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RESEARCH ARTICLE

Updating the programming of a precision grip is a function of recent history of available feedback

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Abstract In a recent study (Whitwell et al. in Exp Brain Res 185:111–119, 2008), we showed that the visuomotor system is "cognitively impenetrable" to the extent that explicit predictive knowledge of the availability of visual feedback on an upcoming trial fails to optimize grasping. The results suggested that the effects of trial history, rather than the anticipatory knowledge of the nature of an upcoming trial, plays the most significant role in how the availability of visual feedback is exploited by the visuomotor system when programming grip aperture (e.g., opening the hand wider when visual feedback is unavailable). Here, we provide direct evidence that trial history indeed plays a critical role in the programming of grip aperture. Twelve individuals grasped objects of three different sizes placed at one of two distances either with or without visual feedback of the hand and object (closed- or open-loop trials, respectively). Runs of four consecutive closed- or open-loop trials were interleaved with sequences of closed and open-loop trials that alternated back and forth from trial to trial. Peak grip aperture (PGA) decreased linearly with successive closed-loop trials and increased linearly with successive open-loop trials. We also compared PGA for trials that were preceded by a run of four consecutive closed- (or open-loop) trials with trials that were preceded by only one closed- (or open-loop) trial. This analysis indicated that consistency in the runs of closed- or open-loop trials significantly reduced the effect of the availability of feedback on grasping in the trial following the run. We conclude that while the margin of error observed in precision grasping is largely a function of the availability of visual feedback on the current trial, it is evidently also a function of the recent history of the availability of visual feedback on previous trials.

Keywords Prehension · Visual feedback · On-line control · Motor learning · Trial history

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Introduction

When we reach out to pick up an object we use vision to direct our hand to the location of the object and scale our grip aperture in flight to the object's size. Even though our grip aperture shows this systematic scaling, we open our thumb and fingers wider than the actual size of the object. We "over-size" our grip aperture in order to establish a stable grip on the object and avoid bumping or knocking the object away. Put another way, over-sizing grip aperture on route to the object helps ensure that the pads of the fingers and thumb approach the object at an angle perpendicular to its contact surface (Smeets and Brenner 1999, 2001). Not surprisingly, when visual information is unavailable during the execution of the grasp, we open our hand even wider, a strategy that increases the 'safety margin' in the face of increased uncertainty and reduces the probability of missing or bumping the object.

Although the presence or absence of visual feedback has a clear influence on the kinematics of grasping on the current trial (e.g., Fukui and Inui 2006), it is equally

clear that the consistency of visual feedback (or no visual feedback) across a series of trials also plays a role (Jakobson and Goodale 1991; Whitwell et al. 2008). Thus, Jakobson and Goodale (1991) showed that randomizing the availability of feedback from trial to trial greatly reduces the difference in grip aperture between visually open-loop and visually closed-loop trials that is evident when these two visual feedback conditions are blocked separately. This result suggests that the scaling of grip aperture is influenced by what happened on earlier trials and is not simply reactive to the availability of feedback during the execution of the movement. In a recent study (Whitwell et al. 2008), we replicated this finding but went on to explore whether or not participants were using explicit knowledge about the pattern of trials that had occurred earlier to predict what was going to happen next. To do this we included an additional block of trials in which the open- and closed-loop trials alternated back and forth from trial to trial in a predictable manner. Despite the fact that participants knew what the feedback condition was going to be on every trial (just as they did in the blocked trials), the difference in grip aperture between open- and closed-loop trials was reduced on the alternating trials just as it was on the randomized trials. This finding is consistent with evidence from a range of different paradigms showing that individuals will use experience with previous trials to prepare for an upcoming trial (for review, see Dixon and Glover 2004) and that this preparation can emerge quite independently of any conscious prediction of what might happen on that trial (e.g., Cheng et al 2008; Song and Nakayama 2007).

The design of the Whitwell et al. (2008) study did not permit us to carry out an analysis of specific trial-to-trial effects on grip aperture. In the present experiment, we addressed this issue by using a design that allowed us to examine how grip aperture on a particular trial was affected by the availability of feedback on preceding trials. We interleaved runs of four consecutive closed- or four consecutive open-loop trials within sequences of alternating closed- and open-loop trials. This allowed us to compare grasp kinematics on trials in which visual feedback differed from the immediately preceding trial (switch trials) to those on trials in which the visual feedback conditions repeated over several trials. We predicted that the difference in grip aperture between closed and open-loop trials would be larger for the runs of the same feedback trials than for the runs of alternating trials. In addition, we could test whether or not the difference in grip aperture between closed and open-loop trials would continue to increase with the number of successive trials of a particular feedback condition, and whether or not these effects would influence the subsequent switch trial.

Methods

Participants

Twelve right-handed individuals (six males and six females) aged 18–31 ($M = 20.4$), volunteered to take part in the experiment and were given $10 for their time. Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield 1971). The experiment was approved by the local ethics committee.

Apparatus and stimuli

Visual feedback was controlled with liquid crystal goggles (PLATO goggles; Translucent Technologies, Toronto, ON, Canada). Kinematic data were collected at 200 Hz using an OPTO*TRAK* (Northern Digital, Waterloo, ON, Canada) optoelectronic recording system which measured the 3D spatial location of three infrared emitting diodes (IREDs) attached with adhesive tape at three positions on the right (reaching) hand: on the distal left corner of the index finger nail, on the distal right corner of the thumb nail, and on the skin opposite the styloid process of the ulna. The leads from the IREDs were taped to the medial portion of the right forearm to ensure complete freedom of movement. The experimenter ensured that the pads of skin on both digits were uncovered to ensure normal tactile feedback from the goal objects when grasped. On a given trial, one of the three objects was presented on the surface of the table where participants were seated. Each object was presented at the participant's midline 20 or 35 cm from the centre of a small black button located 15 cm from the edge of the tabletop facing the participant. The experimenter ensured that all participants could grasp the objects comfortably at the furthest distance without leaning forward before the experiment began. The stimuli consisted of three metallic-silver painted rectangular wooden objects 60 mm long and 15 mm high with widths of 15, 30, and 45 mm.

