

RESEARCH ARTICLE

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Bimanual coupling during the specification of isometric forces

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Abstract The present study investigated the generalizability of the hypothesis of transient coupling during the preparation of bimanual movements (Spijkers and Heuer 1995) to the specification of isometric forces. In the first experiment we used the timed response paradigm (TRP) to examine the time course of the specification process. Subjects had to generate bimanual isometric force pulses while preparation time was controlled by the TRP. Target forces were weak (20% of maximal voluntary force, MVF) or strong (40% MVF) and assigned randomly to each hand. The first experiment revealed the predicted pattern of correlations between the peak forces but, because the subjects tended to delay responding when time for preparation was very brief, the time course of the specification process did not fully match expectations. In the second experiment we improved force–trajectory feedback and presented two initial cues that were expected to induce better preparation of the default force (30% MVF). Both changes were successful and the results further corroborate the transient-coupling hypothesis.

Key words Bimanual coordination · Programming · Transient coupling · Isometric forces

Introduction

Recent research on interlimb coordination is mainly concerned with temporal and spatial coupling of movements performed concurrently. Studies of temporal coupling are focused on movement duration (Kelso et al. 1979, 1983; Marteniuk et al. 1984) or relative phase (e.g.

Kelso et al. 1981). Research on spatial coupling is predominantly aimed at amplitude (e.g. Marteniuk et al. 1984; Sherwood 1990, 1991, 1994a, 1994b; Spijkers and Heuer 1995; Heuer et al. 1999, 1998a, 1998b) and, to a lesser extent, at direction (Franz et al. 1996; Swinnen et al. 1997, 1998).

The present study focuses on isometric forces, because isometric contractions are likely to have certain advantages in the study of interlimb coordination. For example, different movement amplitudes tend to be associated with different movement durations, and there is a fairly tight temporal coupling between bimanual movements (Kelso et al. 1979, 1983; Franz et al. 1996). Hence, the study of bimanual movements with different amplitudes suffers from temporal coupling, which again can affect the amplitudes. Temporal coupling between movements of different amplitude seems to be responsible for an often observed asymmetry: when one hand performs a long movement, the amplitude of a concurrently performed short movement of the other hand is significantly increased, while a corresponding shortening is not observed for the long movement (cf. Heuer et al. 1998b; Marteniuk et al. 1984; Sherwood 1994b). In contrast, the duration of isometric contractions has been reported not to depend on the peak force (pulse height control, cf. Gordon and Ghez 1987), so coupling with respect to peak forces can be studied without confounding effects from temporal coupling. While investigating a broad range of isometric forces, but concentrating on peak force variability, Newell and Carlton (1985) also found no influences of peak force on force rise time when peak force was between 20 and 70% of maximal voluntary force (MVF).

Spijkers and Heuer (1995) proposed a model of bimanual coupling that assumes cross-talk to occur at the level of movement execution and at the level of parameter specification. Cross-talk at the execution level occurs when the neural signals which control muscle activity for different movements influence each other, thus resulting in a deviation from the specified movement (cf. Marteniuk et al. 1984). Cross-talk at the execution

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level can also be observed when only one hand acts. Todor and Lazarus (1986), for example, asked children to exert an isometric force unimanually and measured the involuntary co-contraction of the contralateral limb (index finger). They found that the amplitude of the contralateral contraction (motor overflow) depends on the amount of force exerted with the active limb.

Cross-talk at the level of parameter specification (or programming level) occurs when neural signals involved in the setting of the parameters influence each other, so that the parameters deviate from the intended movement characteristics. These influences can be transient or static in nature. Static coupling at the programming level seems to exist in tasks in which the spatio-temporal patterns of the movements are incompatible, e.g. in drawing a circle and a square simultaneously with the left and right hand. Most people fail regardless of the amount of time available for preparation. Transient cross-talk at the programming level, in contrast, depends on the change in the preparatory state, that is, carry-over effects are present while parametrization proceeds but disappear as soon as the final steady state of parameter specification is reached. Thus, the coupling strength varies over time.

According to previous evidence the dynamics of transient coupling depend on whether the parameters for movements of the two hands are the same or different (Heuer et al. 1998b). If identical movements have to be performed, the parameters to be specified are equal. Therefore, coupling strength remains high during parametrization. However, it is necessary to decouple the parametrization processes when two different movements have to be performed, and therefore coupling strength decreases as parametrization proceeds. Decoupling is a time-consuming process, and until it is complete or reaches its final (static) level, mutual cross-talk between the parametrizations occurs. (In the Appendix we present a formalization of the model and fit this model to the experimental data.)

Since the present study aims at identifying cross-talk at the programming level, it is important to have criteria that distinguish it from cross-talk at the execution level. The amount of cross-talk that occurs at the execution level relates to the difference between the strength of the signals that control the limbs (cf. Walter and Swinnen 1990; Todor and Lazarus 1986). Hence, the amount of cross-talk should be small when the difference between the movements is small and larger when it increases. The opposite prediction holds for the interference caused by transient coupling at the programming level: it should be large at early stages, when there is little difference between the parametrization processes, and vanish with increasing differences. Thus, the pattern of interference allows us to distinguish whether the interference is caused by cross-talk at the execution or programming level.

Three predictions can be made on the basis of the hypothesis of transient coupling during parameter specification. First, when different movements have to be performed, more time is needed to prepare for them because

mutual cross-talk during movement specification results in a delay in all preparatory states. This prediction has been confirmed for bimanual reversal movements (Spijkers et al. 1997). The second prediction concerns the time course of the parametrization processes. Transient coupling is related to the change in the parameters, so coupling strength is initially high and then diminishes. Thus, compared to the time course of parametrization of movements that are the same, the parametrization of different movements should show strong assimilation effects at its beginning that decrease as parametrization proceeds. The third prediction derives from the assumption that the dynamics of coupling strength can be adjusted to task requirements. When movements are the same, parametrization processes remain coupled, resulting in strong correlations between the movement characteristics no matter how much time is available for preparation. In the other case, if different movements have to be performed, the correlations between the movement characteristics should be strong during the early stages of the parametrization process, just as they are when the movements are the same, but should decline when the time available for preparation increases, because the parametrization processes are gradually decoupled.

A suitable method for investigating the time course of parametrization processes is the timed response paradigm (TRP), originally developed by Schouten and Becker (1967) for the study of speed-accuracy trade-offs. Its logic is as follows. Subjects are required to initiate a response at a predictable point in time which is indicated, for example, by the fourth of a series of four tones of increasing pitch. The tones are of the same duration and the interval between them is constant, thus allowing subjects to anticipate the onset of the fourth tone. The information about which movement to produce is given by an additional cue (e.g. a visual one) which is presented a certain time in advance of the fourth tone. By way of systematic variation of the interval between cue and last tone (cueing interval) the amount of time available for the preparation of the correct movement can be varied. When the cueing interval is sufficiently short, subjects have to act although preparation is not complete; the actual preparatory state is then reflected in the movement characteristics which approach the required ones as the cueing interval increases. Hence, the TRP allows the time course of the preparation process to be traced. Using the TRP, Hening et al. (1988; see also Ghez et al. 1990) could show that the parametrization process needs time and proceeds gradually.

Studies that used the TRP mainly examined unimanual movements. However, it turned out to be applicable also to investigating the time course of the parametrization of bimanual reversal movements (Heuer et al. 1998b). This study revealed cross-talk during amplitude specification, with its dynamics corresponding to the dynamics predicted by the hypothesis of transient coupling during movement parametrization (Spijkers and Heuer 1995; Heuer 1993). The purpose of the present study was to test the transient-coupling hypothesis with the TRP

for bimanual isometric contractions and thereby to examine its generality.

Materials and methods: Experiment 1

Subjects

Sixteen students participated in the first experiment. All were right-handed (Edinburgh Handedness Inventory, Oldfield 1971) and had normal or corrected-to-normal vision. They were paid DM 72.50 for their participation.

Task and apparatus

Subjects sat in front of a computer monitor. The force-recording device (Fig. 1) was placed on the table between the subjects and the monitor. Subjects grasped two handles (A in Fig. 1), each of 2.6 cm diameter, with their left and right hands. Both thumbs were abducted and placed on the ends of two levers (B in Fig. 1) so that they touched two mechanical stops (C in Fig. 1). Their correct placement was monitored by means of photoelectric make-and-breaks (D in Fig. 1). The lever transmitted the force exerted by the subjects with their thumbs to two load cells (Kyowa LM-A; E in Fig. 1) with an amplification of approximately 1.6. The amplified output of the load cells (Kyowa bridge amplifiers, model WGI-300 series) was fed into a Stemmer analog-to-digital converter (STE 6111). The signal was sampled with 500 Hz. Sampling range was from 0 to 196 N with a resolution of 0.12 N.

