the end point, so a strategy S can be identified with the mean end point $(\bar{x}, \bar{y})$ that results from adopting strategy S. As in previous experiments, we found that subjects' movement variance was the same in the vertical and horizontal directions (and stable throughout the experiment). Thus, we assume that the movement end points (x, y) are distributed according to a spatially isotropic Gaussian distribution with variance σ^2,

$$p(x, y|\bar{x}, \bar{y}, \sigma^2) = \frac{1}{2\pi\sigma^2} \exp\left[-\left[(x-\bar{x})^2 + (y-\bar{y})^2\right] \Big/ 2\sigma^2\right]. \tag{2}$$

The probability of hitting region R_i is

$$P(R_i|\bar{x}, \bar{y}, \sigma^2) = \int_{R_i} p(x, y|\bar{x}, \bar{y}, \sigma^2)\mathrm{d}x\mathrm{d}y. \tag{3}$$

As in our previous experiments, the probability of a timeout is effectively constant over the limited range of relevant screen locations. Thus, the optimal movement strategy corresponds to the mean end point $(\bar{x}_{\text{MEG}}, \bar{y}_{\text{MEG}})$ that maximizes

$$\Gamma(\bar{x}, \bar{y}) = \sum_{i=1}^{2} G_i P(R_i|\bar{x}, \bar{y}, \sigma^2). \tag{4}$$

In our experiment, the optimal strategy $(\bar{x}_{\text{MEG}}, \bar{y}_{\text{MEG}})$ varies with the position and magnitude of the penalty. When the penalty is zero, the optimal mean end point is the center of the target region. For non-zero penalties, the optimal mean end point shifts away from the penalty region and, therefore, away from the center of the target. This shift is larger for greater penalties, for penalty regions closer to the target, and for subjects with greater motor uncertainty σ^2 (Trommershäuser et al. 2003a, b).

Motor trajectories in the presence of visual information provided after movement onset have been found to be different from motor trajectories directed at a stimulus configuration present before movement onset (e.g., Glover and Dixon 2002). For penalty values presented after target onset (Delay = 200 or 400 ms), the subject does not have all the information required to compute the MEG aim point until after movement initiation. Thus, a calculation of an updated aim point and a mid-course correction may be required during the movement. This could increase the value of σ^2 or change the shape of the movement end point distribution. Changes in value or shape of the end point distribution can result in different optimal motor strategies. However, we did not find differences in σ^2 for different times of penalty onset (see below). We therefore compared performance under the three delay conditions with the optimal performance defined by Eq. 4 based on a single estimate of σ^2.

Data analysis

For each trial, we recorded *reaction time* (time from target onset to release of the space bar), *movement time* (time from release of the space bar to arrival at the touch screen), the (x, y) *screen position* that was hit, and the *score*. After movement start, the Optotrak recorded the finger position at a rate of 200 Hz. Trials in which the subject initiated the movement less than 100 ms after presentation of the start signal or hit the screen later than 700 ms after presentation of the start signal were excluded from the analysis. End points on the screen that were further than 6 cm from the target center were classified as errors (e.g., knuckle hits) and were excluded from the analysis. Each subject contributed approximately 864 data points (36 repetitions of each condition). Movement end point data were collapsed across left-right symmetric configurations. Movement end points were recorded relative to the center of the target circle. We calculated movement speed profiles as the distance traveled in space between successive time samples divided by the time between samples.

Reaction and movement times

Once the training session was completed, reaction and movement times differed significantly across subjects, but were consistent across conditions and throughout the experiment (Tables 1 and 2).

We asked whether reaction times differed for motor responses when information about the position of the penalty was provided at target onset (Delay = 0 ms) or after target onset (Delay = 200 or 400 ms). We performed pairwise comparisons of the distribution of reaction times for the Delay = 200 and 400 ms conditions with the Delay = 0 ms condition using a Wilcoxon Signed Rank Test. As penalty values were held constant within a block of trials, reaction times were analyzed separately for penalty values of zero and 500.

