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Visual feedback reduces bimanual coupling of movement amplitudes, but not of directions

Received: 4 July 2003 / Accepted: 18 August 2004 / Published online: 3 November 2004
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Abstract To what extent does visual feedback shape the coordination between our arms? As a first step towards answering this question, this study compares bimanual coupling in simultaneous bimanual reversal movements that control cursor movements on a vertical screen. While both cursors were visible in the control condition, visual feedback was prevented in the experimental condition by deleting one or both cursors from the screen. Absence of visual feedback for one or both arms significantly increased the reaction times of both arms and the movement amplitude of the occluded arm. Temporal coupling between the arms remained unchanged in all feedback conditions. The same was true for spatial coupling of movement directions. Amplitude coupling, however, was significantly affected by visual feedback. When no feedback for either arm was available, amplitude correlations were significantly higher than when feedback for one or both arms was present. This finding suggests that online visual feedback decreases bimanual amplitude coupling, presumably through independent movement corrections for the two arms. The difference between movement amplitudes and movement directions in their susceptibility to visual feedback supports the idea that they are subserved by different control mechanisms. Analysis

of eye movements during task performance revealed no major differences between the different feedback conditions. The eye movements of all subjects followed a stereotypical pattern, with generally only one saccade after target onset, directed towards the average position of all possible targets, irrespective of feedback condition and target direction.

Keywords Bimanual coordination · Visual feedback · Eye-hand coordination · Human

Introduction

Bimanual motor activities are typically characterized by specific patterns of spatial and temporal coupling between the movements of both arms (Kelso et al. 1979a, 1979b; Marteniuk et al. 1984; Fowler et al. 1991; Kazennikov et al. 1994; Franz et al. 1996; Boessenkool et al. 1999; Perrig et al. 1999; Heuer et al. 2001; Summers 2002). This coupling may either be the result of constraints of our motor system that are hard to override, or, alternatively, may actually be desired and necessary for the task at hand. For example, drummers initially suffer from our strong tendency to produce in-phase arm movements, and need a lot of practice to be able to produce different rhythms with different arms (for a review of the constraints of bimanual rhythmic movements, see Summers 2002). On the other hand, we can easily produce quite precise and complex patterns of spatio-temporal coordination between our hands in many everyday activities, such as when tying our shoelaces or unscrewing a bottle. Constraints of bimanual performance seem to arise automatically due to some features built-in to our motor system, such as interference between motor commands for both arms. On the other hand, purposeful bimanual coordination patterns require deliberate and precise spatio-temporal regulation of the movement patterns of each hand. What information is used to achieve this regulation? One possibility is that proprioceptive information from the moving limbs is monitored in order to keep track of the current status of the

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moving limbs and to adjust the movements of other body parts (on the same or on different limbs) correspondingly. There is evidence that the coordination of ongoing movements uses proprioception (see Cordo et al. 1995), and deafferented patients exhibit clear coordination deficits (Sainburg et al. 1993; Ghez and Sainburg 1995; Bonnard and Pailhous 1999; Simoneau et al. 1999; Verschueren et al. 1999; Jackson et al. 2000; Jackson et al. 2002).

However, proprioception cannot account fully for all motor coordination phenomena in general, and for bimanual coordination in particular. Coordination deficits in deafferented patients normally become apparent only if vision is absent (Sainburg et al. 1993; Ghez and Sainburg 1995; Bonnard and Pailhous 1999; Simoneau et al. 1999; Verschueren et al. 1999; Jackson et al. 2002). These results clearly suggest that visual feedback also plays a substantial role in motor coordination. The first positive evidence for this assumption comes from cyclical bimanual movements. Although cyclical bimanual performance maintains its characteristics even when the arms are invisible, more sophisticated manipulations of visual feedback have resulted in subtle effects on movement performance. For example, between-limb asynchrony can be influenced by the instruction to focus visual attention on one or the other hand (Swinnen et al. 1996). Compatibility between the direction of a visual stimulus and arm movement direction within a circular task can stabilize bimanual coordination beyond the normal level (Byblow et al. 1999), and augmented feedback can help when learning new difficult cyclical bimanual patterns (Wishart et al. 2002). Furthermore, the phase stability of anti-phase bimanual movements could be enhanced if altered visual feedback was provided that made movements appear to be in-phase (Bogaerts et al. 2003). Mechsner et al. (2001) even reported that the phase-stability seemed to be completely dominated by the visual perception of its phase-relations.

While the above-mentioned studies do suggest a role for visual feedback in cyclical movement, its contribution to discrete bimanual movements has not been specifically assessed. When a small target must be hit, visual information is indispensable for learning the task and should therefore have a particularly strong impact on such goal-directed movements. In this study, we investigate the role of visual feedback in a discrete bimanual movement task with well-defined and fast goal-directed movements, and in which visual feedback could be controlled. Both arms had to move simultaneously to separate movement targets, hit them, and move back towards the origin. Subjects were instructed to make quick, smooth reversal movements. The advantage of such reversal movements as opposed to one-way movements is that the end of each movement at the target is very clearly defined as the reversal point. Targets were presented on a computer monitor in front of subjects, and visual information about hand movements was supplied by cursors, while direct vision of the arms was prevented. This set-up allowed us to occlude feedback for one or both arms, by deleting the appropriate cursor(s) from the screen. We assessed

bimanual coordination as bimanual coupling of movement parameters, by quantifying the relations between the spatial and temporal parameters of the two hands in simultaneous trials, and compared them in different feedback conditions. Since very little is known about the active collection of visual feedback through eye movements in bimanual reaching movements (Honda 1982; Müri et al. 1999), we also measured eye movements during task performance. Specifically, the registration of eye movements served as a control for the possibility that observed effects of visual feedback could be related to different visuomotor strategies.