Subjects had to produce bimanually isometric force pulses at a certain point in time. Target forces were indicated by visual cues: Two vertical bars which indicated the required peak forces by their height were presented on a monitor at eye level. Each bar was 1.1 cm wide and of one of three different heights (3.8 cm, 7.6 cm, 11.4 cm) representing 20, 30, and 40% of the subject's maximal voluntary force (MVF). The two bars were yellow on a blue background and separated by 1.7 cm. Their bases were aligned. The start of the force pulses had to be synchronized with the last of four predictable tones of increasing pitch (from 1000 Hz to 2000 Hz in steps of 333 Hz; 20 ms duration; 480 ms interstimulus interval). The visual cues were presented with a variable cueing interval (onset of cue to onset of the fourth tone) of 0, 125, 250, 375, 500, 750, and 1000 ms.

Design and procedure

Initially, the individual MVF of each subject was determined. Subjects were instructed to produce brief bimanual force pulses with their thumbs as forcefully as they were capable of. Five bimanual force pulses were recorded. When a force pulse contained more than one maximum, the measurement was repeated; force rise time was not restricted. For each hand the maximal peak force was taken as the MVF for this hand (hand-specific best-of-five procedure).

All subsequent measurements were scaled relative to the individual level of each hand.

Subjects initiated a trial by positioning their thumbs on both levers. The correctness of their placement was indicated on the screen by means of two colored circles, one for each hand, which changed from red to green when the correct position had been maintained for at least 500 ms. After 500 ms of presentation of the two green circles the screen was cleared, and after an interval of 1000 ms presentation of the tone series began. Within the series the visual cues were presented with the appropriate cueing interval. Both cues (for left and right hand) appeared simultaneously.

Subjects were instructed for each trial to prepare a force pulse of medium intensity (30% MVF) as long as the visual cues were not yet presented and to use the remaining time from the onset of the cues until the fourth tone to prepare for the cued peak forces. Simultaneously with the fourth tone they had to produce the bimanual pulses as accurately as possible, no matter whether the correct peak force had already been specified or not. Sampling of the force data started with the presentation of the first tone and continued for 2000 ms after presentation of the fourth one.

After each thumb-press subjects received feedback about their synchronization accuracy (interval between the force onset and the fourth tone). At cueing intervals of 1000 ms they were also provided with feedback about their force trajectories (i.e. peak force and duration). The onset of each force pulse was defined as the start of a 30-ms interval within which the force change exceeded 0.7 N/30 ms (1.1 N/30 ms at the load cell). Synchronization was indicated to be good when the first of the two force pulse onsets did not deviate more than ± 40 ms from the tone onset. In this case, the German word for good ("gut") was displayed at the bottom of the screen. Otherwise the deviation was presented numerically, together with the German word for deviation ("Abweichung: x ms"). Responses that were too early were indicated by a negative sign.

Trajectory feedback was given separately for each hand. Two outline rectangles were in the left and right half of the screen. Their height was 3.8, 5.7 or 7.6 cm for 20, 30, and 40% MVF, respectively, and their width of 3.8 cm represented 400 ms. The force-time curves were drawn with their onsets aligned to the left edge of the rectangle and the baseline aligned to the bottom line. Thus, when the peak force was correct the force-time curve just touched the rectangle's upper line, and when the duration was 400 ms the curve's fall back to the base line coincided with the rectangle's right edge. Feedback was shown for 2000 ms. Subjects were instructed to produce force pulses that fit in their height as accurately as possible in the outlined rectangle, while their width was not to exceed the boundaries of the rectangle (i.e. pulse duration should not be longer than 400 ms). The experimenter who monitored performance received synchronization as well as trajectory feedback after each trial on a separate screen. He gave corrective feedback if the subject's performance deviated consistently too much from the constraints.

After determination of MVF five blocks of training were given in which subjects learned the task step by step. During the first block of training (60 trials) they practiced identical bimanual force pulses of 20, 30 or 40% MVF with a constant cueing interval of 1000 ms. They were instructed to pay attention to the accuracy of force production and received feedback about the force trajectories after each trial. The focal task characteristic of the second training block (70 trials) was the accuracy of synchronization. Target forces for both hands were constant (30% MVF), but six cueing intervals were variable and randomized (0, 125, 250, 375, 500, 750 ms). The seventh cueing interval of 1000 ms occurred on every seventh trial, thus ensuring trajectory feedback at constant intervals. This procedure was retained for all the following blocks.

In the third block of training (112 trials) variable target forces (20% MVF and 40% MVF) were combined with variable cueing intervals. Only identical target forces for the two hands were used, while in the fourth training block the cues indicated different target forces in each trial. Finally, in the fifth block of training all cueing intervals and pairs of target forces were presented. Each of the four combinations of cues and seven cueing intervals was replicated four times, thus resulting in 112 trials. This fifth block was in all aspects identical to the following experimental blocks.

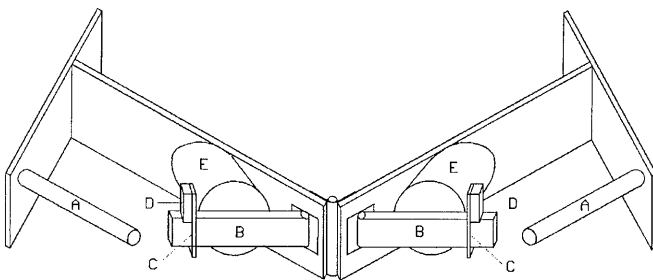
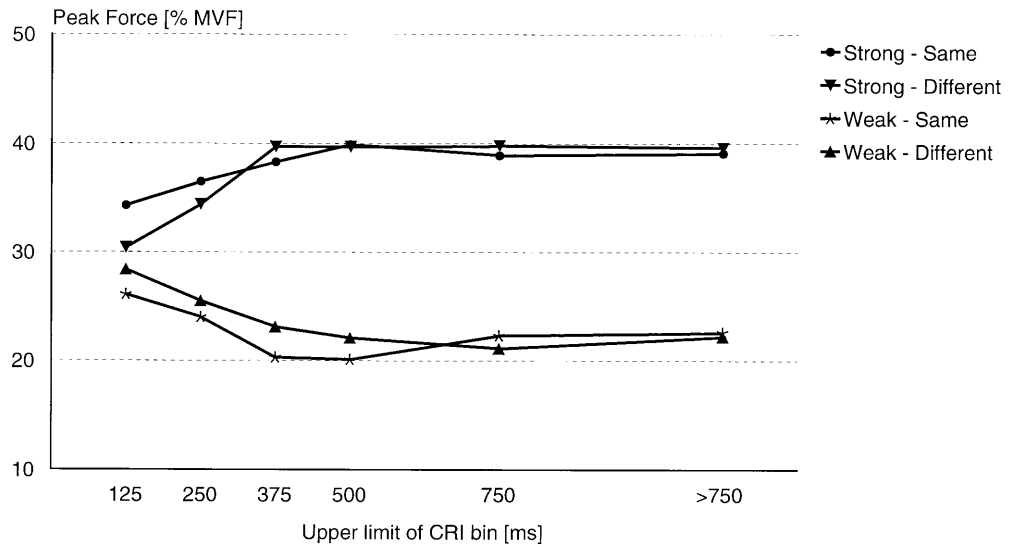


Fig. 1 Sketch of the apparatus: A handles, B levers, C stops, D photoelectric make-and-breaks, E housings of load cells

Fig. 2 Experiment 1: mean peak forces, expressed as a percentage of maximal voluntary force (MVF) related to the time available for response preparation, for each target force (strong, weak) and cued force of the other hand (same, different). Target force in the strong and weak conditions were 40 and 20% of MVF respectively



The experiment was split into two sessions on two successive days. In the first session subjects performed the five blocks of training and three experimental blocks; during the second session they performed training blocks one and five again, followed by five experimental blocks. (The first subject performed only six experimental blocks, two in the first and four in the second session.)

Data analysis

Data analysis was restricted to the experimental blocks. The signals were low-pass filtered (fourth order Butterworth filter with a cut-off frequency of 10 Hz, forward and backward to eliminate phase shifts). The first and second derivatives were computed using standard differentiation techniques; signals were again low-pass filtered after each differentiation. The criterion for the onset and the end of a force pulse was a threshold of 20% MVF/s.

Results

Trials were excluded from analysis when the asynchrony between the onsets of the pulses of the two hands exceeded 80 ms, when subjects produced only a single pulse with one hand or no pulse at all. In total 10.25% of 14 112 trials were rejected by these criteria, almost all of them because of synchronization errors.

For each valid trial the cue-response interval (CRI), the interval from cue presentation to the onset of the force pulse, was computed separately for each hand. The mean of both hands was used to assign each trial to one of the six CRI bins (0–125; 125–250; 250–375; 375–500; 500–750; 750–). Three subjects were excluded from further analyses because they did not achieve cue-response times of less than 125 ms in some of the conditions.