We asked whether movement times differed for motor responses when information about the position of the penalty was provided with target onset (Delay = 0 ms) or after target onset (Delay = 200 or 400 ms). Movement times were compared using a one-factor repeated

Table 1 Median reaction times for the three delay and two penalty conditions (approx. 144 data points per condition, data averaged across the four spatial conditions)

		ABH	AJK	AOO	MD	SWU
Penalty = 0	Delay = 0 ms	253 ms	310 ms	300 ms	246 ms	172 ms
	Delay = 200 ms	259 ms	301 ms	291 ms	238 ms	180 ms
	Delay = 400 ms	246 ms	302 ms	298 ms	237 ms	171 ms
Penalty = 500	Delay = 0 ms	262 ms	298 ms	319 ms	238 ms	203 ms
	Delay = 200 ms	253 ms	296 ms	321 ms	232 ms	193 ms
	Delay = 400 ms	251 ms	291 ms	309 ms	227 ms	199 ms

Table 2 Mean movement times for the three delay and two penalty conditions (approx. 144 data points per condition, data averaged across the four spatial conditions)

		ABH	AJK	AOO	MD	SWU
Penalty = 0	Delay = 0 ms	273 ms	275 ms	208 ms	319 ms	341 ms
	Delay = 200 ms	280 ms	277 ms	207 ms	337 ms	331 ms
	Delay = 400 ms	290 ms	276 ms	211 ms	345 ms	337 ms
	ANOVA	$F(2,413)=3.110$ $P=0.046$	$F(2,425)=0.129$ $P=0.879$	$F(2,496)=0.162$ $P=0.851$	$F(2,424)=8.781$ $P<0.001$	$F(2,557)=2.366$ $P=0.095$
Penalty = 500	Delay = 0 ms	271 ms	309 ms	218 ms	306 ms	329 ms
	Delay = 200 ms	294 ms	313 ms	232 ms	332 ms	351 ms
	Delay = 400 ms	314 ms	320 ms	240 ms	360 ms	363 ms
	ANOVA	$F(2,383)=16.078$ $P<0.001$	$F(2,410)=2.136$ $P=0.119$	$F(2,482)=2.185$ $P=0.114$	$F(2,418)=26.299$ $P<0.001$	$F(2,492)=22.353$ $P<0.001$

measures ANOVA, the factor being the delay condition (see Results and Table 2).

Consistency of motor responses across subjects

Movement end points and movement end point variability were similar for all subjects ($\sigma=3.79$ mm for MD to $\sigma=4.54$ mm for ABH). We therefore pooled data across subjects (average movement end point variability $\sigma=4.23$ mm). Movement end point variability did not depend on delay condition. Also, movement end points did not differ with respect to spatially symmetric configurations. Therefore, for the analysis of movement end points in the x-direction, data were pooled across conditions that were spatially symmetric. We computed the deviations from the center of the reward circle for symmetric conditions (e.g., "left, far" and "right, far") and then multiplied the deviations for the "left" condition by -1 to reflect them about the center. After reflection, we pooled the right and left deviations.

Differences in mean end points across spatial and penalty conditions

The x- and the y-coordinate of movement end points were compared across spatial, delay and penalty conditions using a three-factor, repeated measures analysis of variance (ANOVA) for each subject individually. As end points differed in the x-direction across delay conditions (see Results), we also compared end points in a post-hoc analysis using linear contrasts.

Efficiency of end points for different delays of penalty onset

We asked whether subjects were still able to plan their movements efficiently with delayed information about the penalty location. We define efficiency in our task as the actual score divided by the optimal score derived from the model of optimal movement planning. Our model predicts clear differences in mean movement end points in the "near" condition when the penalty is large and not far from the target. We computed efficiencies for the near condition as the ratio of the subject's cumulative score and the optimal score (i.e., the maximum expected gain) predicted by the model of optimal movement planning. The optimal score was computed based on each subject's movement variability. The 95% confidence interval of optimal performance was computed across all subjects for an optimal movement planner in a Monte Carlo simulation consisting of 100,000 runs of the optimal movement planner performing the experiment with the average movement end point variability of $\sigma=4.23$ mm (for the "left, near" and "right, near" conditions, for penalty values of zero and 500, respectively). Performance was classified as significantly different from optimal when the actual score fell outside the 95% confidence interval of optimal performance.