Materials and methods

Participants

25 male, right-handed (Oldfield 1971) volunteers between 19 and 34 years of age were paid for their participation. All had normal vision, did not know the purpose of the study, and gave their informed consent prior to inclusion. The experiments were approved by the local ethics committee and complied with The Code of Ethics of the World Medical Association (Declaration of Helsinki), printed in the British Medical Journal (18 July 1964).

Task and apparatus

Throughout the experiment, participants wore a headset for the measurement of eye movements (EyeLink, SMI). Head position was stabilized by a chinrest attached to the table. Subjects sat in front of a computer monitor (distance: ~83 cm, diagonal image size: 21") and performed rapid bimanual reversal movements in the horizontal plane. Only the index fingers were in contact with the smooth glass surface covering the table. Mineral oil was used to lubricate the fingertips, reducing friction. A shield prevented the subjects from viewing their forearms and hands. Positions of the tips of the index fingers were continuously monitored and sampled at 100 Hz (mini-BIRD 800; Ascension Technology Corporation, Burlington, Vermont, USA). Eye movements were recorded at a sampling rate of 250 Hz. Two white crosses on the monitor ("cursors") provided online continuous feedback about the measured finger position. With a sampling rate of 100 Hz, and a screen refreshment rate of 60 Hz, the maximal delay between a measured position and the display on the screen was about 27 ms. Starting positions ("origins") and targets were displayed as open white circles (diameter: 15 mm) on the monitor (see Fig. 1). Each trial began with a drift control for eye position measurements. For this procedure, a small fixation target was presented in the center of the screen. The eye position during stable fixation of this point was used to calibrate the offset in the eye position measurements. After this drift control, the fixation target disappeared and two origins were presented on the screen (see Fig. 1). Subjects were

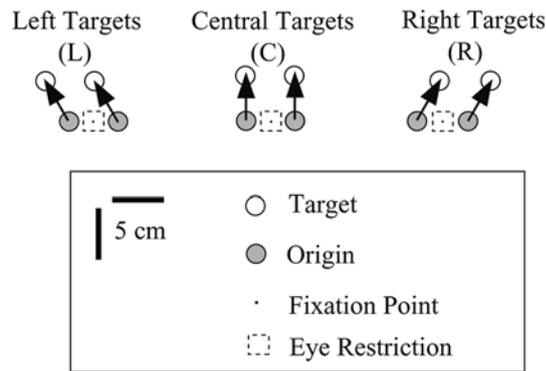


Fig. 1 Sketch of the task design. Movements were executed in the horizontal plane on the surface of a table. Index finger positions were displayed as cursors on a vertical screen in front of the subjects. Movement origins and movement targets were depicted on the screen as white open circles on a black background (different colors are used in this figure for clarity). When the targets appeared, the subjects had to perform quick reversal movements towards the targets, reverse the movement direction at around the target position, and then return toward the origins. The three possible target locations are designated by “L” (for left target), “C” (for central target) and “R” (for right target)

required to position each of the cursors in the middle of its corresponding origin circle. One and a half seconds after the origins were presented another small fixation target (diameter: 3 mm) was presented in the middle between the two origin circles. Subjects had to fixate this target and maintain eye position within a square of 20 mm side length centered around the fixation target for a period of 500 ms (starting 500 ms after eye target onset). If the measured eye position left this area, the trial was aborted and a new trial was initiated. If subjects successfully maintained fixation, the trial continued, the fixation point disappeared and two targets were added to the display. Targets remained visible for 1.5 s. As soon as the target came on, subjects were free to move their eyes. Upon target onset, the cursors had to be moved as quickly as possible and in a straight line to the target circle. Subjects were asked to attempt to “hit” each target by the respective cursor (to move the cursor into the target circle), and then immediately reverse direction to the origin, without pausing at the target. As soon as both cursors had crossed the respective target circles, a tone signaled that the movement was executed correctly. The whole movement was to be completed within the 1.5 s of target presentation, requiring a single, swift reversal movement. The temporal constraint ensured that movements were basically straight without substantial corrections. After each movement, there was a one second inter-trial interval during which the

screen was blank. Different movement types were presented at pseudo-random order. Unsuccessful trials were repeated. We intentionally chose reversal movements for this experiment since they have several advantages over single goal-directed movements. First, in reversal movements, the end of movement at the target is much more easily detectable than in single movements, which may show a considerable slowing down before the target, requiring an algorithm to detect the end of the movement (for instance, on the basis of a velocity threshold). These algorithms can give incorrect results, especially if subjects approach the target slowly. Second, single movements may entail a slow phase of homing-in to the target, during which the endpoint will be regulated by visual feedback. This would necessarily be independent for both arms and would reduce bimanual coupling. Furthermore, bimanual coupling has repeatedly been demonstrated in reversal movements (see Weigelt and Cardoso de Oliveira 2003; Heuer et al. 2001).

Experiments

Figure 1 shows the possible target arrangements and the corresponding arm movements. In all cases, the origins were 5 cm apart and the distances from the origins to the targets were also 5 cm. The arrows represent the movements required to hit the targets on the screen. In the control condition (full feedback of both hands), the positions of both arms were displayed as cursors on the feedback screen.

In the experimental condition, one or both cursors could be deleted from the display as soon as the targets appeared on the screen and remained invisible for the rest of the trial. Subjects were randomly assigned to one of four experimental groups, each of which was tested in one of four different experimental conditions (see Table 1), as well as in the control condition. The first group also received full visual feedback for both cursors also in the experimental condition (Full Feedback Group). The second group only received feedback for the cursor controlled by the right arm during the experiment condition (Right Feedback Group). The third group only received feedback for the cursor controlled by the left arm during the experiment condition (Left Feedback Group). In the fourth group, no cursors were visible during the experiment (No Feedback Group).