Peak force

The major dependent variable was the peak force of the left and right hand. Figure 2 shows the mean peak forces

as a function of the CRI (classified into bins). Peak forces matched the instructed 20% and 40% when there was sufficient time to prepare for the response; that is, at long CRIs. At short preparation times (less than approximately 400 ms CRI) the peak forces did not reach the target level. The less time available for preparation, the more the forces approached the instructed default value of 30% MVF, although in particular the peak forces in conditions with the same target forces did not reach this value at the shortest CRIs (first bin).

The critical prediction of the transient coupling hypothesis concerns the initial phase of the specification process. The specification process of different forces should lag behind the process of same forces until decoupling is complete. The data show that at the shortest CRIs peak forces were still closer to the instructed default value of 30% when different target forces were required than when the same forces were required. This initially strong coupling is assumed to be due to coupling at the programming level, because it decreases while the difference between the actually specified forces increases. In contrast, coupling at execution level should increase with increasing difference between the forces that are produced (cf. Walter and Swinnen 1990).

The peak forces were averaged individually for each experimental condition and submitted to an ANOVA with the four factors Relevant Cue, Irrelevant Cue, CRI, and Hand ($2 \times 2 \times 6 \times 2$ factorial design with repeated measures on each factor). The factor Relevant Cue represents the cue that specified the target force for the hand that produced the force which was entered in the ANOVA (weak or strong). The factor Irrelevant Cue represents the cue for the other hand, which could be the same as or different from the relevant cue.

Peak forces were larger when the cue indicated a strong target force and smaller when it indicated a weak target force [$F(1,12)=163.88, P<0.001$]. Starting at a level near the instructed default value of 30% MVF, the peak forces increased or decreased towards the cued tar-

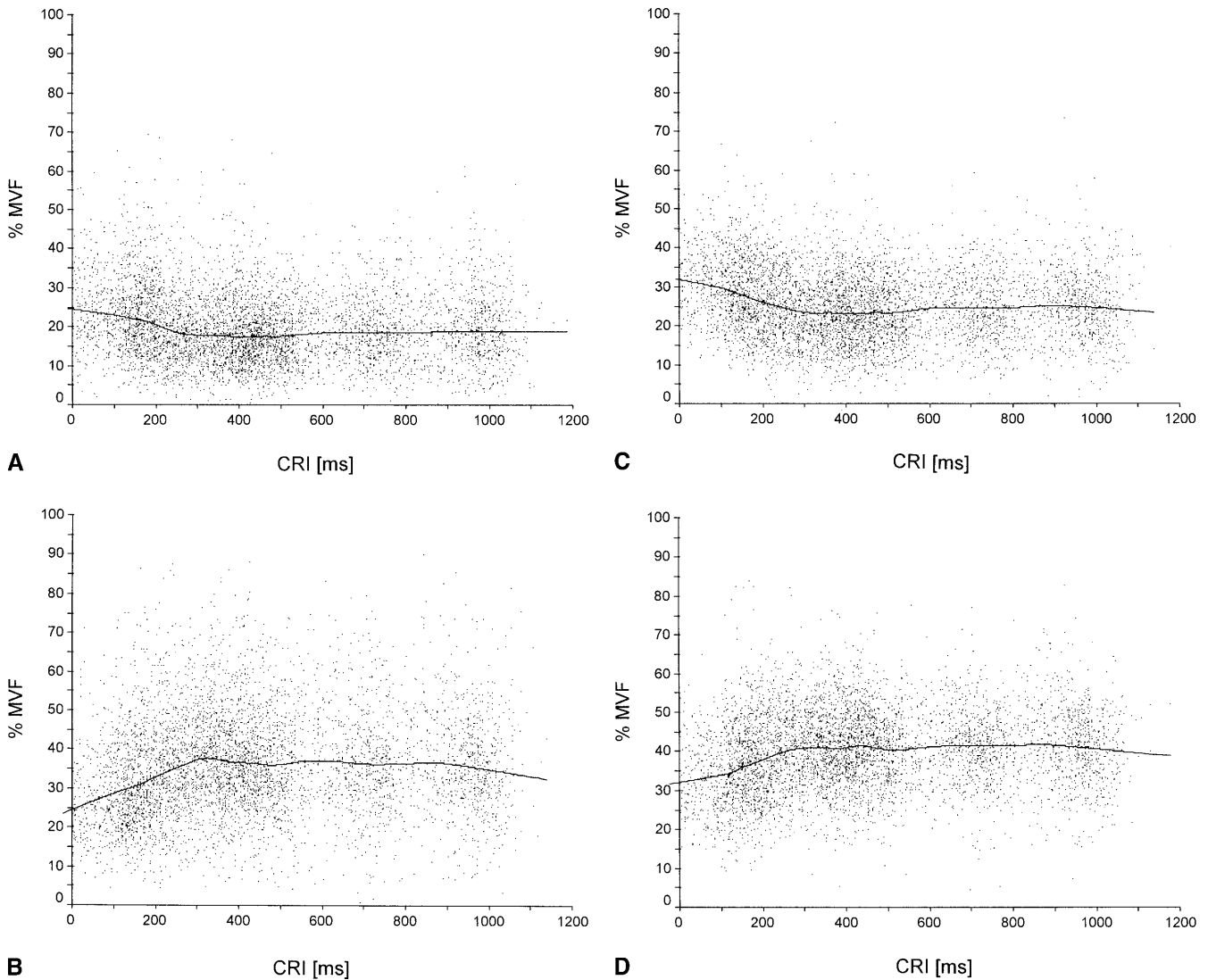


Fig. 3 Experiment 1: scatterplots of all experimental data. Peak forces were plotted against the CRI, separately for each hand and target force. **A** weak forces with left hand, **B** strong forces with left hand, **C** weak and **D** strong forces with right hand. The solid lines are fitted by LOWESS

get forces depending on whether the cue indicated 20 or 40% MVF and depending on the available preparation time, that is, the CRI [$F(5,60)=38.79$, $P<0.001$]. This interaction reflects the gradual specification process of the peak forces and thus confirms the findings of Hening et al. (1988; see also Ghez et al. 1990), who studied unimanual isometric flexions of the elbow.

To control for the possible artifact that the apparently gradual specification results from a mixture of different forces (default value and target force) that have been prepared – at short cueing intervals at chance level and then with increasing probability of the correct target force – peak forces of individual responses were plotted against the CRI (i.e. preparation time). Figure 3 shows these plots separately for each hand and target force. The solid lines were fitted with the LOWESS procedure

which computes a locally weighted regression (Chambers et al. 1983). No hints of a bimodal distribution of peak forces were visible.

As indicated by the interaction between Relevant Cue, Irrelevant Cue and CRI, the time course of the specification process depended not only on the relevant cue but also on the cue for the other hand [$F(5,60)=3.98$, $P<0.01$]. When the cue for the other hand was different from the relevant cue, the specification of strong forces had not proceeded as far as when the irrelevant cue was the same at the shortest CRIs (bin 0–125 ms), that is the actually produced forces were somewhat weaker ($P<0.05$). The opposite difference could be observed for weak target forces at short CRIs: when the irrelevant cue was different, the peak forces were somewhat stronger, but this difference was significant only at bin 250–375 ms ($P<0.01$). This kind of assimilation between the specification processes for the same and different peak forces at short preparation times was predicted by the hypothesis of transient coupling, but not its different timing for strong and weak force pulses. Finally, the interactions between Irrelevant Cue and CRI [$F(5,60)=4.41$,

Fig. 4 Experiment 1: correlations between the peak forces of the two hands as a function of CRI and cue for the other hand