Results

We first report evidence that subjects initiated their movement independent of whether they had complete knowledge about where the penalty region would be located and when it would be displayed. We then demonstrate that movement dynamics remained unaffected by the presentation of the penalty region in the penalty zero condition, indicating that the sudden visual onset did not interrupt movement execution. We finally provide evidence that subjects were still able to plan their movements with high efficiency if information about the penalty location was first available at movement onset, but that they fail to do so if information was presented with a delay of 400 ms, about 200 ms before movement end.

Subjects initiate movement independent of whether they know where and when the penalty will appear

We first asked whether reaction times differed for movements when the penalty was presented together with the target region, i.e., prior to movement onset, or some time later in the trial. We found that reaction times did not differ significantly whether the penalty appeared together with the target region or during the movement (Wilcoxon Signed Ranks Test, $P > 0.064$, except for reaction times of ABH, penalty values of 500, Delay = 400 ms vs. 0 ms; $z = -3.057$; $P = 0.002$, $N = 144$; see Table 1). This is also evident from Fig. 2 which shows no difference in speed profiles for different times of penalty onset.

Movements were not disrupted by the sudden display of the penalty during the movement, and still exhibited the same bell shaped velocity profiles as found for trials in which the penalty was zero (Fig. 2). In the penalty zero condition, mean movement end points did not differ significantly from the center of the green target (Fig. 3a), independent of time of display of the penalty region. In addition, movement dynamics remained unaffected by the delayed presentation of the penalty region. Movement times did not differ systematically across the three conditions of time of penalty display in the penalty zero condition (Table 2).

Subjects still compensate for delayed presentation of penalty position at movement onset

We next asked whether performance was affected by the delayed presentation of the penalty display. Consistent with the predictions of our model of optimal movement planning, movement end points did not differ significantly in the *y*-direction across spatial, delay and penalty conditions ($P > 0.05$ for all conditions and subjects). We found that subjects still managed to adjust their movement when the penalty region was presented with a 200 ms delay. Stimulus presentation with a delay of 200 ms fell in the range of times of movement onset with median reaction times ranging from 171 to 321 ms (Table 1). Movement end points did not differ significantly across the three delay conditions. This lack of overall effect is due to identical shifts in end points for the 0 and 200 ms delay conditions (Fig. 3a, lower panel).

To check for effects in the condition of highest delay (400 ms) compared to the other delay conditions, we