Subjects performed four blocks of 60 trials (each with 20 repetitions per target direction) in the control condition and four blocks of 60 trials (again, each with 20 repetitions

Table 1 Experimental design (for explanation see the “Methods” section)

Feedback group	Control condition	Experimental condition	Number of subjects
Full Feedback Group	Both cursors visible	Both cursors visible	6
Left Feedback Group	Both cursors visible	Only the cursor controlled by the left hand is visible	6
Right Feedback Group	Both cursors visible	Only the cursor controlled by the right hand is visible	6
No Feedback Group	Both cursors visible	No cursors visible	7

per target direction) in the respective experimental condition (see Table 1). To avoid performance deterioration caused by the lack of feedback, experimental blocks were alternated with control blocks with full feedback. Furthermore, even though visual feedback was fully or partly prevented in the experimental condition, auditory feedback upon target hit was provided.

Only subjects for which eye movements could be registered reliably and that complied well with our instructions (swift movements without corrections), with a minimal performance level of 30% correct movements were included in this study. Since the no feedback condition was clearly the most difficult one (see “Results” section for performance in the different groups), we originally tested ten subjects in this group, and six people in the other groups. Seven subjects in the No Feedback Group, and six subjects in the other groups complied with these criteria and were used in this study.

Data analysis

Only successful movements in which both cursors hit the target were analyzed in this study, in order to make sure that movements complied with the instructions. We analyzed only the first part of the reversal movement (towards the target, until reversal). Hand position data were smoothed by a second-order Butterworth filter (forwards and backwards to eliminate phase shifts, cut-off frequency 10 Hz).

In order to determine reaction times (RT), we first calculated velocity profiles by differentiating the position signal. Movement onsets (directly corresponding to RTs) were then defined as the first measurement of monotonically increasing velocity before exceeding 5% of the maximal amplitude. The time between movement onset and movement reversal was called “movement time”. Movement amplitudes were defined as the Euclidian distance between the starting position and the reversal point. Movements that deviated considerably from the average reaction time (<200 ms or >1200 ms), average amplitude (>20 cm) or the average time interval between the RTs (>100 ms) were excluded from the analysis. To investigate bimanual coupling, we calculated the correlation coefficients (r values) between RTs, the movement times and the movement amplitudes of the two arms in all repetitions of the same type of movement in the control condition and in the experimental condition for each person. In all subsequent analyses, r values were z-transformed before averaging and statistical analysis, and retransformed to r values for display. To study directional coupling over the whole movement, we calculated correlation coefficients between the instantaneous movement directions of both arms at each point in time (obtained by triangulating movement direction between subsequent position samples), beginning at the time of the earliest onset of movement in all trials and ending at the mean time of movement reversal. After z-transforming the r values, we averaged the time-resolved correlations over all

time-points to yield an average correlation coefficient for each movement type and person. Alternatively, correlation coefficients were computed between the directions of straight-line connections between arm positions at movement onset and at movement reversal. Since the former analysis gave very similar results to the latter, but had the advantage of being much less noisy, we only describe the results obtained using the average of the time-resolved correlation coefficient here.

For each of the experimental groups, the effects of the feedback condition were evaluated by ANOVA. For the movement parameters of the individual hands, 2 Hands (left, right) \times 2 Conditions (control condition, feedback condition) \times 3 Directions (left, central, right) ANOVAs with repeated measures on all factors were calculated for movement amplitudes, RTs, movement times and times to peak velocity. In order to evaluate bimanual coupling, 2 Conditions (control condition, feedback condition) \times 3 Directions (left, central, right) ANOVAs with repeated measures on all factors were calculated for the Fisher-Z-transformed correlation coefficients of movement times and reaction times, and the average correlation coefficients of amplitudes and directions. The averaged z-values were retransformed to r values for graphical display.

In addition to these within-group analyses, we also performed ANOVA analyses between groups, in which the between-group factor Group was included in addition to the above-mentioned within-group factors. We either used all four groups for these between-group ANOVAs, or, where we found a significance of the factor group, we ran an additional ANOVA in which only the three experimental groups were inserted. Post hoc analyses were performed using Tukey’s Honestly Significant Difference (HSD) test. The general significance limit was set to an error probability of $p < 0.05$. For the purpose of this study, we focus on main effects and interactions including the factor Condition.

Analysis of eye movements

For the purpose of this study, eye movements were mainly recorded as a control for potential differences in different feedback conditions. The analysis presented in this manuscript serves only to assess this point. Further analyses and comparisons between bimanual and unimanual movements will follow in a forthcoming, separate study.

We focused our analysis on saccades, since they represent the main type of eye movement observed in our task. Saccadic eye movements were automatically detected by the software package provided with the EyeLink system. Since we were interested only in eye movements that were related to goal-directed arm movements, we restricted our analysis to a time window beginning 80 ms after target onset and ending at the end of the trial (1500 ms after target onset). We also separately analyzed the first saccades that occurred before arm movements (that started before the first hand started

moving) and those that occurred after arm movement onset (after the second hand started moving). The parameters analyzed in this study were reaction times and end positions of the first saccade after target onset. Only data from the right eye were analyzed.

We evaluated the temporal relations between arm movement and eye movement onsets, quantified as correlation coefficients between the reaction times of eyes and arms in identical trials. Since not all subjects had enough saccades in each direction and condition before arm movement onset to allow the correlation coefficients to be calculated (a minimum number of five saccades was required), we could not perform an ANOVA. Rather, we compared the corresponding direction with and without feedback for each group (*t*-test, significance limit: 0.05). The end positions of the first saccades were also compared in such *t*-tests.