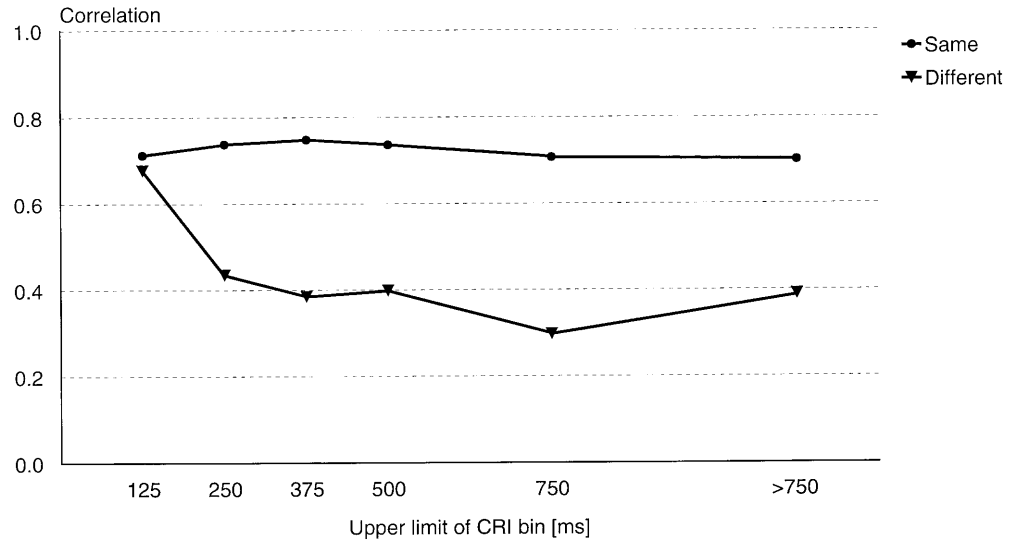
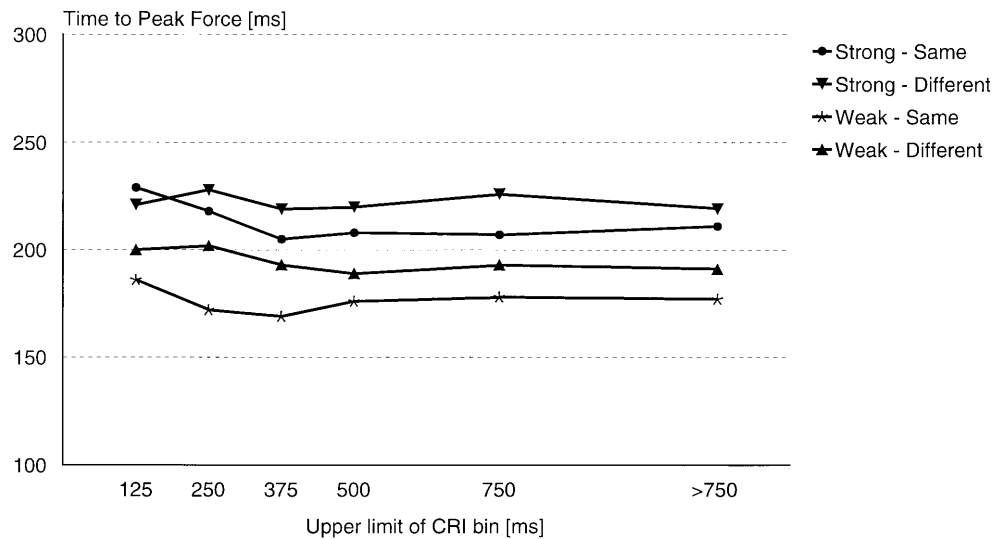


Fig. 5 Experiment 1: force rise times for each target force and cued force of the other hand, depending on CRI



$P < 0.01$] and Irrelevant Cue, CRI, and Hand [$F(5,60) = 2.45$, $P < 0.05$] reached significance.

Correlational analysis

Another major prediction of the transient-coupling hypothesis concerns the changes in the correlation between peak forces of the left and right hand while the peak-force specification proceeds: when different forces are required, these correlations should initially be high and decline as programming time increases. In contrast, when the same forces are required, the correlations should remain high and not vary when the CRI becomes longer. Therefore, correlations between the peak forces of left and right hand were computed for each condition and subject (Pearson r). The individual correlations were submitted to an ANOVA after Fisher- z transformation.

Figure 4 shows the mean correlations (based on mean z values) as a function of the relation between the cues

and the time available for preparation (CRI). At the shortest CRIs (bin 0–125 ms) the correlations in the same-cue and different-cue conditions were almost identical. This indicates a rather tight coupling between peak forces of both hands regardless of the irrelevant cue. Then, while the correlations between the peak forces remained high with increasing preparation time for the same target forces of the hands, they declined for different forces. Thus, when target forces were different, the hands became more and more independent from each other as programming time increased. Statistical analysis yielded significant main effects of Irrelevant Cue [$F(1,12) = 74.11$, $P < 0.001$] and CRI [$F(5,60) = 7.10$, $P < 0.001$]. The significant interaction between Irrelevant Cue and CRI [$F(5,60) = 8.00$, $P < 0.001$] reflects the decline of the correlations between different peak forces of the two hands with increasing CRI, while the correlations between the same peak forces stayed at a high level.

Time to peak force

Figure 5 shows the mean rise times of the force pulses. Rise times were longer when force was strong than when it was weak. They were also longer when the irrelevant cue was different than when it was the same as the relevant cue. Only when little time was available for preparation were rise times between the same-cue and different-cue conditions almost identical for both strong and weak target forces. With further processing of the cues, rise times declined more when the irrelevant cue was the same as the relevant cue than when it was different. The described effects were substantiated by statistical analysis which yielded significant main effects for Relevant Cue [$F(1,12)=51.86$, $P<0.001$] and Irrelevant Cue [$F(1,12)=16.25$, $P<0.01$] as well as significant interactions of Irrelevant Cue and CRI [$F(5,60)=4.31$, $P<0.01$] and of Relevant Cue, Irrelevant Cue, and CRI [$F(5,60)=4.86$, $P<0.01$].

Discussion

Overall, the results of the first experiment conform to expectations based on the hypothesis of transient coupling during peak-force specification. Mean peak forces exhibited an assimilation at short CRIs when the target forces were different, and this assimilation disappeared when the time available for peak-force specification increased. As already mentioned, this kind of assimilation (strong at early stages of the specification, absent at its end) provides strong evidence for coupling at the programming level, since coupling at the execution level should show up with the opposite pattern. This result is well in line with the evidence for transient coupling at the programming level as revealed by reaction times for bimanual movements (Spijkers et al. 1997) and imagined movements (Heuer et al. 1998a). In the latter study subjects had to perform sequences of bimanual reversal movements. During the middle phase of a trial subjects had to withhold the physical movement of one hand while they continued moving the other hand. Subjects were told to “perform” imaginary movements with the hand that stopped moving during this phase. Although the hand did not move physically, yet cross-talk effects showed up in the moving hand. Because there was actually no movement of the other hand, the effects could not be attributed to cross-talk at the execution level. Hence, the coupling effects must occur at the programming level.

Correlations between the peak forces of both hands were high at the start of the parametrization process, no matter whether the cues for the two hands were the same or different. However, as the CRI increased the correlations declined when the target forces were different, indicating decoupling, whereas they remained high when the target forces did not differ, because then decoupling is not necessary.

Although, in spite of the very noisy peak forces of individual responses, the findings basically conform to

expectations, there are some slightly disturbing aspects. In particular, for weak pulses the effect of the Irrelevant Cue was not statistically significant for the shortest CRIs, but only for later bins. From Fig. 2 it is apparent that the peak forces already depended on the relevant cue at the shortest CRIs. This indicates that subjects had to some degree prepared the correct peak force in advance. The only way to specify the correct peak force at zero cueing intervals is to delay execution. In fact, in this experiment responses were frequently delayed at the shorter cueing intervals, and very short CRIs were rare.

One difficulty, as revealed by introspection, consisted of preparing the default response (medium force) in advance of the presentation of the cues. Without this, responses cannot be produced at very short CRIs. Therefore we decided to make preparation of the default response easier by providing at the beginning of each trial an initial cue of medium length that reminded the subject to prepare medium forces. In this way we hoped to obtain shorter CRIs in a follow-up experiment and stable individual data for early CRI bins (cf. Experiment 2, below).

Contrary to our initial expectations the times to peak force turned out to depend on peak force. A possible explanation for this result comes from Gottlieb et al. (1989), who claimed that subjects use two different strategies to control movements, depending on the type of task. They distinguished between a speed-sensitive strategy, used when the task imposes temporal constraints, and a speed-insensitive-strategy, used when subjects do not have to control the temporal properties of the movement. The difference is the way the neural signals generating the forces that move the limb are modulated. In the speed-sensitive strategy the amplitude of the pulse is varied, whereas in the speed-insensitive strategy the width of the neural signal, assumed to be a rectangular pulse, is changed. Because the motor neuron pool is supposed to act like a low-pass filter, integrating the signals over time, changing the pulse's height results in responses of different amplitude but equal duration, while changing its width affects amplitude as well as duration. Newell and Carlton (1985) controlled time-to-peak force by providing a template pulse of fixed rise time after each trial, together with the actually produced force pulse, thus urging the subjects to use a speed-sensitive strategy. In agreement with Gottlieb et al. (1989) they found no influences of peak force on force rise time when peak force was between 20 and 70% MVF. Since we did not constrain the force rise time much (we only set an upper limit) the subjects may have chosen the speed-insensitive strategy that then caused the differences in force rise time.