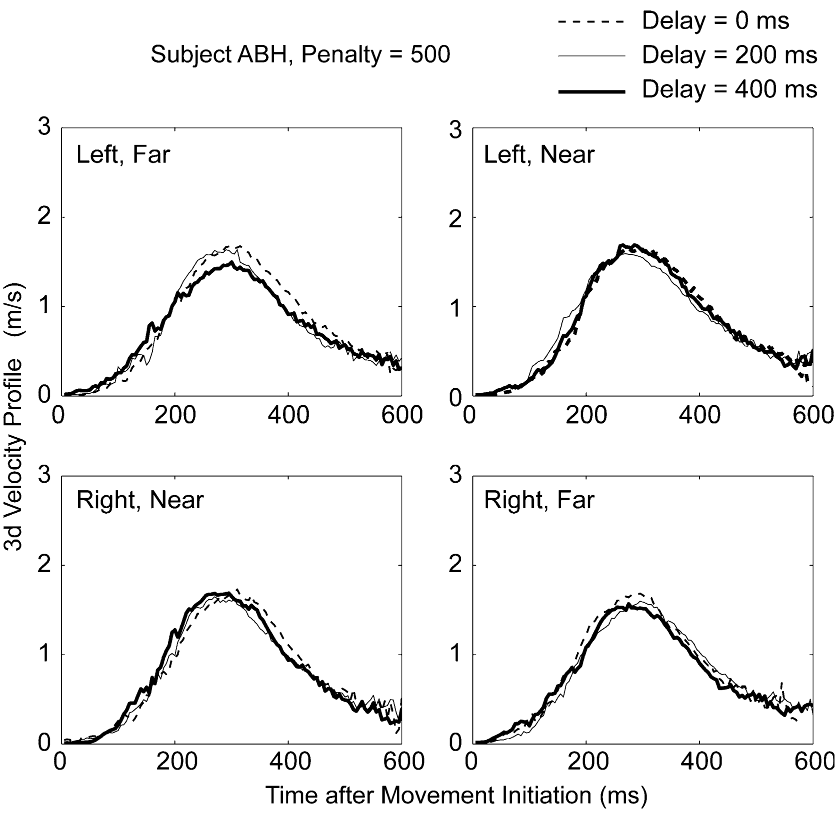

Fig. 2 Speed profiles for different times of presentation of the penalty region (penalty value of 500 only); data presented for a single subject (ABH)

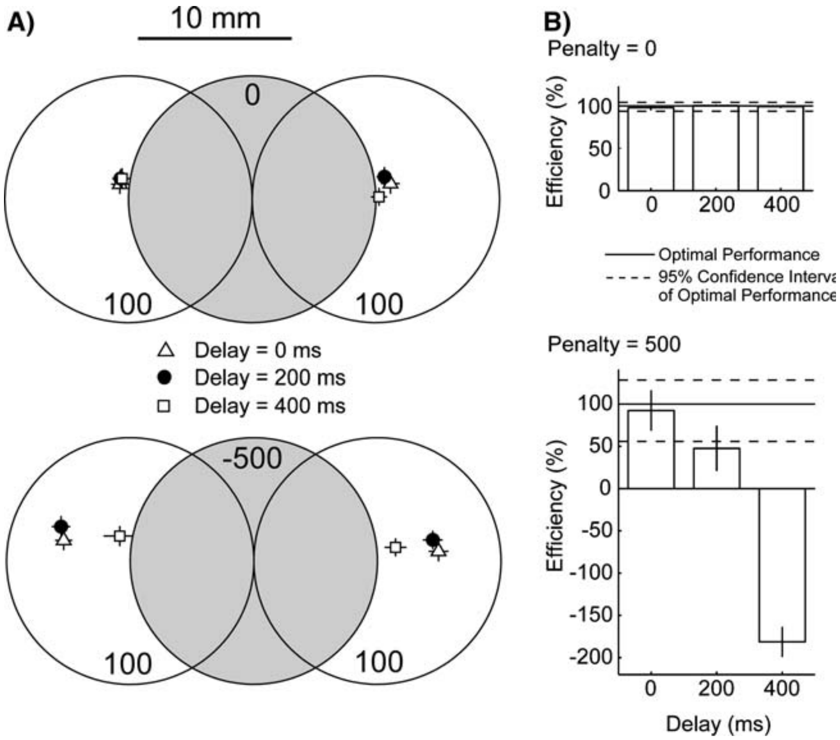

Fig. 3 Mean movement end points and efficiencies for different times of presentation of the penalty region. **a** Mean movement end points for the "Near" condition, with penalty values of zero (*top panel*) and 500 (*lower panel*). Data pooled across five subjects. Error bars indicate ± two standard error of the mean, standard error computed across subjects and trials (approximately 196 data points per condition). **b** Efficiencies for the "Near" condition (averaged across spatially symmetric conditions), with penalty values of zero (*top panel*) and 500 (*lower panel*). Efficiencies computed for each subject individually, based on the subject's movement variability. Data pooled across five subjects. Error bars indicate ± standard error of the mean, standard error computed across subjects. *Solid lines* indicate optimal performance for a subject with average movement variability of $\sigma = 4.23$ mm; *dashed lines* the 95% confidence interval

