Bilateral Interactions During Contractions of Intrinsic Hand Muscles

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Zijdewind, Inge and Daniel Kernell. Bilateral interactions during contractions of intrinsic hand muscles. J Neurophysiol 85: 1907–1913, 2001. During demanding voluntary contractions (e.g., high force or fatigue), activation is not restricted to the target muscle but extends to other ipsilateral muscles; even contralateral muscles become activated. The contralateral “irradiation” of activity was measured in five subjects during submaximal and maximal voluntary contractions (MVCs) of the first dorsal interosseous (FDI) (index finger abduction) and during unfatigued and fatigued conditions. All subjects were tested five times with at least one week between tests. Unilateral MVCs were associated with a substantial amount of contralateral FDI activation [mean = 7.9 ± 6.7% (SD) MVC prior to fatigue]. The amount of such contralateral irradiation was significantly different between different individuals and was positively correlated between dominant and nondominant hands. During fatigue tests, the contractile activity of the contralateral “nontarget” index finger showed progressive increase (force, electromyogram) as was measured during both the submaximal task and interspersed MVCs of the target finger. In addition, a superimposed saw-tooth pattern of intermittently waxing and waning contractions commonly appeared contralaterally. The expression of contralateral irradiation force was itself fatigue-sensitive: less irradiation was seen in a recently fatigued muscle than was seen before the fatigue test. These fatigue effects could not be explained as having been caused by changes in muscle properties. Possible anatomical sites of contralateral irradiation are briefly discussed.

INTRODUCTION

In motor behavior, nonintended interactions between commands to different muscles and different limbs are of common occurrence. This is particularly noticeable under conditions of high levels of effort, for instance, when working at high absolute force levels or when moderate force production is difficult because of fatigue. Under such conditions, the consequences of voluntary muscle activation are not restricted to the original set of “intended” target muscles; the activation patterns tend to “irradiate” to other ipsilateral and even to contralateral muscles (see, for example, Dimitrijevic et al. 1992; Gandevia et al. 1991; Gellhorn 1947; Kristeva et al. 1991; Mayston et al. 1994, 1999). The general existence of such irradiation phenomena has long been known (cf. ipsilateral irradiation of muscle activation in strong withdrawal reflexes; see, for example, Sherrington 1906) and these phenomena are of considerable theoretical and practical interest. The contralateral irradiation that is seen at high levels of motor activation may reveal basic inborn patterns of motor organization that are successfully suppressed under normal conditions of motor behavior. The ipsilateral deficits in motor control that are seen after stroke (Brodal 1973; Colebatch and Gandevia 1989; Jones et al. 1989) could be a consequence of this motor control organization. In a more applied perspective, the appearance of unintended contractions in states of motor fatigue would be expected to compromise the precision of (bimanual) motor coordination which, in work situations, might lead to errors and accidents.

The main purpose of the present study was to describe to what extent contralateral contractions are actually seen in hand muscles during unilateral voluntary activation. This was done during brief maximal contractions (MVCs) and long-lasting submaximal contractions that were maintained until exhaustion. Such a quantitative description is a necessary first step toward a better understanding of these intriguing irradiation phenomena.

Beside the observations concerning the behavior of contralateral irradiation, we also studied the possible relationships between this phenomenon and another example of bilateral interaction, the so-called “bilateral deficit.” Bilateral deficit refers to the fact that the amount of force produced by two simultaneously activated contralateral homologous muscles is often lower than the forces obtained when the two muscles are activated independently (see, for example, Herbert and Gandevia 1996; Howard and Enoka 1991; Vandervoort et al. 1984). The mechanisms underlying the bilateral deficit are not yet clear.

METHODS

Data were obtained from five healthy subjects (2 males and 3 females aged 20–25 yr). One female and one male were left-handed. All subjects gave informed consent to participate in the study and the local ethics commission for human experimentation approved the project.

The experiments were repeated five times with at least one week between experiments. To eliminate the influence of the time of day on force production (Gauthier et al. 1996; Martin et al. 1999), all experiments started at 10:00 a.m. Subjects were instructed to keep their normal daily routines (e.g., caffeine intake). Results dealing with the reproducibility of target contractions, fatigue tests, and voluntary activation levels (estimated using “interpolated twitches”) (Allen et al. 1995; Merton 1954) will be described elsewhere.