Materials and methods: Experiment 2

As outlined for Experiment 1, subjects failed to produce responses with only small deviations from the synchronization signal at zero cueing intervals. To obtain more responses with very short CRIs

we added a signal that reminded the subjects to prepare the default response. Two bars of medium height were presented at the beginning of each trial, which changed to the appropriate length (short or long) when the cueing interval started. In addition we modified the training procedure as described below, and gave feedback on the force trajectory after each trial, similar to the procedure of Hening et al. (1988) who provided online feedback when they studied unimanual isometric contractions by means of the TRP. These measures were intended to reduce the noise of peak forces in individual trials.

Subjects

Eight subjects participated. All were right-handed (Edinburgh Handedness Inventory, Oldfield 1971), had normal or corrected-to-normal vision and had not participated in Experiment 1. They were again paid for their service.

Design and procedure

Task and apparatus were the same as in Experiment 1. The first step again consisted of determining the maximal voluntary forces of the subjects. Thereafter each subject performed four pairs of two blocks of training. The training procedure was modified in that subjects first learned to produce a force combination without needing to synchronize their response with a tone. The first of each pair of blocks of trials consisted of such self-timed trials; in the second block of each pair the synchronization task was added (synchronization trials).

A synchronization trial started when the thumbs were placed in position. After a blank screen for 1000 ms two bars of medium height were displayed. After an additional 1000 ms the series of four tones began. At the time specified by the cueing interval the cue appeared: the bars of medium height changed their size according to the actual combination of target forces. The six cueing intervals varied randomly (0, 125, 250, 375, 500, 750 ms). Sampling continued for 2000 ms after the fourth tone. Subjects were then given feedback about the force trajectories of each hand and their quality of synchronization after each trial (2000 ms duration). During the self-timed trials cues were presented at the same point in time as in a synchronization trial, but the series of four tones was omitted. Instead a single tone was presented together with the cue (2000 Hz, 20 ms). Subjects were instructed to produce the target forces as accurately as possible when preparation was complete. After each response they received feedback about the force trajectories.

In the first two blocks (48 trials each) subjects had to produce only medium forces with both thumbs. The forces required in the second pair of blocks (48 trials each) were both strong or both weak, and in the third pair (48 trials each) there were different target forces for each thumb. In the last two practice blocks (96 trials) all four combinations of target forces were presented. Experimental blocks were identical to the last practice block (four cue combinations \times six cueing intervals \times four replications), but were preceded by eight warming-up trials.

Subjects took part in two sessions on successive days. In the first session they completed the training procedure and four experimental blocks. At the beginning of session 2 the fourth pair of training blocks was repeated, followed by eight experimental blocks. Each session lasted about two hours.

Data analysis

The data were analyzed in the same way as in Experiment 1. There were more trials with very short CRIs, so the bins could be finer grained (0–50 ms; 50–100; 100–150; 150–200; 200–300; 300–400; 400–600; and 600–). Applying the selection criteria as in Experiment 1 yielded 8368 valid trials out of 9216 (9.2% invalid trials).

Results

Peak force

In general, the pattern of the mean peak forces (Fig. 6) was similar to that of the first experiment, but there were some important differences. As in the first experiment, the peak forces developed towards the instructed target values as programming time (CRI) increased. Inspection of the peak forces of individual pulses again revealed no indication of bimodality at any CRI (Fig. 7). In contrast to the first experiment, peak forces in the four cueing conditions did not differ at the shortest CRIs (first bin). Thus, the presentation of the medium cues had served its purpose: Subjects produced responses at very short CRIs and their peak forces were close to the instructed default value of 30% MVF. A further obvious difference from the results of Experiment 1 concerns the peak forces in the two strong-force conditions. While the forces of the strong–different condition reached the target value of 40% MVF, this was not the case in the strong–same condition: significant differences between the two conditions appeared at long CRIs, beginning at bin 200–300 ms. The weak-force conditions produced a different pattern in that the conditions weak–different and weak–same differed significantly at short CRIs only (at bins 50–100 and 100–150 ms; analysis of simple effects), with the forces of the weak–different condition being stronger. Hence, the pattern of the weak forces' conformed to predictions but that of the strong forces did not. We will return to this issue in the Discussion and provide a quantitative analysis in the Appendix.

The mean peak forces of each subject and condition were subjected to a four-way ANOVA (Relevant Cue \times Irrelevant Cue \times CRI \times Hand = $2 \times 2 \times 8 \times 2$ conditions with repeated measures on each factor). The main effect of Relevant Cue reached significance [$F(1,7)=110.5$, $P<0.001$], indicating that the subjects performed conforming to the cues. Subjects pressed harder when the Irrelevant Cue was different [$F(1,7)=12.12$; $P<0.05$], and this difference was more pronounced at later bins of the CRI [$F(7,49)=2.31$, $P<0.05$]. The peak forces approached their target values with increasing CRI [Relevant Cue \times CRI: $F(7,49)=47.65$, $P<0.001$], but their time course differed depending on whether the cues were the same or different [Relevant Cue \times Irrelevant Cue \times CRI: $F(7,49)=3.58$, $P<0.01$].

In addition, there were a number of differences between the two hands which gave rise to a number of significant interactions in the statistical analysis (CRI \times Hand: $F(7,49)=3.78$, $P<0.01$; Relevant Cue \times Hand: $F(1,7)=7.13$, $P<0.05$; Relevant Cue \times CRI \times Hand: $F(7,49)=2.93$, $P<0.05$; Irrelevant Cue \times CRI \times Hand: $F(7,49)=3.37$, $P<0.01$). However, the basic pattern of Fig. 6 was present in both hands.

Fig. 6 Experiment 2: mean peak forces as a function of preparation time, expressed as a percentage of maximal voluntary force, for each target force (strong, weak) and cued force of the other hand (same, different). Target force in the strong and weak conditions were 40 and 20% of MVF respectively

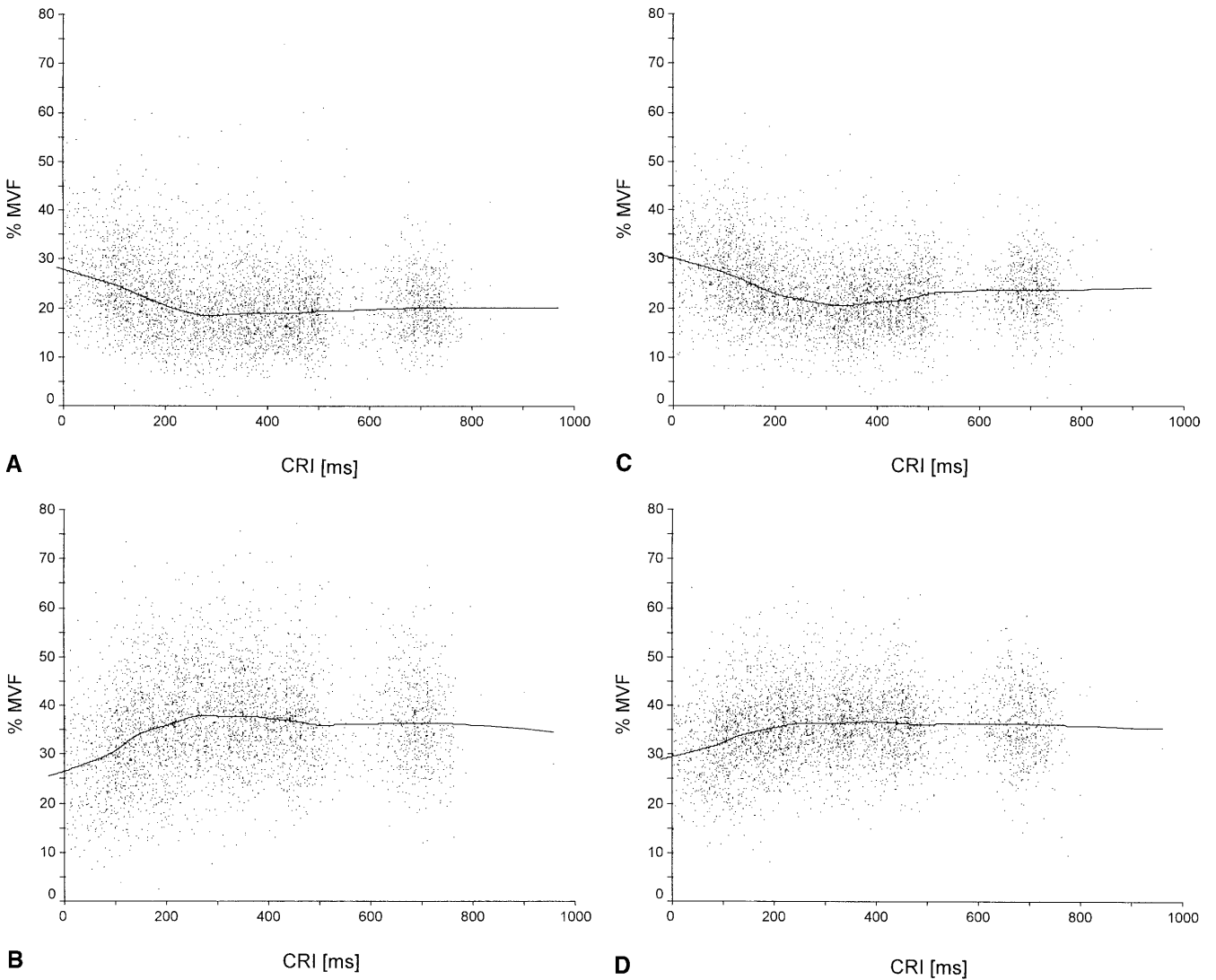
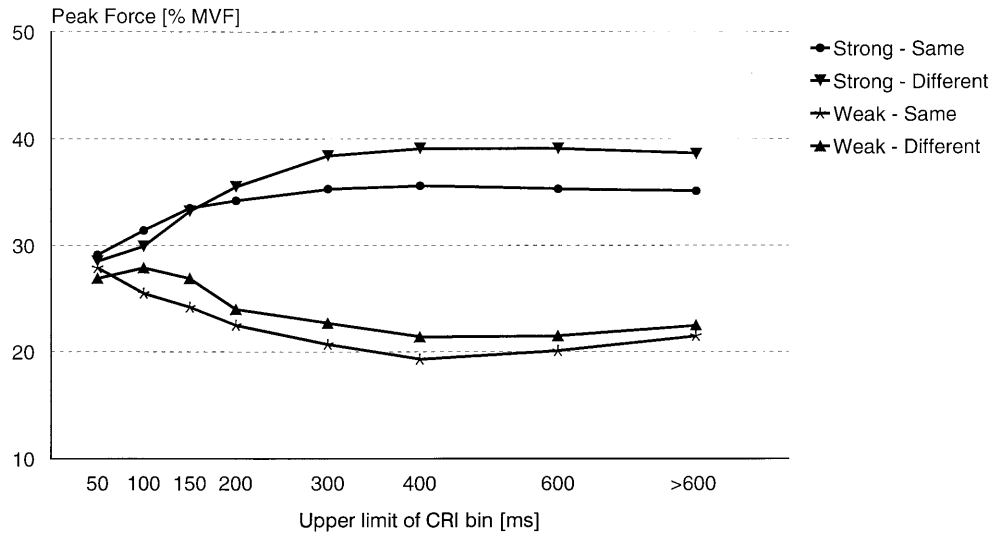