computed a linear contrast between the combined 0 and 200 ms delay conditions and the 400 ms delay condition (separately for targets located to the right or left of the penalty region, near condition only). We found significant effects for most subjects ($P < 0.05$ except for AJK, right configuration: $t(102) = -0.335$, $P = 0.246$; data Bonferroni corrected for three tests). Accordingly, efficiencies in the 200 ms delay condition were almost as high as in the 0 ms delay condition (> 70%; Fig. 3b). However, efficiency was very low when the penalty region was presented with a 400 ms delay. In fact, all subjects lost points in this condition, as they failed to shift their movements in time to avoid the penalty region (Fig. 3a). Although velocity profiles did not differ significantly for the different penalty delays (Fig. 2), movement times increased slightly with delayed onset of penalty presentation (Table 2).

Information about penalty value is integrated during the movement

Finally, we asked whether we have evidence when information about the penalty region is integrated into the movement plan. Subjects do not shift their movement end points in response to the purely visual display of the penalty region, i.e., when the assigned penalty value is zero (Fig. 3a). Furthermore, we found no evidence that their movements were disrupted by the unexpected visual display of a colored disk, either with penalty values of zero or 500. Subjects do shift their movement end points away from the penalty region in trials in which the penalty value is non-zero, as long as information about the penalty location is available prior to or around movement onset, but fail to do so if information about the penalty location is provided during the movement (Fig. 3b). Figure 4 makes clear that this shift develops gradually across the reach and occurs later in the reach the later information about the penalty region is available. If penalty information is not available prior to movement onset, that information is still integrated during the course of the movement.

Discussion

The purpose of our study was to investigate whether information about the movement goal can be updated after a movement has begun. We studied human movement planning in a task in which subjects attempted

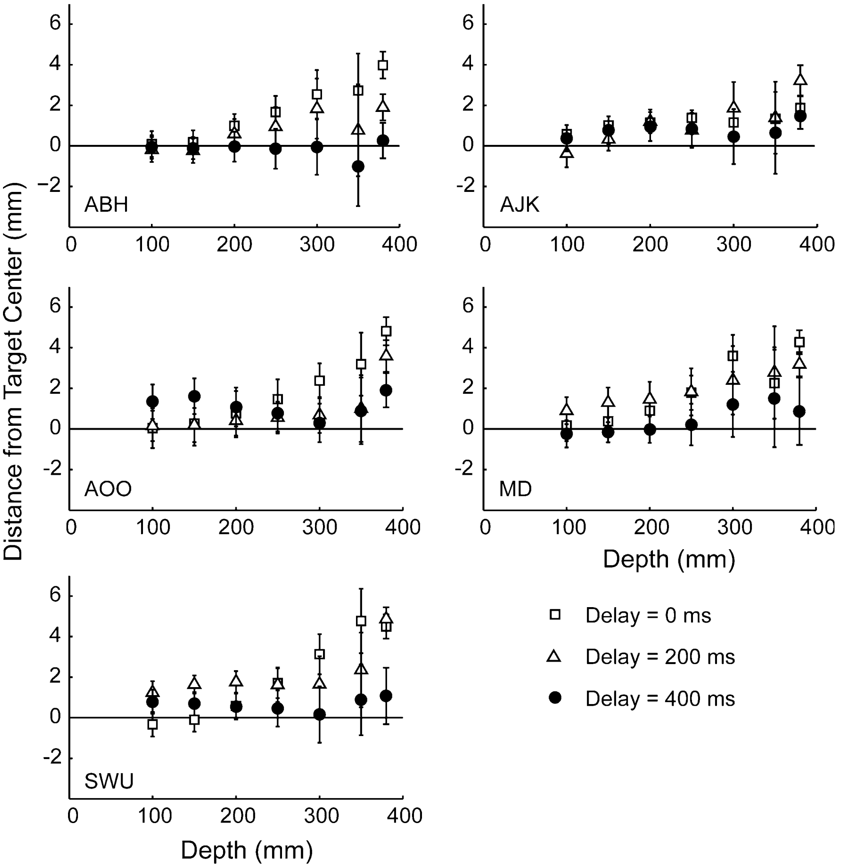

Fig. 4 Change in mean movement end point in the *x*-direction during the movement. Mean fingertip locations in the *x*-direction were computed as a spatial average within the *xy*-plane for different distances in the *z*-direction. Data are displayed for each subject individually; error bars indicate ± one standard error of the mean, approx. 144 data points per delay condition (penalty value of 500, near condition only). Data were pooled for the "left, near", "right, near" conditions