Mechanical recording

Each subject was seated at an experimental table and the subject’s elbow was slightly flexed (~135° angle). Both of the subject’s hands were clamped in a vertical position and were held immobile with pressure plates and Velcro tape. An index finger was slightly abducted and its abduction force was measured at the proximal interphalangeal joint. The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

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failed to maintain 30% MVC force for as long as 5 s. After a brief rest (4.5 s), an MVC (MVC-F1) was performed by the subject. This sequence was repeated until the subject could not maintain a 22-s maintained contraction at 30% MVC, a 4-s MVC, and 4 s of rest formed two submaximal endurance tests, first with their nondominant hand and then for the nondominant hand. Finally, a new series of unilateral (D, nD) and bilateral (L&R) MVCs (MVC-F2) were performed.

joint with a transducer (see Zijdewind and Kernell 1994). To prevent abduction of the whole hand, a horizontal plate secured the middle finger and the hand was further stabilized by a C-shaped plate around the wrist. Force signals of the left and right index fingers were amplified and saved on magnetic tape (PCM-3000A, Vetter Digital, Rebensburg, PA).

Electromyographic recordings (EMG) were made of the first dorsal interosseous muscles (FDI) of both hands; one surface electrode was placed over the muscle belly and a reference electrode was placed at the metacarpophalangeal joint of the index finger. A band-shaped earth electrode was positioned around the left wrist.

General experimental procedures

The general procedures (repeated fatigue tests in both hands) (Fig. 1) resembled those of Zijdewind et al. (1998). After thorough immobilization of their hands, the subjects performed three series of brief contractions (index finger abductions, each ~4 s): six MVCs with the dominant hand, six MVCs with the nondominant hand, and six MVCs with both hands simultaneously. The first three MVCs of the series were performed without electrical stimulation of the target muscle; the last three were performed with electrical stimulation (supramaximal double pulse stimulation of the FDI or “twitch interpolation”). During the contractions, visual feedback of the force of the target muscle(s) was provided on an oscilloscope. The interval between consecutive MVCs was ~½ min and the largest MVC force during unilateral contractions was considered to be the “true” MVC value for the respective hand. The mean contralateral force for the six contractions was used as an indication of the amount of contralateral activity. During bilateral contractions, force was calculated as a percentage of the MVC for each hand (dominant and nondominant) separately.

After performing the MVCs, the subjects were asked to briefly match their force production (6–8 s) to different target forces (20, 40, 60, and 80% MVC). The target forces were indicated on an oscilloscope in front of the subject. This procedure was done first for the dominant hand and then for the nondominant hand.

Instructions to the subject

No instructions were given concerning co-contractions of the contralateral hand and subjects were not aware of our interest in the nontarget hand.

Endurance test

After the MVC and force-level measurements, all subjects performed two submaximal endurance tests, first with their nondominant hands and then with their dominant hands. Each endurance test started with an MVC and continued as a series of 30-s cycles consisting of a 22-s maintained contraction at 30% MVC, a 4-s MVC, and 4 s of rest (Figs. 1 and 4). This sequence was repeated until the subject could not maintain the 30% force for more than 5 s. During the first 5 s of each segment of the 30% contraction, subjects were asked to rate their effort on a scale of 0–10. After the first test and a pause of ~4.5 s, the subjects performed a final MVC (MVC-F1) with their nondominant hands, after which the endurance test was repeated for the dominant hand (see Fig. 1). Following a brief pause of ~4.5 s after the end of the second fatigue test, the subjects were asked to perform 1–3 MVCs (MVC-F2) for each hand separately (dominant and nondominant) and for both hands together.

EMG and force measurements were analyzed offline with a personal computer equipped with a data acquisition interface (1401plus interface, Cambridge Electronic Design, Cambridge, UK; sampling frequency 2 kHz both for EMG and for force recordings). In relation to the MVC measurements, we measured the mean rectified EMG for 0.2 s before each relevant force peak.