Procedure

In general, the procedure differed little from our previous study (see Whitwell et al. 2008). Briefly, participants began each trial holding the tips of their right index finger and thumb pressed together while depressing the start button. Participants were instructed to reach out, grasp, and lift the object using a precision grip (index finger and thumb) across the width of the object as soon as the goggles became transparent. The object was always positioned such that the long axis was perpendicular to the mid-sagittal axis of the participant. Participants were asked to use a ''natural'' grasp paced at their own speed—neither laboured nor speeded—and to avoid bumping or

missing the object. During the visual closed-loop trials, the goggles remained transparent for 1,500 ms after the release of the start button, permitting a full view of the hand and the object during the execution of the movement. During the visual open-loop trials, the goggles closed as soon as the start button was released, thereby ensuring that neither the hand nor the object was in view during the execution of the movement.

Runs of four consecutive closed- or four consecutive open-loop trials were interleaved within sequences of alternating closed- and open-loop trials. There were 18 runs of consecutive closed-loop trials and 18 runs of consecutive open-loop trials for a subtotal of 144 trials. These 36 runs of four-trial sequences were embedded within 72 alternating closed- and open-loop trials. The number of alternating trials between each run of four same-feedback trials varied pseudo-randomly (0, 2, or 4 trials). The runs alternated with respect to feedback from one run to the next. For example, a given run of four consecutive closed-loop trials was preceded by four consecutive open-loop trials and followed by four consecutive open-loop trials (with a sequence of alternating closed- and open-loop trials separating at least two of the three runs if not all of them). Each object size and distance combination was presented three times for each of the four trial positions within the runs of closed- and open-loop trials. Thus, the trial total (216) and session time (approximately 40 min) were equivalent to that used in our previous study (Whitwell et al. 2008). The trial orders were pseudo-randomized with the following additional criteria: (1) no object of a particular size was repeated on successive trials, (2) no object location was repeated more than twice successively, and (3) for the runs of four same-feedback trials, size and distance combinations were counterbalanced with respect to their position within the runs such that each size and distance combination was replicated at each position three times. Participants were given two 5-min rest periods: one after trial 72 and again after trial 144.

Participants were not told of the nature of the order of the availability of visual feedback. Although unlikely, it is possible that participants could have consciously exploited the trial sequence rules for location and feedback. Therefore, after the experiment was finished, the experimenter asked each participant to explain what he or she thought was the purpose of the experiment. None of the participants indicated that the order or history of visual feedback was the focus of the current study. The experimenter then asked each participant whether or not he or she noticed a pattern in the order of visual feedback, object size, or object location. None of the participants indicated that he or she could discern a systematic pattern for any of these variables. In short, the participants appeared to believe that the sequence of trials was entirely random.

Data collection

Movement onset (or reaction time, RT) was defined as the first of 40 consecutive frames during which the wrist IRED exceeded 40 mm/s. The initial grip aperture (IGA) was defined as the vector distance between the index and thumb IREDs at movement onset. Movement offset was defined as the first of 40 consecutive frames during which the grip aperture velocity (the rate of change in the distance between the thumb and first finger IREDs) fell below 40 mm/s. Peak grip aperture (PGA) was defined as the maximum vector distance between the index and thumb IREDs between movement onset and movement offset. The time to PGA (tPGA) was defined as the elapsed time from movement onset to the PGA. The duration of the post-PGA phase was defined as the elapsed time from tPGA to movement offset. The movement time (MT) was defined as the time between movement onset and movement offset.

Data and statistical analysis

All data were analyzed offline. A number of trials were discarded due to participant or experimenter error (e.g., missing IREDs). For a given dependent measure the experiment-wise average number of trials discarded was 22 of 2,592 (0.8%). The highest discard rate occurred for the post-peak grip aperture phase, 28 of 2,592 (1.1%), while the lowest discard rate occurred for MT, 13 of 2,592 (0.5%). The discard rate for our primary measure of interest, peak grip aperture, was 25 of 2,592 (1.0%).

Trials that were immediately preceded by a trial of the opposite feedback condition were "switch" trials. Thus, in addition to the trials in which feedback conditions were alternated, the first trial of each embedded run of four consecutive closed- or open-loop trials was a switch trial; that is, in terms of immediate trial history the first trial of a run of same-feedback trials was just like an alternating trial. The trial that immediately followed a run of four consecutive closed- or open-loop trials was also, by definition, a switch trial, but this trial had the distinction of being preceded by a considerable number of trials of the opposite feedback type. We were therefore able to compare grip aperture on these switch trials with grip aperture on switch trials that were preceded by only one trial of the opposite feedback condition. Within a run of trials with the same feedback conditions, the second, third, and fourth trials of the runs were preceded by an increasing number of same feedback trials. Thus, to analyze the effects of previous trial history on

performance, we conducted separate 2 × 5 × 3 × 2 feedback (closed- and open-loop) × trial history (those trials that were preceded by: a run of four trials of opposite feedback, only one trial of opposite feedback, and two-, three-, or four-trials of the same feedback) × object size (1.5, 3.0, and 4.5 cm) × object distance (20 and 35 cm) repeated measures analyses of variance (rmANOVA) on the means for each dependent measure.

We followed up this omnibus analysis with trend analyses for all the kinematic measures and targeted Student's paired *t* tests for peak grip aperture. For effects involving trial history, however, the trend analyses were restricted to the runs of closed and open-loop trials where each successive trial, by definition, was separated by the same time interval (approximately 6 s). The significant interactions in the trend analyses were followed up with tests of the simple main effects.

To test for changes in the effects of trial history on grip aperture across the session, a rmANOVA was employed; mean PGAs were collapsed across object size and object distance to create a 2 × 3 feedback (closed- and open-loop) × block (first, second, and third blocks of 72 trials) design. This analysis was followed by Student's paired *t* tests comparing the first block of 72 trials with the last block within each feedback condition to test for possible change in performance over the course of the session.