to touch a target region and avoid a nearby overlapping penalty region. The reward region was always visible at the beginning of the trial. The penalty region could appear together with the target region, or delayed by 200 or 400 ms after presentation of the target location. The subject did not know whether the penalty would appear immediately or how long it might be delayed. The position and orientation of the stimulus configuration were varied unpredictably from trial to trial.

The subject was required to complete the response in 700 ms, independent of the penalty delay. This time window of 700 ms included the time for movement initiation as well as the time for movement execution. Median reaction times (time to movement onset) were approx. 200 ms, i.e., the time of display of the penalty region in the condition with medium delay.

We found that, in the longest delay condition, mean movement end points were too close to the penalty region leading to performance that was significantly suboptimal. On the contrary, efficiencies were high in the condition with medium delay, indicating that humans are able to plan their movements with high efficiency even if knowledge of the exact movement goal was provided only at the time of movement onset.

We also found that performance did not suffer appreciably when the movement goal was only available at the time of movement onset (200-ms-delay condition). While movement trajectories diverged less rapidly from the center toward the optimal aim point in comparison with the movement trajectories of the 0-ms-delay condition (Fig. 4), the distribution of mean end points and the measures of efficiency of the conditions in these two conditions did not differ significantly. Note that the movement goal in our task is defined by a complex combination of factors, including the spatial arrangement of the penalty and target regions, the pay-offs assigned to each region, and the subject's movement variability. Yet, efficiencies in the 200-ms-delay condition were only slightly lower than in the 0-ms-delay condition or than those found in our previous studies (Trommershäuser et al. 2003b, 2005). In contrast, if the movement goal was only available 200 ms after the initiation of movement (400-ms-delay condition), efficiency dropped substantially.

To summarize: if the goal of a movement changes shortly after movement is initiated (at about 200 ms after the start of a trial), the motor system can still gradually integrate the changed goal into the movement plan as it unfolds over the next 500 ms. If it is changed more than 200 ms after movement initiation, the motor system is unable to compensate for the changed goal in the roughly 300 ms remaining until contact.

Our results complement findings reported from studies using the so-called double-step paradigm in which a visually specified target is displaced at movement onset of a pointing response (Bridgeman et al. 1979; Komilis et al. 1993; Pélisson et al. 1986; Sarlegna et al. 2004). These studies demonstrated that subjects can rapidly modify arm movements after an unexpected change of target position. It takes subjects about 320 ms to adjust their movements to the displacement in target position when the hand was visible and 390 ms without visual feedback of the hand, indicating that visual feedback of the hand contributes to online corrections of hand movements. Subsequent studies have attempted to further identify contributions of different sources of feedback to the online control of movements. Perturbations of visual feedback of the hand have lead to corrections as early as ~120 ms after the perturbation if they occur in the movement direction and within ~150 ms if orthogonal to movement direction (Saunders and Knill 2004, 2005).

We emphasize that a penalty region is defined by information that is not simply visual in nature, but also by non-visual information such as the pay-off assigned to the penalty region. In particular, our results indicate that subjects only adjust their movements in conditions in which non-zero pay-offs are associated with the penalty region, but manage to ignore the sudden visual display altogether if hitting the penalty region comes without additional cost for the subject. These results indicate that subjects in our experiment indeed adjust their movements in response to changes in the reward structure and not due to the sudden onset of a visual distractor (Castiello 2001; Tipper et al. 1997). We conclude that relevant information concerning the reward structure is required between 200 and 400 ms prior to the end of the movement, but is not necessarily required prior to movement initiation.