Results

As expected, all within-group ANOVAs revealed that the control group did not show any difference between the control and the experimental conditions, since in this group, the two conditions were actually the same (always full feedback). This fact will not be mentioned specifically in the following text again, although the respective data will be shown in all figures. Therefore, we will focus on the within-group analyses for the three other experimental groups, and on between-group analyses.

General movement parameters

Performance in the task

Whenever one or both cursors were not visible, it was more difficult to hit both targets, as reflected in lower performance rates for all groups (besides the Control Group) in the experimental condition. In the Left Feedback Group, average performance dropped from 72% to 62% successful trials. In the Right Feedback Group, the drop in performance was even bigger (from 65% to 47%). The most difficult condition was clearly when both cursors were invisible (No Feedback Group), as shown by a decrease in the performance rate from 76% to 44%. In the following analyses, only successful movements were included. Since our data acquisition software automatically repeated unsuccessful trials, we could ensure an equal number of successful movements in all conditions. Figure 2 shows typical trajectories and velocity profiles of single movements from individual subjects in the different feedback conditions. Quantitative parameters of movement execution in the different conditions will be described below.

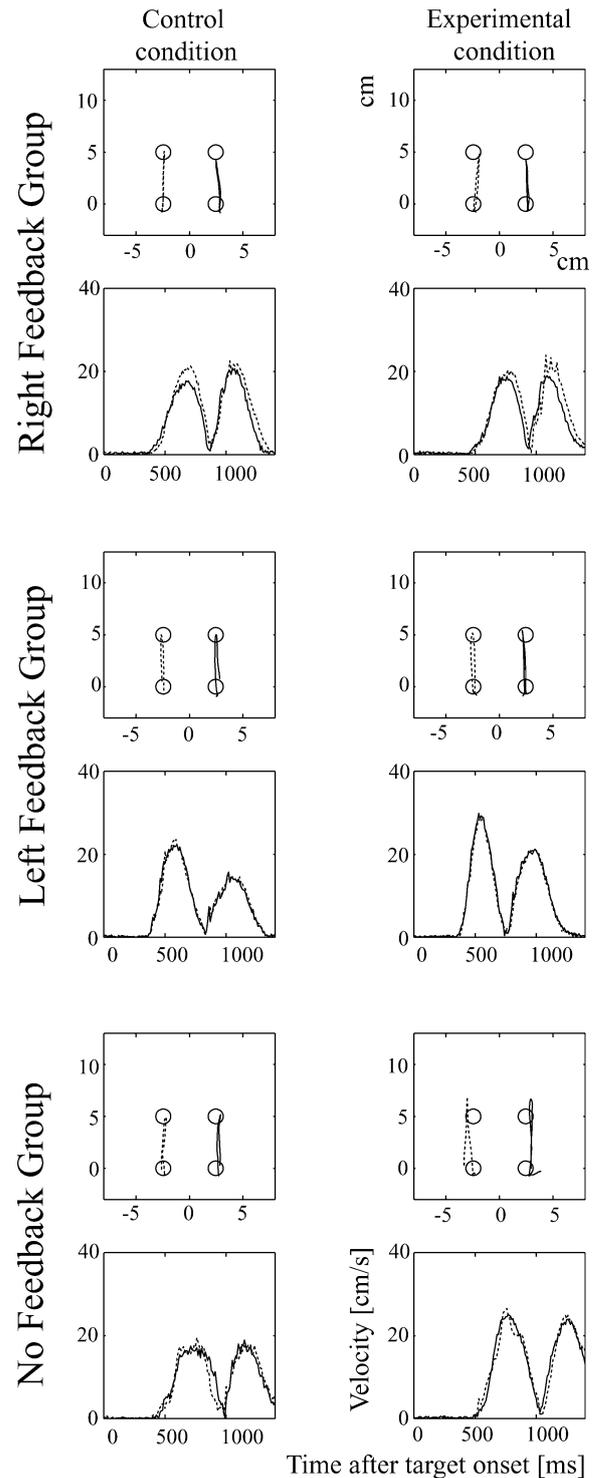


Fig. 2 Typical examples of movement trajectories and velocity profiles (single trials) for three different subjects, each from a different feedback group, in the control condition (left) and in the experimental condition (right). *Solid lines* depict data from the right hand, *dashed lines* data from the left hand. Since the movements were reversal movements, the velocity profiles have two peaks, the first one reflecting the movement towards the target, the second one the movement back towards the origin. Only the movement towards the target was evaluated in this study

Movement amplitudes

As is typified in Fig. 2 (especially in the No Feedback Group), movement amplitudes significantly increased when visual feedback was missing. When all four groups were inserted in the ANOVA, this effect led to significant interaction of the factors Condition×Group ($F_{(3,21)}=12.593$, $p<0.000$). In order to examine the effects of Condition in the experimental groups more closely, we performed another ANOVA in which only the three experimental groups were inserted. This analysis revealed a main effect of Condition ($F_{(1,16)}=35.741$, $p<0.000$). When the feedback for only one arm was taken away, movement amplitudes increased mainly in the arm for which no feedback was provided, as indicated by a substantial change in movement amplitudes of the left hand in the Right Feedback Group (left hand: 5.7 with, versus 6.14 cm without feedback), and of the right hand in the Left Feedback Group (right hand: 5.41 with, versus 6.29 cm without feedback). In the Left Feedback Group, these changes resulted in a significant Hand×Condition interaction ($F_{(1,5)}=11.61$, $p<0.019$). This was due to the phenomenon that the left arm's amplitudes were higher than those for the right arm under normal vision, but this relation reversed when only feedback for the left arm was present. In the Right Feedback Group, there was also a significant increase in movement amplitude, as indicated by a significant main effect of Condition ($F_{(1,5)}=7.108$, $p<0.045$). However, there was no significant interaction of Hand×Condition ($F_{(1,5)}=1.710$, $p<0.248$), since the left arm's movements in control conditions were already longer than those of the right arm. This difference between the Left and Right Feedback Groups resulted in significant interaction of the factors Condition×Group in the between-group analysis containing the three experimental groups ($F_{(2,16)}=9.191$, $p<0.002$), and a significant interaction of Condition×Hand ($F_{(2,16)}=4.984$, $p<0.040$).