Fig. 7 Experiment 2: scatterplots of all experimental data. Peak forces were plotted against preparation time, separately for each hand and target force. **A** weak forces with left hand, **B** strong forces

with left hand, **C** weak, and **D** strong forces with right hand. The solid lines are fitted by LOWESS

Fig. 8 Experiment 2: correlations between the peak forces of the two hands, depending on the preparation time and cue for the other hand

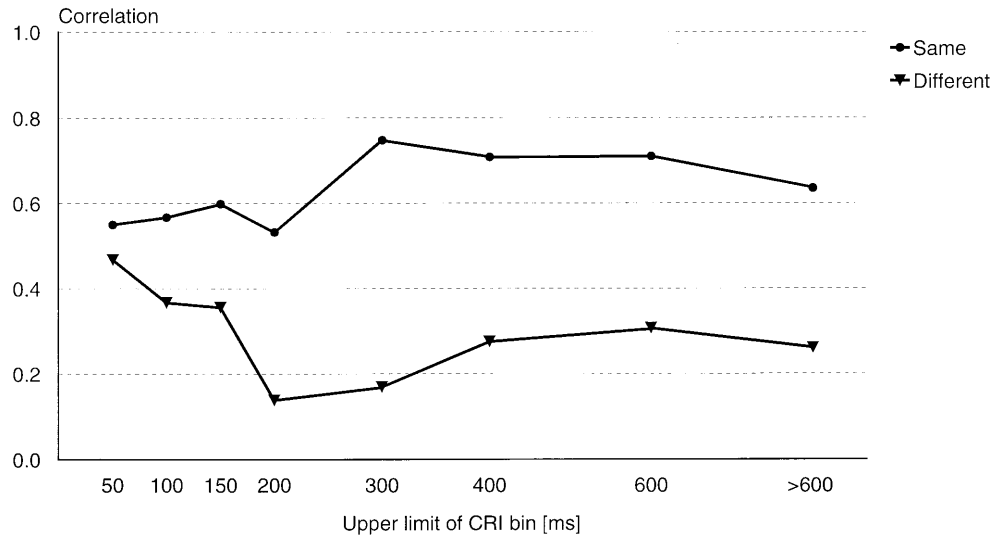
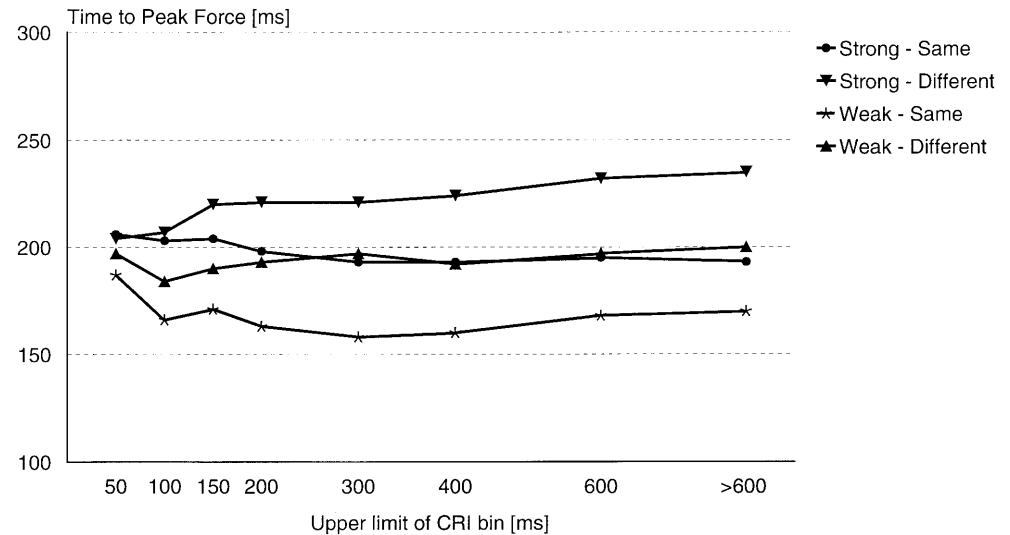


Fig. 9 Experiment 2: force rise times for each target force and cued force of the other hand, depending on the time available for response preparation



Correlational analysis

Two subjects had to be excluded from the correlational analysis because there were not more than two valid trials in some CRI bins. The mean correlations between peak forces of the two hands are shown in Fig. 8. As predicted, correlations between the peak forces were high initially and not affected by the irrelevant cue. As the specification process proceeded, the correlations in different-force conditions declined, whereas for same-force conditions they remained high. The ANOVA of the Fisher- z -transformed correlations yielded a significant main effect of Irrelevant Cue [$F(1,5)=53.62$, $P<0.001$] and a significant interaction between Irrelevant Cue and CRI [$F(7,35)=3.52$, $P<0.01$]. (The unstable data for early CRI bins are probably due to the small number of trials in these bins.)

Time to peak force

Like peak forces and correlations the pattern of the force rise times (Fig. 9) largely corresponded to the results of Experiment 1, but the differences between same-force and different-force conditions were larger. Rise times were longer when the target force amounted to 40% MVF than when it was 20% MVF [$F(1,7)=19.41$, $P<0.01$], and when the irrelevant cue was different rather than the same [$F(1,7)=7.18$; $P<0.05$]. Both differences became more pronounced with increasing CRI [Relevant Cue \times CRI: $F(7,49)=3.34$, $P<0.01$, and Irrelevant Cue \times CRI: $F(7,49)=12.63$, $P<0.001$]. Rise times with all four cue conditions were close to each other in the first CRI bin. The changes in the force rise times with increasing CRI depended on the combination of relevant and irrelevant cue, as indicated by a significant three-way interaction [$F(7,49)=2.48$, $P<0.05$], especially across the first four CRI bins. The difference between the strong-same and strong-different conditions developed earlier (bin

100–150 ms; $P < 0.05$, simple effects analysis) than the difference between the weak–same and weak–different conditions (bin 150–200 ms; $P < 0.05$).