Greenhouse–Giesser epsilon multipliers were applied to the degrees of freedom to all rmANOVAs to compensate for potential violations of sphericity and equivalency of the variance–covariance matrices. The alpha criterion for statistical significance was set to 0.05 for each statistical analysis. The 95% within-subject confidence intervals (95% CI) extracted from the MS_{error} for the significant effects are appended wherever condition means are reported in-text. Where condition means are illustrated in figures, the 95% confidence intervals extracted from the MS_{error} for the effect is included as error bars in the figure (see Loftus and Masson 1994; Masson and Loftus 2003).

Results

Reaction time

The analysis of reaction time (RT) revealed a significant main effect of distance [$F(1,11) = 8.7$, $P < 0.05$, $\eta_p^2 = 0.44$]. Reaction times for objects placed at the 20 cm position ($M = 263$ ms) were significantly faster than those for objects placed at the 35 cm position, $M = 275$ ms; 95% CI ± 35 ms. This 12 ms increase in RT with increased object distance is nearly identical to that observed with similar distances used in our previous study (Whitwell et al. 2008).

Peak grip aperture

The analysis of peak grip aperture (PGA) yielded three main effects (feedback, size, and distance) and three-two-way interactions (feedback × trial history, feedback × size, and feedback × distance). The main effects of feedback [$F(1,11) = 100.9$, $P < 0.001$, $\eta_p^2 = 0.90$], size [$F(2,11) = 416.3$, $P < 0.001$, $\eta_p^2 = 0.97$], and distance [$F(1,11) = 8.8$, $P < 0.05$, $\eta_p^2 = 0.45$] have to be interpreted in terms of the interactions involving feedback. The interaction between feedback and trial history [$F(3,25) = 29.2$, $P < 0.001$, $\eta_p^2 = 0.73$] and the trend analyses are shown in Fig. 1. The trend analysis revealed a significant linear feedback × trial type interaction, $F(1,11) = 108.0$, $P < 0.001$, $\eta_p^2 = 0.91$. Testing the simple main effect of repetition number on mean PGA for closed- and open-loop trials separately indicated that the mean PGA increased linearly for the closed- [$F(1,11) = 75.1$, $P < 0.001$, $\eta_p^2 = 0.87$] and decreased linearly for the open-loop conditions, $F(1,11) = 86.9$, $P < 0.001$, $\eta_p^2 = 0.89$. No non-linear components were significant for either feedback condition.

We carried out two sets of planned *t* test comparisons to explore how the two types of switch trials related to each other and to the runs within each visual feedback condition. Figure 2 depicts these contrasts for the closed- and open-loop conditions separately. We first tested whether the runs of four successive closed- or open-loop trials would influence the next trial in the sequence (a switch trial) by comparing the mean PGA of these trials to the mean PGA of trials that were preceded by only one trial of the opposite feedback condition. As Fig. 2 shows, the mean PGA of the closed-loop trials that followed four consecutive open-loop trials was significantly larger than the mean PGA of the closed-loop trials that were preceded by only one open-loop trial, $t(11) = 2.5$, $P < 0.05$. We found a similar yet opposite influence for the open-loop condition: the mean PGA of the open-loop trials that were preceded by four consecutive closed-loop trials was significantly smaller than the mean PGA of the open-loop trials that were preceded by only one closed-loop trial, $t(11) = -2.6$, $P < 0.05$. Thus, the cumulative influence of successive closed- and open-loop trials on PGA reduced the degree to which the availability visual feedback was exploited on the subsequent switch trial.

We next examined whether one or two repetitions of closed- or open-loop feedback was sufficient to influence grip aperture by comparing the mean PGA of switch trials that were preceded by only one trial of the opposite feedback condition with the second trial position (i.e., one repetition) and then the third trial position (i.e., two repetitions) within the runs of four consecutive closed or open-loop trials. Figure 2 depicts these contrasts separately within the closed- and open-loop conditions. As can be

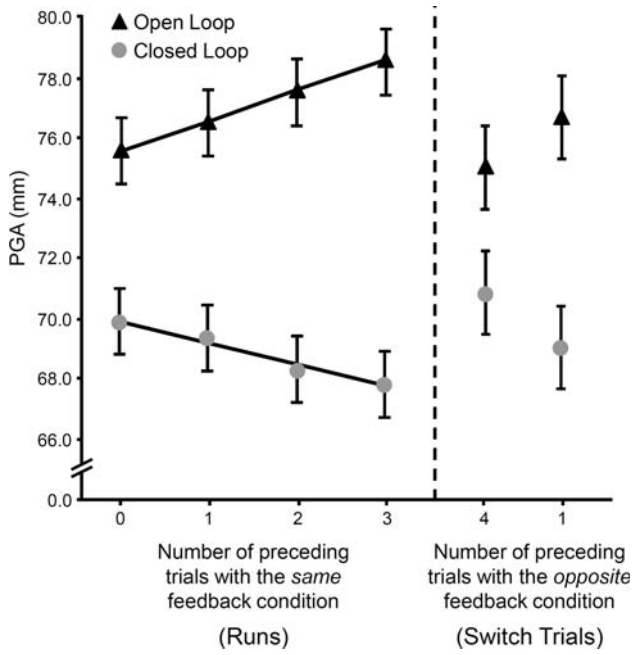

Fig. 1 The cumulative trial-to-trial influence of consistent feedback (closed-loop: *grey circles*; open-loop: *black triangles*) on peak grip aperture (*PGA*). Within a run of four successive closed- or open-loop trials, the zero repetition trial is the first trial in the run of four consecutive visual feedback (or no visual feedback) trials. The zero repetition trials (together with the three successive trials that followed within the run) were analyzed in the trend analyses but these trials were grouped as switch trials in the omnibus ANOVA. Note that peak grip aperture increases linearly as the run of open-loop trials progresses and decreases linearly as the run of closed-loop trials progresses. The switch trials were grouped into two feedback histories: those that were preceded by four consecutive trials of the opposite feedback condition and those that were preceded by only one trial of the opposite feedback condition. Peak grip aperture on the open-loop switch trials was smaller when the trial was preceded by four consecutive closed-loop trials than when preceded by only one closed-loop trial. A similar but opposite result was observed for PGA on closed-loop trials: PGA was larger on closed-loop trials that were preceded by four consecutive open-loop trials than when preceded by only one open-loop trial. *Solid black error bars* represent the 95% confidence intervals extracted from the mean square error term of the feedback × trial interactions