The lengthening of movement amplitudes for the arm for which no visual feedback is available suggests that the amplitude of a given arm's movements is restricted by visual monitoring. The fact that only the right arm's amplitudes were appropriate under normal conditions, while the left arm's amplitudes tended to overshoot the target, could then be explained by a preferential monitoring of the right arm's movements under full vision conditions (at least for right-handers, which constituted all of our experimental subjects).

Differences between the movement amplitudes of the two arms

The effect of visual feedback on movement amplitude was also reflected in the differences between movement amplitudes, as indicated by a main effect of Condition when analyzing all four groups ($F_{(1,21)}=14.863$, $p<0.001$). This main effect persisted when only the three experimental groups were analyzed ($F_{(1,16)}=16.732$, $p<0.001$). Interestingly, the differences between movement ampli-

tudes increased when no feedback was available. The sign of this difference depended on the group. Under normal (full feedback) conditions, the right arm's amplitudes were always shorter than those of the left arm. When feedback for the left arm was taken away (Right Group), the difference between the amplitudes of the left arm and the right arm became even bigger, since the left arm's amplitude was increased further. Whenever feedback for the right arm was not available (Left Group), however, the left arm's amplitude became longer than that of the right arm.

Reaction times

Whenever visual feedback was prevented for one or both arms, reaction times for both arms increased significantly (Fig. 3), as revealed by an interaction of Condition×Group in the ANOVA containing all four groups ($F_{(3,21)}=12.260$, $p<0.000$), and a main effect of Condition in an ANOVA containing only the three experimental groups ($F_{(1,16)}=50.130$, $p<0.000$). This fact was even visible in single trials (see the example in Fig. 2). Since the increase was greatest for the No Feedback Group, there was also a significant interaction of Condition×Group ($F_{(2,16)}=6.770$, $p<0.007$).

Movement times

Average movements times were 479 ms. Consistent with the increase in movement amplitudes when no feedback was available, movement times also slightly increased without feedback. This effect, however, just failed to reach

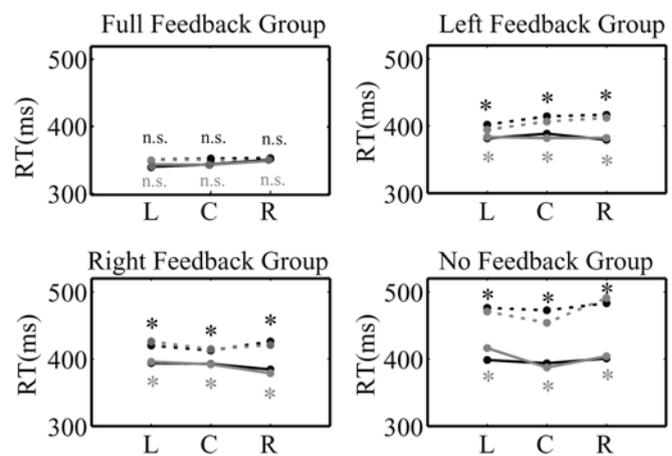


Fig. 3 Mean reaction times for both hands, all target directions and all conditions averaged over all subjects. Data from the control condition (with full feedback) are drawn as *solid lines*, data in the experimental condition (with full feedback in the Full Feedback Group, only feedback for the right arm in the Right Feedback Group, only feedback for the left arm in the Left Feedback Group, no feedback for either arm in the No Feedback Group) are drawn in *dashed lines*. Right arm values are shown in *gray*, left arm values in *black*. Asterisks highlight significant post-hoc differences between the two conditions for a given hand and target. Target directions are indicated by L, C and R (see Fig. 1)

significance over all experimental groups ($F_{(1,16)}=3.078$, $p<0.098$).

Bimanual coupling

Temporal coupling

As is evident from the examples shown in Fig. 2, the movements of the two arms were initiated and reversed almost simultaneously. The mean RT-difference of the two arms was 36 ms and did not show any significant dependence on the feedback condition ($F_{(1,21)}=1.041$, $p<0.323$) or interaction of Condition \times Group ($F_{(3,21)}=3.010$, $p<0.053$). The mean difference in reversal times was even smaller (26 ms). It showed a dependence on the feedback condition ($F_{(1,21)}=5.804$, $p<0.025$) and a significant interaction of Condition \times Group ($F_{(3,21)}=3.593$, $p<0.031$). However, this interaction also persisted when analyzing only the three experimental groups ($F_{(2,16)}=4.778$, $p<0.024$), since the effect of the feedback was inconsistent in the different groups.

Although the RTs and reversal times in different trials could vary substantially from trial to trial, these variations were highly coupled between the arms, resulting in extremely high correlations of the RTs (on average 0.88, ranging from 0.1 to 0.99 for individual subjects and conditions) and movement times (on average 0.87, ranging from -0.20 to 0.99) of both arms over trials. There were no significant effects of the feedback condition on the RT correlation ($F_{(1,21)}=1.424$, $p<0.246$) and reversal time correlation ($F_{(1,21)}=2.725$, $p<0.114$), and no significant interaction of Condition \times Group (RT: $F_{(3,21)}=1.083$, $p<0.378$, time of reversal: $F_{(3,21)}=1.566$, $p<0.227$).