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References

Brainard DH (1997) The psychophysical toolbox. Spat Vis 10:433–436

Brenner E, Smeets JB (2004) Colour vision can contribute to fast corrections of arm movements. Exp Brain Res 158:302–307

Bridgeman B, Lewis S, Heit G, Nagle M (1979) Relation between cognitive and motor-oriented systems of visual position perception. J Exp Psychol Hum Percept Perform 5:692–700

Castiello U (2001) The effects of abrupt onset of 2-D and 3-D distractors on prehension movements. Percept Psychophys 63:1014–1025

Connolly JD, Goodale MA (1999) The role of visual feedback of hand position in the control of manual prehension. Exp Brain Res 125:281–286

Desmurget M, Pélisson D, Rosetti Y, Prablanc C (1998) From eye to hand: planning goal-directed movements. Neurosci Biobehav Rev 22:761–788

Diedrichsen J, Werner S, Schmidt T, Trommershäuser J (2004) Immediate spatial distortions of pointing movements induced by visual landmarks. Percept Psychophys 66:89–103

Elliott D, Binsted G, Heath M (1999) The control of goal-directed limb movements: correcting errors in the trajectory. Hum Mov Sci 18:121–136

Glover S, Dixon P (2002) Dynamic effects of the Ebbinghaus illusion in grasping: support for a planning/control model of action. Percept Psychophys 64:266–278

Goodale M, Westwood DA (2004) An evolving view of duplex vision: separate but interacting cortical pathways for perception and action. Curr Opin Neurobiol 14:203–211

Hamilton AFC, Wolpert DM (2002) Controlling the statistics of action: obstacle avoidance. J Neurophysiol 87:2434–2440

Howard LA, Tipper SP (1997) Hand deviations away from visual cues: indirect evidence for inhibition. Exp Brain Res 113:144–152

Jeannerod M (1988) The neural and behavioral organization of goal-directed movements. Oxford University Press, Oxford

Keele SW, Posner M (1968) Processing of visual feedback in rapid movements. J Exp Psychol 77:155–158

Komilis E, Pélisson D, Prablanc C (1993) Error processing in pointing at randomly feedback-induced double step stimuli. J Mot Behav 25:299–308

Pélisson D, Prablanc C Goodale MA, Jeannerod M (1986) Visual control of reaching movements without vision of the limb. II. Evidence of fast unconscious processes correcting the trajectory of the hand to the final position of the double step stimulus. Exp Brain Res 62:303–311

Pelli DG (1997) The VideoToolbox software for visual psychophysics: transforming numbers into movies. Spat Vis 10:437–442

Rosenbaum DA, Loukopoulos LD, Meulenbrock RJ, Vaughan J, Engelbrecht SE (1995) Planning reaches by evaluating stored postures. Psychol Rev 102:28–67

Sabes PN, Jordan MI (1997) Obstacle avoidance and a perturbation sensitivity model for motor planning. J Neurosci 17:7119–7128

Sarlegna F, Blouin J, Bresciani JP, Bourdin C, Vercher JL, Gauthier GM (2004) Online control of the direction of rapid reaching movements. Exp Brain Res 157:468–471

Saunders JA, Knill DC (2004) Visual feedback control of hand movements. J Neurosci 24:3223–3243

Saunders JA, Knill DC (2005) Humans use continuous visual feedback from the hand to control both the direction and distance of pointing movements. Exp Brain Res 162:458–473

Schmidt T (2002) The finger in flight. Real time motor control by visually masked color stimuli. Psychol Sci 13:112–118

Tipper SP, Howard LA, Jackson SR (1997) Selective reaching to grasp: Evidence for distractor interference effects. Vis Cognition 4:1–38

Trommershäuser J, Maloney LT, Landy MS (2003a) Statistical decision theory and trade-offs in the control of motor response. Spat Vis 16:255–275

Trommershäuser J, Maloney LT, Landy MS (2003b) Statistical decision theory and the selection of rapid, goal-directed movements. J Opt Soc Am A 20:1419–1433

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

Woodworth RS (1899) The accuracy of voluntary movement. Psychol Rev Monographs 3:1–114