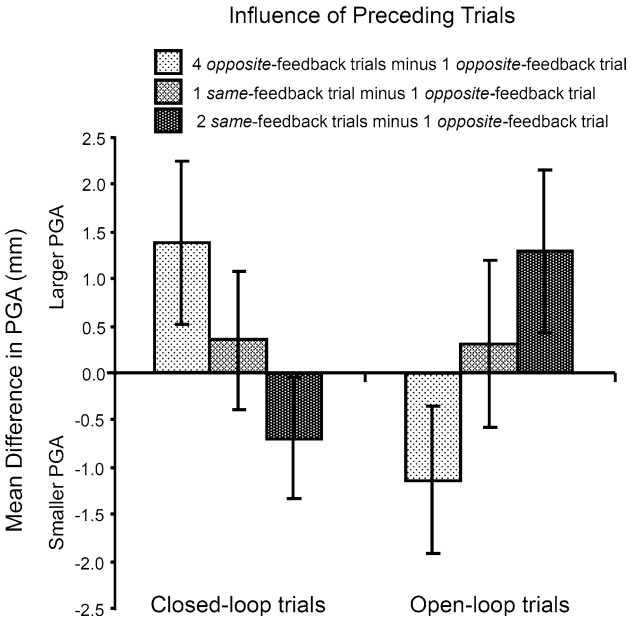

Fig. 2 Mean difference scores (in mm of PGA) between trials with different feedback histories. Difference scores were derived from three different contrasts for both open-loop and closed-loop trials: PGA on trials preceded by four trials of opposite feedback minus PGA on trials preceded by only one trial of the opposite feedback condition; PGA on trials preceded by only one trial of the same feedback condition minus PGA on trials preceded by only one trial of the opposite feedback condition; and, finally, PGA on trials preceded by two trials of the same feedback condition minus PGA on a trial preceded by only one trial of the opposite feedback condition. Note that PGA was larger on closed-loop trials that were preceded by a run of four open-loop trials and smaller on open-loop trials that were preceded by a run of four closed-loop trials. One repetition of either closed- or open-loop feedback failed to significantly influence PGA on the second trial of that run. PGA was significantly larger on the third trial of the runs of closed-loop feedback and significantly smaller on the third trial of the runs of open-loop feedback. *Solid black error bars* represent the 95% confidence intervals around the mean difference score

seen in Fig 2, one repetition of closed-loop feedback failed to reduce the mean PGA in-flight [$t(11) = -0.9$, ns), but two repetitions of did, $t(11) = 2.3$, $P < 0.05$. Similarly, one repetition of open-loop feedback failed to increase mean PGA in-flight [$t(11) = -0.6$, ns] whereas two repetitions of open-loop feedback did, $t(11) = -2.4$, $P < 0.05$. The influences of the trial history of the availability of visual feedback on grip aperture can be seen in Fig. 3, which illustrates the normalized grip aperture profiles for the switch trials and the runs of consecutive feedback within each visual condition. As this figure makes clear, the influence of previous feedback conditions can be seen throughout the movement and not just at the moment of peak grip aperture.

The feedback × size interaction [$F(2,17) = 20.6$, $P < 0.001$, $\eta_p^2 = 0.65$] reflected the fact that while the mean PGA increased with object size and was larger on open-loop trials than on closed-loop trials, the closed-loop trials elicited a sharper linear increase in mean PGA with object size [$F(1,11) = 256.0$, $P < 0.001$, $\eta_p^2 = 0.96$] than did the open-loop trials, $F(1,11) = 529.6$, $P < 0.001$, $\eta_p^2 = 0.93$ (closed-loop trials: 1.5 cm, $M = 58.3$ mm, 3.0 cm, $M = 69.6$ mm, 4.5 cm, $M = 79.3$ mm; open-loop trials: 1.5 cm, $M = 68.0$ mm, 3.0 cm, $M = 77.4$ mm, 4.5 cm, $M = 85.3$ mm; 95% CI ± 1.9 mm). We observed a similar finding in our previous study (Whitwell et al. 2008). One explanation offered in that study noted that because individuals oversize their grip aperture while reaching out to grasp the object, larger objects would elicit grip apertures that approach the natural limits of the extent to which individuals can open their fingers (see also

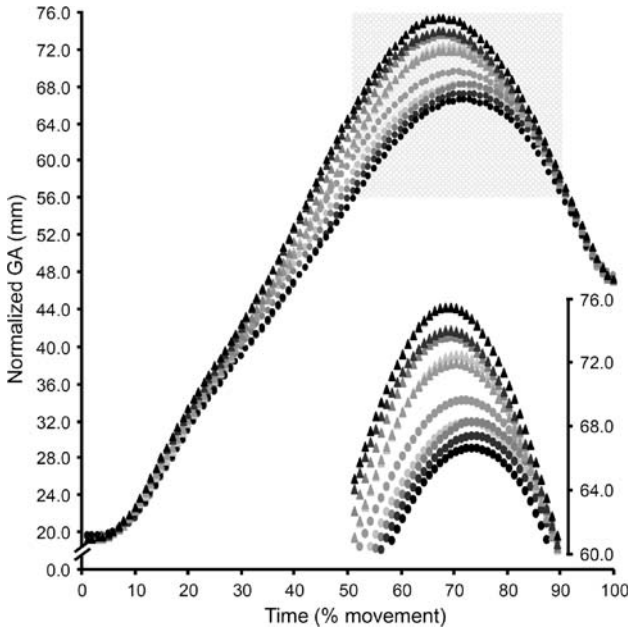

Fig. 3 Grip aperture normalized for movement time for successive closed- and open-loop trials. Although these data are presented for illustrative purposes only and were not analyzed statistically, it is qualitatively apparent that grip aperture diverges with each successive closed- (*filled circles*) or open-loop trial (*filled triangles*) following a series of switch trials (*lightest shaded* profiles) on through to the final closed- or open-loop trial of the runs of four consecutive trials (*darkest shaded* profile) earlier than the peak grip aperture. The *inset* depicts the profiles in the shaded region using the same temporal scale but an approximately doubled scale for grip aperture