In summary, therefore, it seems that temporal trial-by-trial coupling between the arms is not consistently affected by visual feedback.

Spatial coupling: amplitude correlations

The manipulation of visual feedback significantly affected the movement amplitude correlation, as indicated by a significant interaction of Condition \times Group in an ANOVA in which all four groups were used ($F_{(3,21)}=5.167$, $p<0.008$). In order to analyze the effect of visual feedback in detail, we performed another ANOVA with only the three experimental groups. Correlations between movement amplitudes of the two arms were significantly higher when feedback was absent than when feedback was present (Fig. 4), as was revealed by a main effect of Condition in the experimental groups ($F_{(1,16)}=7.219$, $p<0.016$). Since the effect of condition was only highly significant in the No Feedback Group ($F_{(1,6)}=11.209$, $p<0.015$), and not significant in the Right Group ($F_{(1,5)}=0.991$, $p<0.365$) or in the Left Group ($F_{(1,5)}=4.157$, $p<0.097$), there was an additional highly significant interaction of Condition \times Group ($F_{(2,16)}=5.582$, $p<0.014$). Therefore, it appears that correlation between

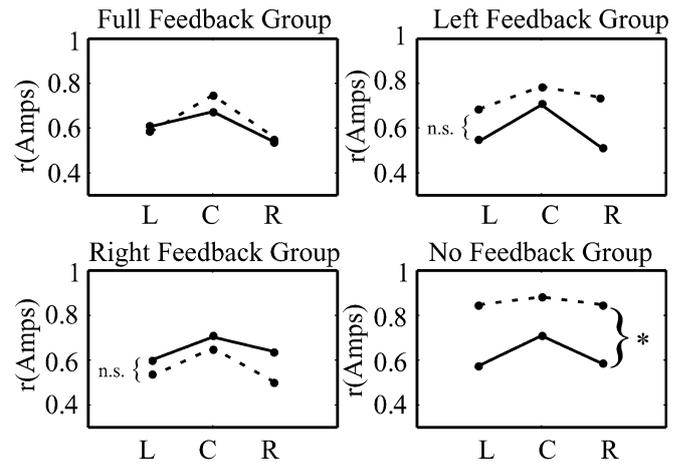


Fig. 4 Average movement amplitude correlation coefficients for all subjects in each group, target direction and condition. As in Fig. 3, data from the control condition are drawn as *solid lines* and data from the experimental condition are drawn as *dashed lines*. The significant main effect of the factor Condition is highlighted by an asterisk

the amplitudes of the two arms significantly increased compared to the other conditions only when feedback for both hands was missing. Since the amplitude correlations were higher during straight forward than during oblique movement directions, there was an additional main effect of direction ($F_{(2,15)}=6.182$, $p<0.011$).

Spatial coupling: directional correlations

Directional coupling between the arms varied systematically with target direction, with correlations close to 0

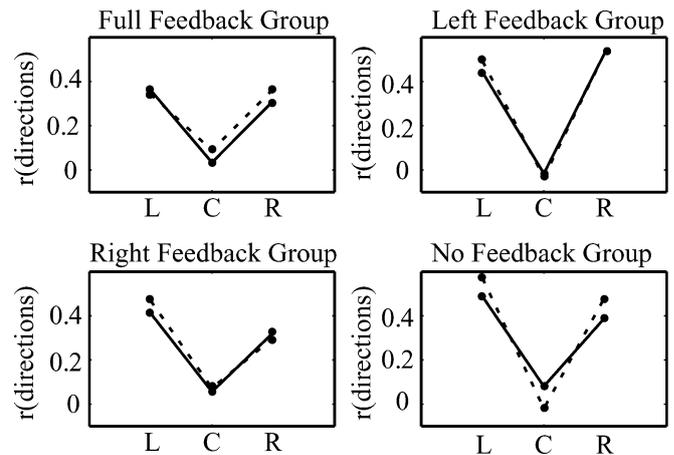


Fig. 5 Average movement direction correlation coefficients for all subjects in each group, target direction and condition. Correlation coefficients were determined for each point in time after the earliest onset of movement until the average time of reversal. The z-transformed time-resolved correlation coefficients were then averaged for each subject over time and reconverted to r values for display. As in Fig. 3 and 4, data from the control condition are drawn as *solid lines* and data from the experimental condition are drawn as *dashed lines*. There were no significant post hoc differences between the feedback conditions in any of the groups

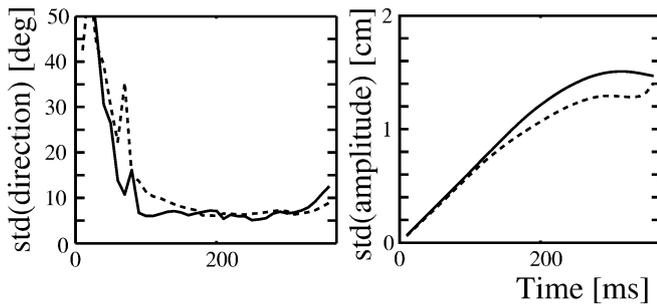


Fig. 6 Representative examples of standard deviations for movement directions (left panel) and movement amplitudes (right panel) over time (displayed starting from the earliest onset of movement until the average time of reversal). Data are from 37 trials of one subject moving to the central targets with full visual feedback. Data for the left hand are displayed as *solid lines*, data for the right hand as *dashed lines*

for straight forward movements and higher correlations for oblique movement directions (Fig. 5). This resulted in significant main effects of movement direction in all four groups ($F_{(2,20)}=81.493$, $p<0.000$). This effect will be considered in an independent, forthcoming study. The visual feedback did not affect this pattern in any way, as indicated by no significant interaction of the factors Condition \times Group ($F_{(3,21)}=0.049$, $p<0.985$). Also within the individual experimental groups, there was no significant effect of Condition.