Discussion

The changes introduced in the second experiment to explore cross-talk effects in the early phases of peak-force specification were successful. Regardless of the target forces, force specification started close to the instructed default value of 30% MVF at the shortest CRI bin (0–50 ms). With increasing preparation time the peak forces approached their respective target levels, i.e. 20% and 40% MVF. This is again in close agreement with the results in earlier studies which showed a gradually proceeding specification process for isometric forces (e.g. Hening et al. 1988; Ghez et al. 1990), extent (Heuer et al. 1998b) or direction (Favilla and de Cecco 1996), and with the results of Experiment 1. However, there is a remarkable difference between the results of the two experiments.

One prediction concerned the cross-manual effect on the peak force at short CRIs when a different peak force is specified for the other hand. In Experiment 1 the cross-manual effect was significant only when the target force was strong, while for weak target forces significance was approached. In the second experiment we observed exactly the opposite pattern. The specification process for weak target forces was significantly affected by cross-talk at CRI bins 50–100 ms and 100–150 ms, but for strong target forces significant differences showed up only at CRI bin 200–300 ms and later on, where peak forces in the strong–different condition reached a higher level than in the strong–same condition.

The latter result of higher forces in the strong–different than in the strong–same condition cannot be attributed to a static coupling component such as the longer amplitude of short movements while performing a long movement with the other hand (Heuer et al. 1998b). The result of a static coupling component would be assimilation in the strong–different condition to the weak target forces of the other hand, but the data show exactly the opposite pattern. This result is essentially impossible to explain in terms of cross-talk effects during motor programming or force production. However, there is the possibility that the difference between the strong forces in the same-force and different-force conditions reflects different target values set by the subjects internally. [Note that when speaking of target force we have to distinguish between the instructed target value and the value actually set by the subject. For the purpose of clarity we shall call the latter the internal target value (force) if the correct meaning does not emerge from the context.]

In the Appendix we describe a formalization of the transient-coupling hypothesis. In this model the time course of the parametrization process is described by the step response of a low-pass filter. One property of such a response is that the amplitude of the step input is ap-

proached in the same time, regardless of its value; when the input amplitude is scaled by a certain factor, the output is scaled by the same factor. Hence, a consequence of different internal target values would be a specification process that proceeds faster from the very start when the target value is higher. This, however, is not what we observed (cf. Fig. 6): while the peak forces in the strong–different conditions were larger than in the strong–same condition at longer CRIs, at the shortest intervals this difference was reversed, although it failed to be significant. This is suggestive of a transient cross-talk effect at short CRIs which is masked by the higher internal target value in the strong–different condition.

Although the assumption of higher internal target forces in the strong–different than in the strong–same condition, together with the assumption of transient cross-talk effects, nicely accounts for our data, there is no obvious reason why target forces should differ when in Experiment 1 there was no such difference. One major change in the second experiment was the introduction of two bars of medium height at the start of each trial, which later changed their height to signal the target forces. Phenomenally, the bars seemed to “jump” to their new lengths. If the perceived amplitude of the “jump” of one bar is now affected by whether the other bar jumps to the same height or a different one (i.e. in the opposite direction), and if this is so especially for long bars, one could explain the different internal target values as resulting from a perceptual effect. We have examined this hypothesis in a psychophysical experiment in which subjects compared the lengths of bars as used in Experiment 2, where the bars changed from medium to long or short, when the second bar changed in the same direction or in the opposite direction. The points of subjective equality in the one display did not deviate significantly from the reference height in the other display. Thus we found no support for a possible perceptual effect which could give rise to the different internal target values for specifying strong forces in conditions with same and different target forces for the other hand.

An alternative explanation for the different internal target forces refers to a strategic effect. One way to overcome the difficulties associated with the production of different forces at short preparation intervals would be to exaggerate the difference between the internal target values, so that the two specification processes diverge more rapidly. This strategy would ideally result in lower weak forces and higher strong forces in the different-force conditions than in the same-force conditions. However, this is not what we found. When the actual forces at long CRIs are taken as estimates of internal target forces, there was enhancement in the strong–different condition compared with the strong–same condition, but also a weak (and non-significant) enhancement in the weak–different condition as compared with the weak–same condition, rather than a reduction (cf. Fig. 6). We observed a similar pattern of forces in two other experiments that used the pre-cueing method to test the transient-coupling hypothesis.

Jaskowski and Verleger (1993) showed that in a reaction-time task the response force increased when the imperative stimulus occurred earlier than expected. Their interpretation is that subjects tried to compensate for the lack of preparation by increasing the force. A similar kind of argument can be applied to our experimental situation: the slower progress of preparation with different cues for the two hands could be associated with overall higher response forces. When such an effect of heightened response forces is added to the strategic contrast effect on internal target forces in different-force conditions, it serves to enhance the increase of strong forces in the strong-different condition and to reduce or even reverse the reduction of weak forces in the weak-different condition. This is the pattern which we observed. The fact that this pattern did not occur in the first experiment might be related to the fewer responses with very short CRIs, which indicate an avoidance of responding in an unprepared state.

On the other hand, Newell and Carlton (1985) found that the maximal voluntary force depends on force rise time: When force rise time is longer, the maximal voluntary force increases. Hence, when force rise time is shorter, as in the strong-same condition when compared with the strong-different condition (cf. Fig. 9), the maximal force that can be produced is smaller, thus leading to the smaller peak force. This interpretation has to be regarded with caution since there were similar systematic differences in the force rise times in the first experiment, but the peak forces in the strong-same condition reached the required 40% MVF.

Turning to the correlations between the peak forces of the two hands, the findings confirm the results of the first experiment and hence strongly support the hypothesis of transient coupling during the specification process. Peak forces remain strongly coupled when target forces are equal for both hands as indicated by the consistently high correlations. When target forces are different from each other the specification processes have to be decoupled. Hence, the correlations decline with increasing preparation time.

General discussion

In the present study we used the timed-response paradigm to investigate the time course of preparation of bimanually performed isometric contractions. Our specific goal was to examine whether the hypothesis of transient coupling during the parametrization process holds for the specification of isometric forces. We conducted two experiments, the data from which agree well with the predictions. These concern primarily the time course of (1) the mean peak forces and (2) the correlations between the peak forces of the two hands when the available time for parameter specification is increased. As mentioned above, the correlation data from both experiments strongly support the transient-coupling hypothesis, and the same results have been found

for amplitudes of bimanual reversal movements (Heuer et al. 1998b).

The observations on mean peak forces are also in general agreement with the transient-coupling hypothesis. Basically, mean peak forces indicate a stronger cross-manual effect after a short specification time, which disappears as specification time increases. Thus, the strongest cross-manual effects occur after durations of the concurrent specification processes at which the final states are not yet reached, so the differences between the peak forces of the two hands are still smaller than at longer CRIs: cross-talk effects do not simply increase as the difference between peak forces increases. This is inconsistent with any account in terms of cross-talk between outflow signals only. Furthermore, with bimanual movements rather than isometric forces, interference also showed up in a study that used a reaction-time approach to investigate coupling effects during the programming phase, so that movements had not yet started when the measurements were made (Spijkers et al. 1997). Cross-talk was also present when, during repeated bimanual movements of different amplitudes, one hand's movements were imagined and not executed (Heuer et al., 1998a). Taken together, these results strongly point at the existence of interference due to coupling at the programming level. This kind of coupling probably also caused the pattern of results which we observed in the present study.

Consistent with our expectation there was no asymmetric cross-manual effect of a strong force on a concurrently produced weak force, whereas such an effect is a typical finding when bimanual movements of different amplitudes have to be performed (e.g. Marteniuk et al. 1984; Heuer et al. 1998b), although this is not invariably observed (cf. Spijkers et al. 1997). As mentioned in the Introduction, the tight temporal coupling between bimanual movements is supposed to account for this effect. Although, contrary to our expectation, the force rise times differed considerably depending on the peak force, they did not show any assimilation (i.e. a prolongation of the force rise time of a weak pulse towards the rise time of a strong pulse when both are performed concurrently). Thus, there could be weaker temporal coupling of bimanually produced isometric forces than of bimanual movements which might account for the "missing" assimilation of the forces.

Alternatively, the characteristic asymmetric assimilation of short and long movements could be accounted for in terms of cross-talk at the execution level (cf. Marteniuk et al. 1984; Spijkers and Heuer 1995; Heuer et al. 1998b), caused by ipsilateral descending pathways. Compared to proximal muscles, the distal muscles involved in the isometric contractions in the present experiments receive less input via the ipsilateral pathways, so cross-talk at the execution level may be reduced.

Finally the absence of assimilation effects could have resulted from a too small difference between the target forces: Sherwood (1994b) showed that spatial assimila-

tion effects are not present in bimanual movements when the difference between the target values is too small.