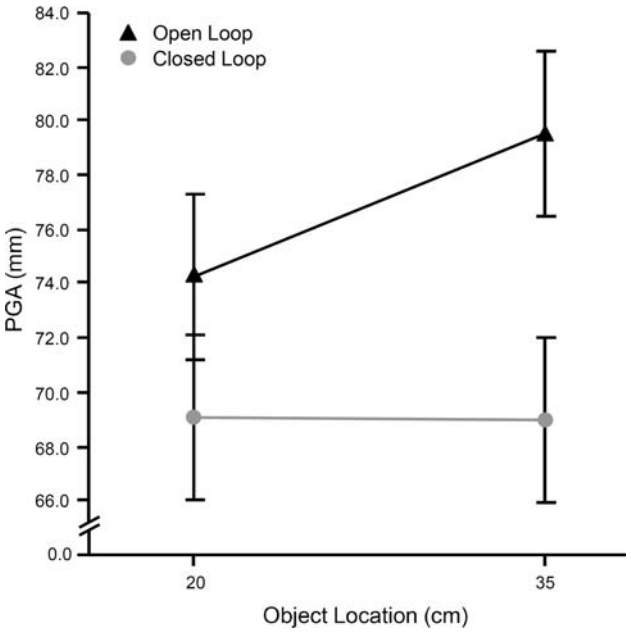

Fig. 4 The influence of visual feedback (closed-loop trials: *grey circles*) and no visual feedback (open-loop trials: *black triangles*) and the two object distances on peak grip aperture (PGA). Note that PGA increases with distance in the open-loop condition but remains constant in the closed-loop condition. *Solid black error bars* represent the 95% confidence intervals extracted from the mean square error term of the feedback × object distance interaction

Bootsma et al. 1994). Open-loop conditions in particular may be more susceptible to this effect, because the removal of visual feedback at movement onset elicits wider grip apertures. Alternatively, the overall sensitivity of grip scaling to object size may be reduced when online visual information is not available.

The feedback × distance interaction [$F(1,11) = 57.8$, $P < 0.001$, $\eta_p^2 = 0.84$] highlights the influence of time on the availability of visual feedback noted in our previous study (Whitwell et al. 2008) and is depicted in Fig. 4. As the figure indicates, the interaction appears to be driven largely by the open-loop conditions and the farthest object distance. Trend analyses of the mean PGAs of the closed- and open-loop trials indicated a significant linear influence of object distance for the open-loop trials [$F(1,11) = 20.2$, $P < 0.001$, $\eta_p^2 = 0.65$] but not for the closed-loop trials, $F(1,11) = 0.1$, ns.

There was no evidence to suggest that the effects of trial history changed over the course of the experiment. The 2 × 3 feedback (closed- and open-loop) × block (first, second, and third blocks of 72 trials) revealed neither a significant main effect of block, $F(1,22) = 1.7$, ns, nor a significant interaction between feedback and block, $F(2,22) = 2.4$, ns. Confirming this failure to detect any change in performance over the session, the Student's paired t test of the mean PGAs of the first and third blocks within the closed-loop trials failed to find a significant difference, $t(11) = -0.4$, ns, as did an identical test conducted within the open-loop trials, $t(11) = -1.7$, ns. Thus, the trial-to-trial influences of visual feedback history on PGA observed within the runs of four consecutive closed- and open-loop trials cannot be explained as an artifact of an increasing difference in the effects of visual feedback across the span of the session.

Time to peak grip aperture, and the post-peak grip aperture phase

The analysis of the time to peak grip aperture (tPGA) revealed three main effects (feedback, size, and distance) and two-two-way interactions (feedback × size and feedback × distance). The main effects of feedback [$F(1,11) = 18.7$, $P < 0.001$, $\eta_p^2 = 0.63$], size [$F(2,16) = 28.3$, $P < 0.001$, $\eta_p^2 = 0.72$] and distance [$F(1,11) = 283.1$, $P < 0.001$, $\eta_p^2 = 0.96$] have to be interpreted in terms of the significant interactions involving feedback. The feedback × size interaction [$F(2,22) = 4.2$, $P < 0.05$, $\eta_p^2 = 0.28$] reflected the fact that while the mean tPGA was longer with increased object size and was shorter on closed-loop trials than on open-loop trials, the closed-loop