Movement variability in amplitudes and directions

Why are the correlations of movement amplitudes affected by visual feedback, while correlations between movement directions are not? One hypothesis is that the drop in amplitude correlations may be caused by independent corrective movements of the two arms. Corrective movements should lead to an increase in signal variability. We assessed the variability of movement amplitudes and

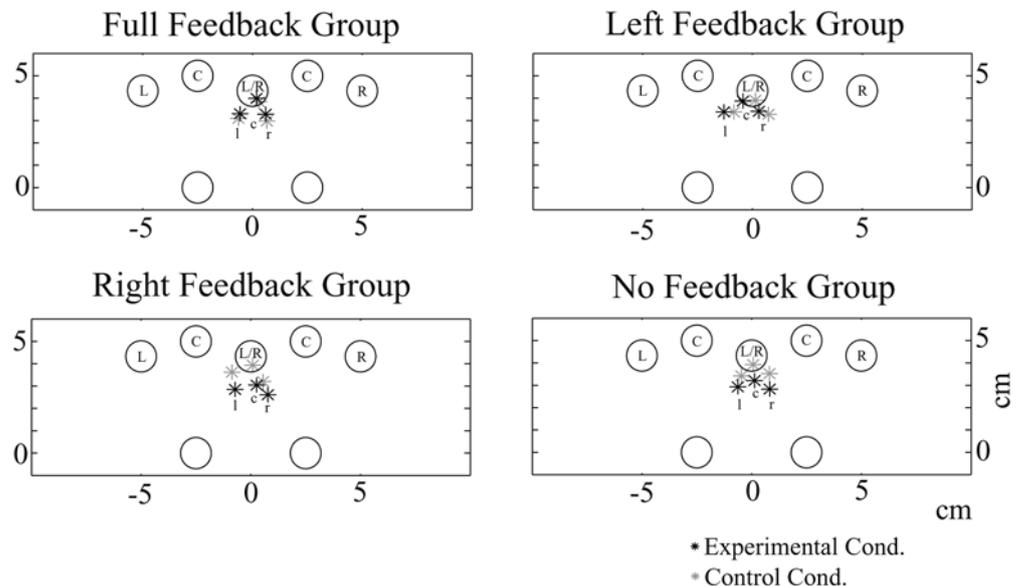
movement directions by calculating the standard deviations of movement amplitudes or directions over time (starting at the first movement onset and up to the average time of reversal). Figure 6 shows a typical example of standard deviations of movement amplitudes and movement directions over time during straight bimanual movements to the front. It is obvious that while the variability of movement directions stays at a constant level (after dropping from an initial high level due to noisy direction measurements before and around movement onset), while the variability of movement amplitudes increases over time. These different patterns of variability can be explained by the different accuracy demands on these two factors posed by the task. Movement direction had to be quite accurate, since the targets had to be hit in order for a movement to be scored as successful. On the other hand, movement amplitude was less restricted, since subjects only had to cross the border of the target, so there was a minimum amplitude for successful movements, but no strict requirement on a maximal amplitude. Therefore, more variability was possible in the amplitude domain.

Eye-hand coordination

In order to assess eye movement strategies during our bimanual task, and to test whether the differences in bimanual coupling observed with and without visual feedback resulted from different eye movement strategies, we evaluated the reaction times and end points of saccades under different conditions.

In all groups and for all target directions, eye movement strategies followed a typical pattern. In 63% of the trials, a saccade occurred after target onset and before the arms began to move, with an average reaction time of 303 ms (as compared to an average arm reaction time of 379 ms). The reaction times of saccades occurring before arm movement onset were only weakly correlated to the

Fig. 7 Mean end positions of first saccades after target onset for all groups and target directions in the control condition (*gray asterisks*) and the experimental condition (*black asterisks*). Capital letters indicate the target positions for the left (L), center (C), and right (R) target, lower case letters indicate the average end points of the saccades when the left (l), center (c), or right (r) targets were presented



* Experimental Cond.
* Control Cond.

reaction times of the arms (with an average correlation coefficient of 0.23). In no group or target direction did we find a significant difference between the correlation of eye and arm reaction times in different feedback conditions.

In only 7% of the trials there was a saccade after arm movement onset. The saccades occurring before arm movement onset invariably pointed towards the middle between the two central targets, corresponding to the average position of all possible targets (Fig. 7). For rightward movements, this corresponded to the position of the left target, while for leftward movements it corresponded to the position of the right target. If a saccade occurred after arm movement onset, it pointed to a similar position as the first saccade. In none of the groups did we find a difference between the number of saccades before movement onset or after movement onset in the different feedback conditions. Moreover, none of the groups showed a significant difference in saccade directions (as quantified by the horizontal end positions of the first saccades), in neither the saccades initiated before arm movement onset (Fig. 7) nor in the ones initiated after movement onset (not shown). The only difference was a slightly (but significantly) smaller saccade amplitude (expressed by lower end-points in the vertical dimension) without feedback for the middle target in the Right Feedback Group, and for all targets in the No Feedback Group.

Discussion

This study was aimed at investigating to what extent online usage of visual feedback influences the performance of discrete bimanual reversal movements. We found that visual feedback not only influenced movement characteristics of each arm, but also affected a specific parameter of bimanual coupling (trial-by-trial amplitude correlations), suggesting that online visual information is used to shape the coordination between the arms.