Statistical analysis

Most variables showed normal distributions when tested with the Kolmogorov-Smirnov test; therefore, comparisons across conditions were analyzed with paired t-tests. Due to the relatively small number of observations (n = 5), comparisons between different experiments of individual subjects were made with the Wilcoxon signed ranking test. Comparisons were made between subjects with a one-way analysis of variance (ANOVA). The level of significance was set to 5%. Tukey post hoc analysis was performed following a significant ANOVA.

RESULTS

Contralateral irradiation during unilateral MVCs in the nonfatigued state

Examples of force and EMG recordings during unilateral maximal voluntary abductions of the right index finger are shown in Fig. 2. No instructions were given to the subject with respect to the contralateral nontarget hand. Every MVC of the target finger was accompanied by a small but evident contraction of the homologous finger in the other hand (Fig. 2).

As calculated across all of the tests (n = 25), the mean MVC force was 42.1 ± 6.8 N (SD) for the dominant hand and 41.2 ± 7.2 N for the nondominant hand (Table 1). During unilateral MVCs, a substantial amount of coactivation of the contralateral FDI (i.e., index finger abduction) was observed in more than half of the experiments (29 of 50 unilateral contractions showed a contralateral force of >5% MVC; mean values are in Table 1). The amount of contralateral nontarget force in the dominant and nondominant hands was significantly correlated (r = 0.44, P < 0.05). When analyzed for all of the subjects
Contralateral irradiation of activation was clearly a graded phenomenon that was related to the degree of target muscle activation. This is demonstrated by the results in Fig. 3A, in which the relative amount of contralateral index finger force is shown for different target-side levels of activation.

**Contralateral irradiation during submaximal endurance tests**

In the submaximal endurance tests, we studied the degree of contralateral irradiation under two conditions: 1) during maintenance of the submaximal force (target level of 30% MVC) and 2) during intermittently interspersed MVCs (Figs. 1 and 4).

During prolonged maintenance of submaximal target force, there was a continuously increasing degree of contralateral force production (Figs. 4 and 5A). In many cases, such contralateral contractions already were seen at the onset of the test (Figs. 4 and 5A). Contralateral activity intermittently assumed a peculiar saw-tooth behavior (Fig. 4), particularly in the latter half of many of the tests. That is, after a slow gradual rise, the force would suddenly reset to zero and start rising anew, often without any connection to the target-side force or to the timing of the interspersed MVCs (Fig. 4, arrows). Also, no movements in the forearms or upper body were visible in relation to the saw-tooth behavior. Therefore, although the mean level of contralateral force increased continuously (Fig. 5, A and B, bottom 3 sets of values) in the same general manner as the expected level of perceived effort, other factors were clearly of importance as well for the detailed timing of contralateral irradiation force (Fig. 4).

With regard to the interspersed MVCs, our initial expectation was that these brief contractions, all delivered at a presumably constant level of maximum voluntary effort, would produce relatively constant contralateral effects throughout the course of the endurance test. However, as for the interspersed MVCs as well, the contralateral irradiation force increased progressively during the test period (Fig. 5, A and B). On average, in the first experiment (nondominant hand), the nonfatigued state, contralateral irradiation of muscle activation was present during MVCs in all subjects and it was consistently more pronounced in some individuals than in others (Fig. 3A).