trials elicited a sharper linear increase in mean tPGA with object size [$F(1,11) = 31.0$, $P < 0.001$, $\eta_p^2 = 0.74$] than did the open-loop trials, $F(1,11) = 43.8$, $P < 0.001$, $\eta_p^2 = 0.83$ (closed-loop trials: 1.5 cm, $M = 455$ ms, 3.0 cm, $M = 484$ ms, 4.5 cm, $M = 503$ ms; open-loop trials: 1.5 cm, $M = 488$ ms, 3.0 cm, $M = 505$ ms, 4.5 cm, $M = 517$ ms; 95% CI ± 21 ms). The feedback × distance interaction [$F(1,11) = 8.3$, $P < 0.05$, $\eta_p^2 = 0.43$] reflected the fact that while the mean tPGA was longer with increased object distance (and, as mentioned above, shorter on open-loop trials than on closed-loop trials), the open-loop trials elicited a sharper increase in mean tPGA with object distance [$F(1,11) = 162.1$, $P < 0.001$, $\eta_p^2 = 0.94$] than did the closed-loop trials, $F(1,11) = 339.3$, $P < 0.001$, $\eta_p^2 = 0.97$ (closed-loop trials: 20 cm, $M =$ 431 ms, 35 cm, $M = 530$ ms; open-loop trials: 20 cm, $M = 445$ ms, 35 cm, $M = 562$ ms; 95% CI ±26 ms). The absence of a main effect or significant interactions involving trial type in the omnibus analysis suggests that the mean tPGA was not affected by trial history. Figure 5 illustrates the mean tPGAs of the closed- and open-loop trials as functions of repetitions of closed- or open-loop trials (the runs) and switch trials. As Fig. 5 indicates, the availability of visual feedback had a clear influence on the tPGA, while trial history did not. As one might expect, the trend analyses of tPGA for the runs of four consecutive closed and open-loop trials failed to indicate significant linear or non-linear components for main effects and interactions involving the trial positions within the runs. Thus, the effects of trial history on PGA were not apparent in measures of time taken from movement onset to the peak grip aperture.

The analysis of the time from peak grip aperture to movement offset [the post-PGA (pPGA) phase] revealed three main effects (feedback, size, and distance) and two–two-way interactions (feedback × trial history and feedback × distance). The effect of size [$F(2,14) = 16.1$, $P < 0.001$, $\eta_p^2 = 0.59$] reflected the linear decrease in the mean duration of the post-PGA phase with increased object size, $F(1,11) = 18.0$, $P < 0.001$, $\eta_p^2 = 0.62$ (1.5 cm, $M = 232$ ms, 3.0 cm, $M = 215$ ms, and 4.5 cm objects, $M = 202$ ms; 95% CI ±35 ms). The main effects of feedback [$F(1,11) = 40.1$, $P < 0.001$, $\eta_p^2 = 0.79$] and distance [$F(1,11) = 105.1$, $P < 0.001$, $\eta_p^2 = 0.91$] have to be interpreted in terms of the significant interactions involving feedback. The interaction between feedback and trial history [$F(4,36) = 9.7$, $P < 0.001$, $\eta_p^2 = 0.47$] can be seen in Fig. 5. The trend analyses indicated that the mean pPGA phase increased linearly with successive closed-loop trials [$F(1,11) = 8.9$, $P < 0.05$, $\eta_p^2 = 0.45$] and with successive open-loop trials, $F(1,11) = 6.3$, $P < 0.05$, $\eta_p^2 = 0.37$. No non-linear components were significant for either condition. The feedback × distance interaction [$F(1,11) = 14.5$, $P < 0.01$, $\eta_p^2 = 0.57$] reflected the fact that while the mean pPGA increased with object distance and on open-loop trials, the mean pPGA phase of the open-loop trials increased more sharply with object distance [$F(1,11) = 76.0$, $P < 0.001$, $\eta_p^2 = 0.87$] than did the mean pPGA phase of the closed-loop trials, $F(1,11) = 14.5$, $P < 0.01$, $\eta_p^2 = 0.57$ (closed-loop trials: 20 cm, $M = 183$ ms, 35 cm, $M =$ 199 ms; open-loop trials: 20 cm, $M = 220$ ms, 35 cm, $M = 264$ ms; 95% CI ±31 ms).

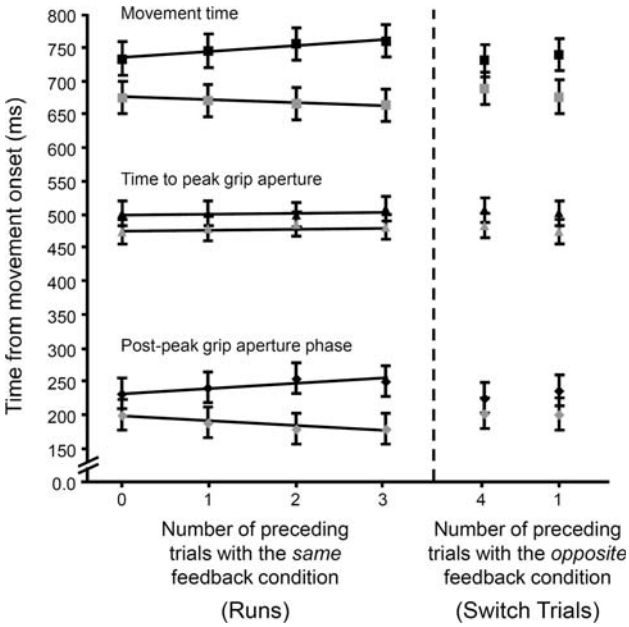

Fig. 5 The cumulative trial-to-trial influence of consistent feedback (closed-loop: *grey circles*; open-loop: *black triangles*) on movement time (MT) and the time from peak grip aperture (PGA) to movement offset [the post-PGA (pPGA) phase]. Although the time from movement onset to PGA (tPGA) was not influenced by trial history, it was influenced by the availability of visual feedback. As in Fig. 1, within a run of four successive closed- or open-loop trials, the zero repetition trial is the first trial in the run of four consecutive visual feedback (or no visual feedback) trials. The zero repetition trials (and the three successive trials that followed within the run) were analyzed in the trend analyses but were grouped as switch trials in the omnibus ANOVA. Again, as in Fig. 1 the switch trials were grouped into two feedback histories: those that were preceded by four consecutive trials of the opposite feedback condition and those that were preceded by only one trial of the opposite feedback condition. Movement time increases linearly as the run of open-loop trials progresses and decreases linearly as the run of closed-loop trials progresses. *Solid black error bars* represent the 95% confidence intervals extracted from the mean square error term of the feedback × trial interactions

Movement time

The analysis of MT revealed two main effects (feedback and distance) and two-two-way interactions (feedback × trial history and feedback × distance). The main effects of feedback [$F(1,11) = 47.4$, $P < 0.001$, $\eta_p^2 = 0.81$] and distance [$F(1,11) = 360.7$, $P < 0.001$, $\eta_p^2 = 0.97$] have to be

interpreted in terms of the significant interactions involving feedback. The interaction between feedback and trial history [$F(4,39) = 9.4$, $P < 0.001$, $\eta_p^2 = 0.46$] is shown in Fig. 5. The trend analysis of the runs of four consecutive closed- or open-loop trials indicated that the mean MT increased linearly throughout the run of open-loop trials [$F(1,11) = 15.2$, $P < 0.01$, $\eta_p^2 = 0.58$] and decreased linearly throughout the run of closed-loop trials, $F(1,11) = 4.5$, $P = 0.057$, $\eta_p^2 = 0.29$. No non-linear components were identified.