The influence of visual feedback on the motor performance of each arm consisted of alterations of two basic movement parameters. First of all, we observed that absence of visual feedback for one or both arms significantly increased reaction times. Assuming that motor programming is a time-consuming process, this suggests that, without being able to use online feedback, a bigger part of motor programming had to be completed before movement initiation. Conversely, if visual feedback is available, some part of the programming process may be left for online specification during movement execution. Interestingly, even if only one arm was deprived of feedback, the initiation of movement in the other arm was also slowed down, so that both arms still started to move almost simultaneously. This observation confirms the idea that temporal coupling of movement initiation of both arms is very tight indeed and cannot be easily overridden (Kelso et al. 1979a; Marteniuk et al. 1984; Fowler et al. 1991; Boessenkool et al. 1999).

Second, absence of feedback resulted in increased movement amplitudes. A similar effect has already been described for unimanual movements (Sheth and Shimojo 2002). Since these authors found that already the early acceleration phase of the movement was influenced, they concluded that visual information must affect the very beginning of movement execution. Such early influences of visual information on movement performance suggest that the visuomotor control loop during ongoing movements may take less time than previously assumed (as in Bushan and Shadmehr 1999, see also reviews about fast visuomotor control loops: Desmurget and Grafton 2000; Paillard 1996). Since increases in movement amplitude appeared primarily in the affected arm, it seems that movement amplitudes are independently controlled for both arms.

Temporal coupling and visual feedback

Correlation coefficients as well as inter-hand-intervals for the RTs and the movement times of the two arms were unaffected by the visual feedback condition. This finding is in agreement with previous studies that show that temporal coupling between hands in a complex bimanual movement sequence is not altered in the dark or when subjects are blindfolded (Kazennikov et al. 1994; Perrig et al. 1999). It lends further support to the idea that temporal coupling is rather rigid and can be overridden less easily than spatial coupling (Schmidt et al. 1979; Kelso et al. 1979a, 1979b; Franz et al. 1996; Jackson et al. 1999). One hypothesis to explain this difference is that temporal coupling may rely mainly on proprioceptive rather than visual feedback during ongoing movements. This assumption is supported by the finding that temporal deficits in movement coordination were observed in centrally deaf-ferented patients (Verschuere et al. 1999; Jackson et al. 2000, 2002).

Spatial coupling and visual feedback

Like temporal coupling, coupling of movement direction was not related to the visual feedback condition. Directional correlations showed a systematic relation to movement direction, with oblique movements being positively correlated and straight forward movements being basically uncorrelated. The fact that this behavior was mainly related to the movement and was not altered by visual feedback is supported by another finding in our group that showed that, in most cases, directional coupling was not affected by visuomotor transformations that distort visual feedback about movement performance (Weigelt and Cardoso de Oliveira, unpublished observations).

On the other hand, movement amplitude correlations were strongly affected by visual feedback. When no feedback for either arm was available, amplitude correlations were significantly higher than when feedback for one

or both arms was available. This finding suggests that online visual feedback decreases bimanual coupling. Two additional findings of this study suggest that this decrease in bimanual coupling is the result of independent movement corrections of the movement amplitudes of both arms. First, the movement amplitude of each arm was independently affected by the availability of visual feedback. The arm for which feedback was absent performed longer amplitude movements, while the other arm was not affected. Second, variability in movement amplitudes increased during movement performance, suggesting that it may be at least partly due to online movement corrections. With movement times of the order of 500 ms, there was enough time available for visual information to induce corrections of ongoing movements. The fact that no such increase in variability occurred in the directions of movement suggests that movement amplitude and direction in our task differed in their susceptibilities to online control processes. This renders more support to the idea that these two movement parameters are subserved by different control mechanisms (Favilla et al. 1990; Bock and Arnold 1992; but see also Bhat and Sanes 1998).

The analysis of eye movement data revealed that the bimanual decoupling of movement amplitudes could not be explained by a difference in eye-movement strategies under different feedback conditions. Upon target onset, subjects invariably moved their eyes towards a central position that represented the middle of all possible target positions. Together with the fact that very few additional eye movements occurred during arm movements, this suggests that both target detection and the visual monitoring process operates mainly with the aid of peripheral vision. This visuo-motor strategy may have been the most “economical” solution for the strict temporal requirements of our tasks, since it minimized both the distance that the eyes had to travel and the number of eye movements generated per trial.

In accordance with a study on a more complex bimanual task (Müri et al. 1999), the temporal coupling of eye-and arm movements was only moderate, and much weaker than the temporal coupling between the arms. In contrast to an early study by Honda (1982), we found no preferential saccades towards the right hand in our bimanual reaching movements. This difference, however, may be accounted for by the different accuracy and speed demands of the two tasks.

Altogether, our study shows that online visual feedback affects bimanual coupling in a very specific way. It selectively influences spatial coupling of movement amplitudes, without affecting coupling of movement directions or temporal coupling. This suggests that movement amplitude may be more susceptible to online visual control than movement direction. Since bimanual coupling was reduced when visual feedback was available, it appears that the “default” mode in bimanual movements is coupled, and visual feedback serves to uncouple the arms, probably by independent corrective movements. This could explain earlier observations of progressive decou-

pling between the arms (Fowler et al. 1991; Gribova et al. 2002).

Acknowledgements This study was supported by the DFG (CA 245), the German-Israeli Project Cooperation (DIP) funded by the German Ministry of Education and Research (BMBF), and the Volkswagen Foundation. We are grateful to Fabian Ottjes for programming the experimental software and to Anja Ruetter for performing the experiments.

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