In summary, we conclude that the experiments reported here provide additional evidence for the transient-coupling hypothesis. Further converging evidence comes from several other studies that used different paradigms to investigate the parametrization of movements (Spijkers and Heuer 1995; Heuer et al. 1999, 1998a; Spijkers et al. 1997, 1999). One major reason for investigating isometric forces was the often-found amplitude scaling, for which the time to peak force is (more or less) constant, regardless of the peak force itself. Although our results did not bear out this assumption (time to peak force was longer for strong target forces), the results nevertheless were as expected: no static coupling occurred in the weak–different condition. Hence, the mere presence of differences in duration is not a sufficient condition for asymmetric coupling and the reason for the commonly observed static coupling in the shorter movement of bimanual movements of different size still remains unclear.

Appendix

The purpose of this Appendix is to give a formal description of the model of transient coupling during the specification of peak forces. The model used here is taken from Heuer et al. (1998b) with some minor modifications. First, the two low-pass filters which represented the time course of stimulus identification and motor programming are collapsed into a single second-order low-pass filter. The advantage of this simplification is that only one time constant has to be determined when the model is fitted to experimental data. Second, the target forces for the specification processes were set to the mean values observed for the longest CRIs (last bin). Thus the target force was set for each condition separately; this procedure takes into account the possible strategic effects that appeared in the different conditions of Experiment 2, in particular the stronger peak forces in the strong–different than in the strong–same condition. Third, we omitted the static-coupling component from the model's equations because we found no evidence for a static coupling and because our focus is on the transient-coupling component. The start value for the parameter-specification process was set to the mean value of the first bin of the CRIs of all four conditions. Hence, the parameters to be estimated by the fitting procedure were the delay and the time constant of the low-pass filter, separately for each of the two same-force conditions, and the dynamic coupling gain that results from fitting the model to the different-force conditions. We will first describe the model equations and then provide the results of fitting them to the data for each of the two experiments separately.

The peak forces as a function of the cue and response (C-R) interval t in the same-force conditions were fitted by the following equations:

$$P_{Ss}(t) = P + A_S h_S(t) \quad (\text{A1})$$

with

$$h_S(t) = 1 - \exp\left[-\frac{t - T_S}{\tau_S} \left(1 + \frac{t - T_S}{\tau_S}\right)\right] \quad (\text{A2})$$

and

$$P_{Ww}(t) = P + A_W h_W(t) \quad (\text{A3})$$

with

$$h_W(t) = 1 - \exp\left[-\frac{t - T_W}{\tau_W} \left(1 + \frac{t - T_W}{\tau_W}\right)\right] \quad (\text{A4})$$

The indices w and s indicate the weak and strong conditions, respectively. P is the start value of the specification process and A the difference from the target value that scales the step response of the second-order low-pass filter $h(t)$.

The following equations were fitted to the peak forces of the different-force conditions:

$$P_{Sw}(t) = P + A_{Sw} h_S(t) - c_{Sw}(t) [A_{Sw} h_S(t) - A_{Ws} h_W(t)] \quad (\text{A5})$$

with

$$c_{Sw}(t) = k_{Sw} [A_{Sw} h'_S(t) - A_{Ws} h'_W(t)]^2 \quad (\text{A6})$$

and

$$P_{Ws}(t) = P + A_{Ws} h_W(t) - c_{Ws}(t) [A_{Ws} h_W(t) - A_{Sw} h_S(t)] \quad (\text{A7})$$

with

$$c_{Ws}(t) = k_{Ws} [A_{Sw} h'_S(t) - A_{Ws} h'_W(t)]^2 \quad (\text{A8})$$

As already mentioned, the start values were the same for all conditions and the properties of the low-pass filters in the different-force conditions were assumed to be the same as in the corresponding (strong or weak) same-force condition. Their output was scaled with the amplitude factor A , which could differ between same-force and different-force conditions. The cross-talk adds to an undisturbed parametrization process. Its amount is proportional to the difference between the current outputs of the parametrization processes of both hands, as if they were proceeding independently, and the time-dependent cross-talk gain $c(t)$. The latter is linked to the change in the parametrization processes and amplified by a constant factor k .

The left part of Fig. A1 shows the functions that resulted from fitting the model equations to the data from the first experiment by means of a least-squares procedure. The right part depicts the time course of the dynamic coupling term $c(t)$. The set parameters were $P=29.8\%$ MVF, $A_W=-7.2\%$ MVF, $A_S=9.3\%$ MVF, $A_{Ws}=-7.6\%$ MVF, and $A_{Sw}=9.8\%$ MVF. The estimated values for the weak–same (strong–same) conditions were $\tau=47$ ms (59 ms) and $T=0$ ms (0 ms), and the RMS error was 1.4 (0.7)% MVF. For the weak–different (strong–different) conditions we obtained dynamic coupling gains of 0.33 (0.42) with the RMS error amounting to 1.0 (1.1)% MVF.

The results of fitting the model to the data from the second experiment are shown in Fig. A2. The set parameters were $P=28.1\%$ MVF, $A_W=-6.6\%$ MVF, $A_S=7.0\%$ MVF, $A_{Ws}=-5.6\%$ MVF and $A_{Sw}=10.5\%$ MVF.

Fig. A1 Model fitted to the data of Experiment 1. Left graph: mean peak forces as a function of CRI. The symbols indicate the observed means, the lines the predicted values of the regression. Right graph: cross-talk gain during the specification of different forces as derived from predicting the different conditions from the same conditions

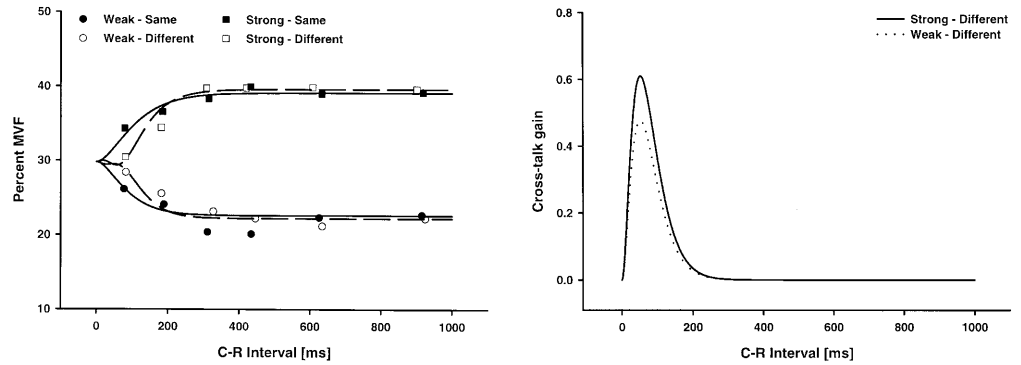
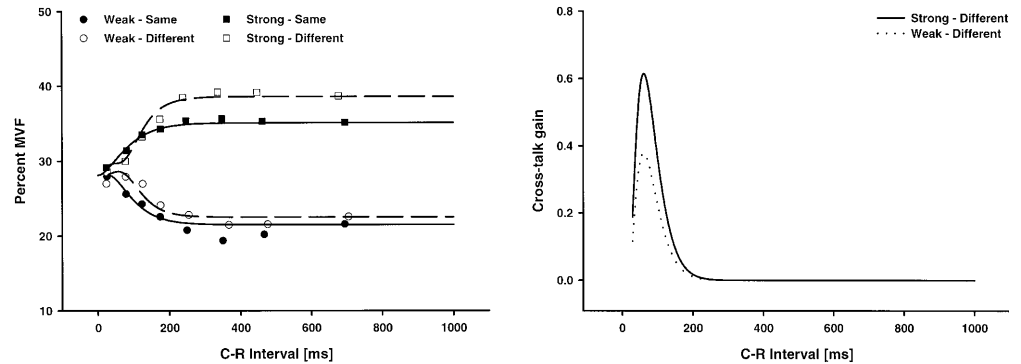


Fig. A2 Model fitted to the data of Experiment 2. Left graph: mean peak forces as a function of CRI. The symbols indicate the observed means, the lines the predicted values of the regression. Right graph: cross-talk gain during the specification of different forces as derived from predicting the different conditions from the same conditions



The parameter estimates were for the weak–same (strong–same) condition: $\tau=41$ ms (46 ms) and $T=31$ ms (0 ms), and the RMS error was 1.0 (0.3)% MVF. In the weak–different (strong–different) condition the fitting procedure yielded a dynamic coupling gain of 0.23 (0.37), and the RMS error was 0.8 (0.6)% MVF.

The coupling functions of the two experiments (right-hand graphs in Figs. A1 and A2) are very similar. This indicates that a similar coupling mechanism is present in both experiments, in spite of considerable differences in data and procedure. Most remarkably, in both experiments there was an asymmetry: at short CRIs the transient influence of the weak isometric contraction on the strong one was stronger than the transient influence of the strong isometric contraction on the weak one. The same kind of asymmetry also appeared when we studied long and short reversal movements (Heuer et al. 1998b).

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