The feedback × distance interaction [$F(1,11) = 24.8$, $P < 0.001$, $\eta_p^2 = 0.69$] reflected the fact that while the mean MT increased with object distance and was longer on open-loop trials than on closed-loop trials, the Trend Analysis indicated that open-loop conditions elicited a sharper increase in mean MT with object distance [$F(1,11) = 230.3$, $P < 0.001$, $\eta_p^2 = 0.94$] than did closed-loop conditions, $F(1,11) = 403.9$, $P < 0.001$, $\eta_p^2 = 0.97$ (closed-loop trials: 20 cm, $M = 615$ ms; 35 cm, $M = 731$ ms; open-loop trials: 20 cm, $M = 666$ ms; 35 cm, $M = 826$ ms; 95% CI ±38 ms).

Discussion

We have shown that the programming of a precision grip is affected by whether or not visual feedback was available on preceding trials. Moreover, the nature of this influence appears to operate in a cumulative manner over the course of at least four trials of consecutive closed or open-loop feedback. This was particularly true for peak grip aperture. When visual information was available throughout the movement for four consecutive trials, we observed a linear reduction in grip aperture with each successive trial. In contrast, when visual information was unavailable throughout the movement for four consecutive trials, we observed a linear increase in grip aperture with each successive trial. Evidently, the programming of grip aperture is subject to the consistency (or inconsistency) of visual feedback. The fact that this occurred despite the unpredictability of target size, distance, and visual feedback strongly suggests that these adjustments in the programming of grip aperture are largely automatic and cognitively impenetrable. This latter conclusion is supported by our earlier study (Whitwell et al. 2008) showing that the visuomotor system did not take advantage of explicit knowledge about the availability of visual feedback on an upcoming trial (for a similar conclusion based on measurements of target-directed reach trajectories and the presence or absence of obstacles see; Jax and Rosenbaum 2007, Exp 2). In short, the programming of our grip aperture is influenced by what happened earlier with little or no conscious mediation.

It is interesting to note that the effect of feedback history on grip aperture increases as a function of repetition of the same trial type. For example, grip aperture on a closed-loop trial preceded by four open-loop trials is larger than grip aperture on a closed-loop trial preceded by only one open-loop trial. Similarly, grip aperture on an open-loop trial preceded by four closed-loop trials is smaller than grip aperture on an open-loop trial preceded by only one closed-loop trial. There is a suggestion in the data that at least two trials of the same feedback condition are required for any influence on the programming of grip aperture to become apparent. Although it is tempting to conclude from this that the visuomotor system controlling grasping must detect some consistency in feedback over at least two trials before altering the initial programming of a subsequent grasp, one must be cautious here. A recent paper examining feedback repetition in pointing, for example, observed effects on the second trial of a run of the same feedback type (Cheng et al. 2008). More experiments are clearly required before a definite answer will emerge about exactly how many repetitions are required.

One way to explain the present findings is to see them as a result of a tradeoff between achieving the objective within the constraints of the task (e.g., what participants are instructed to do with the object; Ansuini et al. 2008) and reducing the biomechanical and processing costs of doing so (e.g., Rosenbaum et al. 2001). In short, the pattern of results we observed may reflect the efforts of the visuomotor system to achieve an optimal movement (Shadmehr and Krakauer 2008; Todorov and Jordon 2002) throughout the trial and over the course of several trials. Over-sizing grip aperture helps ensure that the hand acquires the object in a fashion appropriate for picking it up, i.e., having the fingertips approach the object perpendicular to the near and far surfaces (Smeets and Brenner 1999). Keeping the grip aperture as small as possible, however, reduces the biomechanical costs of the grasp and reduces the probability of a collision with obstacles. When on-line visual feedback is not available throughout the movement, the demands on over-sizing grip aperture increase due to the added uncertainty about the position of the hand and/or object as the movement unfolds. Visual feedback, however, presents the visuomotor system with an opportunity to reduce the demand for over-sizing the grip aperture, conserve biomechanical effort, and avoid obstacles. In other words, visual-feedback offers the visuomotor system the opportunity to minimize cost and maximize benefit.

Thus, when participants in Trommershauser et al.'s (2006) study pointed to a target reward region on a touch-screen display with full visual feedback at their disposal, their end-points deviated from the centre of the reward region in a direction away from a penalty region (located near the reward region) provided the presentation of the penalty region occurred before or very early in the participants' movements. In contrast, participants' end-points

deviated little from the centre of the reward region when the presentation of the penalty region occurred relatively late into their movements. In other words, when the location and timing of the onset of the penalty region is unpredictable, the visuomotor system programs and executes movements directed to the centre of the goal region but can update the trajectory of the hand (while maintaining a smooth or optimal trajectory) only when the system has enough time to process on-line changes to the visual display. Interestingly, the failure to deviate away from the penalty region occurred despite participants' awareness of the cost (in total scores) of landing on this region.

Although Trommershauser et al. (2006) did not examine the influence of trial-to-trial effects on the kinematics of manual aiming movements, the trial-to-trial influences observed in the present study resonate with those of other studies that have (Barden et al. 2005; Jax and Rosenbaum 2007; Jax and Rosenbaum 2008). Blind-folded participants in Barden et al.'s (2005) study replicated an initial pointing movement ten times to a self-selected point in reachable space. The participants reduced the extent by which their movements deviated from their previous movement with each successive trial. In other words, participants used the proprioceptive information gleaned from the previous movement to update future movements and minimize the extent by which their iterative movements deviated from the previous movement on each successive trial. What makes Barden et al.'s (2005) study all the more remarkable is that participants optimized their movements despite the near total lack of information about whether or not their movements were on target. In short, a system that incorporates elements of recent action into future actions can be advantageous under conditions of uncertainty.

Jax and Rosenbaum (2007) examined the trial-to-trial influences of obstacle-present and obstacle-absent conditions on reach trajectories aimed at targets. To do this, the authors employed two non-mixed block formats and three mixed block formats each of which comprised of a different proportion of obstacle-present trials. Not surprisingly, the extent of hand-path deviation was larger for the non-mixed block of obstacle present trials than for the non-mixed block of obstacle absent trials. Of particular interest was the fact that frequency of obstacle-present trials influenced the extent of hand-path deviation averaged across the block. Specifically, the extent of hand-path deviation on obstacle-absent trials increased when the proportion of obstacle-present trials in the mixed blocks increased (from 25 to 50%, and on to 75%). Moreover, the magnitude of the hand-path deviation increased or decreased over the course of a several trials as a function of the consistency of the presence (or absence) obstacles over those trials. In a subsequent effort, Jax and Rosenbaum (2008) replicated and extended their findings to show that the influence of recent trial history of obstacle presence or absence on hand path deviation is reduced with increased inter-trial time. They argue that the reduction in influence reflects a decay of the motor memory.

Although others (e.g., Dixon and Glover 2004; Rosenbaum et al. 2001) have formalized how previous information about the parameters used on earlier trials can influence present performance, there has been little discussion about why this might be adaptive. Jax and Rosenbaum (2007) argued that larger hand path deviations relative to smaller ones reflected greater movement cost. By that same token, larger grip apertures would reflect greater movement costs than smaller ones. In both studies, participants did not adopt costly overarching strategies. Instead, they performed in a more nuanced manner: reducing the biomechanical costs as the task demand relaxed from trial to trial and increasing these costs as the task demands increased. Since the relations between objects in the world and ourselves change in an infinite number of ways when we move from one location to the next, a system that incorporates elements of the previous movement into the current movement would be adaptive under static circumstances. By in large, the environment and the objects within it change little from moment to moment. Objects rarely change size or mass over short periods of time—and even their location in the world remains reasonably consistent. Importantly, the availability of visual feedback is remarkably constant. Thus, under some circumstances it makes adaptive sense to interact with an object in the same way as you did before, using earlier information to help shape the present response. It is perhaps worth adding that participants in the experiments we discussed remained seated for the duration of the experiment, engaged in the same task repetitively from trial to trial wherein relatively few stimuli are changed within a confined region of space. The objects in the present study, for example, were located at one of two positions on the transverse plane along participants' midline. As emphasized by Dixon and Glover (2004), mechanisms that incorporate elements of previous movements into a current movement are more likely to be engaged when the conditions (including the task) remain relatively stable from moment to moment or action to action.

It is important to emphasize, however, that this account does not conflict with the proposal put forward by Goodale and Milner (1992) that visual information is used differentially by perceptual and motor mechanisms. They went on to argue that delayed actions are driven by memories of the goal object originally constructed by perceptual mechanisms in the ventral stream (Milner and Goodale 1995). In the present experiments, of course, the participants were grasping objects that were visible when the

action was programmed, and the influence of earlier trials was reflected in that programming. In delayed grasping, however, where the goal object is not present (or visible) when the command to grasp is given, participants have to remember quite explicitly what it was they had seen earlier. But we have demonstrated both in the present experiment and our earlier study (Whitwell et al. 2008) that explicit retrieval of earlier information is not necessary for exploiting consistency across trials. To reiterate: it makes adaptive sense to have a system in place that uses elements of previous interactions with objects that are consistent from moment to moment (or action to action) to program and execute the current action without having to expend our cognitive resources on monitoring these consistencies.

Of course, the visuomotor system does not rely exclusively on what happened on previous trials to set the parameters of the current motor program. The greatest contribution must always come from the sensory information about the characteristics and state of the current goal. This is true even in the case of visual feedback. Even though we have shown a significant influence of the feedback conditions of earlier trials on current performance, we have also shown that if the target object is far enough away from the hand, then the online availability of visual information will influence grip aperture. Specifically, the difference between closed- and open-loop trials increased as a function of target distance, largely because peak grip-aperture on open-loop trials increased with distance whereas peak grip aperture on closed-loop trials did not. This could reflect increased uncertainty about target size and/or location with longer reaches to distant objects under open-loop conditions. If the sensory information about the object decays over the course of the movement, the motor system would have to rely more and more on proprioceptive feedback and/or stored visual information to modulate the movement as it unfolds. This position simply extends the view that removing components of the visual scene (e.g., the hand, or target) throughout several trials influences subsequent goal-directed movements (e.g., Binsted et al. 2006; Smeets et al. 2006) to the case where full vision is available only up until the point of movement initiation. Alternatively, the increase in grip aperture could reflect the fact that without any direct visual feedback to modulate grip aperture, the grip itself might continue to get larger as the hand moves faster with distance. Future experiments are needed to address these issues.

In conclusion, we have shown that while the availability of visual feedback while grasping can have a substantial influence on grip aperture, there are large trial to trial influences of the presence of visual feedback on the initial programming of grip aperture. This effect seems to be uninfluenced by explicit knowledge of what might happen on an upcoming trial (Whitwell et al. 2008). It is not yet clear whether or not other factors such as the size, orientation, and location of the object grasped on previous trials will have similar effects on the programming of the current trial.

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