**Prefatigue MVC values and contralateral irradiation**

<table>
<thead>
<tr>
<th>Subject</th>
<th>n</th>
<th>MVC-D Unilat, N</th>
<th>MVC-nD Unilat, N</th>
<th>MVC-D Bilat, % MVC</th>
<th>MVC-nD Bilat, % MVC</th>
<th>Non-Target Activity in D, % MVC</th>
<th>Non-Target Activity in nD, % MVC</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>5</td>
<td>41.2 ± 8.2</td>
<td>42.5 ± 6.3</td>
<td>95.8 ± 6.0</td>
<td>95.4 ± 3.2*</td>
<td>0.8 ± 0.2</td>
<td>1.9 ± 0.8†</td>
</tr>
<tr>
<td>2</td>
<td>5</td>
<td>48.5 ± 5.0</td>
<td>48.6 ± 4.8</td>
<td>94.0 ± 9.1</td>
<td>94.5 ± 4.4*</td>
<td>7.8 ± 7.9</td>
<td>0.4 ± 0.2†</td>
</tr>
<tr>
<td>3</td>
<td>5</td>
<td>37.2 ± 2.2</td>
<td>35.8 ± 4.3</td>
<td>95.1 ± 7.3</td>
<td>96.1 ± 6.0</td>
<td>8.8 ± 3.4</td>
<td>8.8 ± 2.1</td>
</tr>
<tr>
<td>4</td>
<td>5</td>
<td>41.8 ± 7.1</td>
<td>44.1 ± 6.3</td>
<td>92.0 ± 4.1*</td>
<td>90.1 ± 4.4*</td>
<td>7.8 ± 2.1</td>
<td>16.1 ± 8.7</td>
</tr>
<tr>
<td>5</td>
<td>5</td>
<td>42.0 ± 6.8</td>
<td>35.2 ± 7.3*</td>
<td>94.4 ± 5.7*</td>
<td>101.7 ± 3.3</td>
<td>12.7 ± 3.3</td>
<td>13.6 ± 7.5</td>
</tr>
<tr>
<td>All</td>
<td>25</td>
<td>42.1 ± 6.8</td>
<td>41.2 ± 7.2</td>
<td>94.3 ± 6.2*</td>
<td>95.6 ± 5.5*</td>
<td>7.6 ± 5.5</td>
<td>8.2 ± 7.9</td>
</tr>
</tbody>
</table>

Values are mean ± SD. Statistical analysis was done using the Wilcoxon signed rank test. Averages were calculated for the maximum MVC of each pre-fatigue experiment; averages were calculated separately for each subject. MVC, maximum voluntary contraction force (index finger abduction); D, dominant hand; nD, non-dominant hand; Unilat, unilateral target contraction; Bilat, bilateral target contraction; non-target activity, forces measured in the hand contralateral (D or nD) to the target side; i.e., contralateral irradiation. * Significant difference between uni- and bilateral contractions (P < 0.05 or better). † Significant difference between dominant and non-dominant values (P < 0.05).
tralateral force that was co-incident with the target-side MVC increased from 9.1 ± 6.6 to 26.0 ± 12.1% MVC (t-test, P < 0.001). However, it should be noted that the timing could be markedly different between the target-side and contralateral contractions: in the latter half of the endurance test, the contralateral force often rose very gradually toward a peak that was coincident with that of the rapidly produced target-side MVC (Fig. 4).

The initial endurance test for the nondominant hand was followed by a final MVC (MVC-F1) of the same hand and was then succeeded by a similar test for the dominant hand (within 25 s after the end of the first endurance test). Because the now contralateral (nondominant) hand was weakened by its own preceding endurance test, one might expect the absolute level of the “irradiated” contralateral co-contractions (as expressed in relation to prefatigue MVC) to be lower during the second test than it was during the first test. This was clearly the case; however, Fig. 5B demonstrates that, when the irradiation forces of the second test were scaled in relation to MVC-F1, the contralateral irradiation forces were initially significantly smaller during the second test than they were during the first tests (* in Fig. 5B; t-tests, P < 0.001). This was also the case for the corresponding EMG signals (P < 0.05; cf. Fig. 5, A and B, vs. Fig. 5, C and D). Therefore, this postfatigue depression of irradiated muscle contraction (Fig. 5, B and D, hatched areas) could not be explained as being caused by changes in muscle properties. The depression was of limited duration; during the last third of the second test the relative rise of contralateral irradiation force and EMG was again as marked as it was during the first test (cf. Fig. 5, A–D).

Contralateral irradiation during unilateral MVCs in the fatigued state

After a pause of 4.5 s, the two endurance tests were followed by a series of unilateral MVCs of either hand (MVC-F2). During these contractions, the relative amount of contralateral irradiation force was 3.9 ± 4.4% (n = 50) of MVC-F2. The amount of irradiation force seen in the most recently fatigued hand (dominant side, 2.3 ± 2.3%) was significantly lower than that obtained prior to both fatigue tests (P < 0.001). Therefore, there was now a postfatigue “irradiation depression” in this hand that was similar to that seen earlier in the nondominant hand (cf. Fig. 5B, *). At this point in time, the nondominant hand had had more time to recover after its own fatigue test. However, on the same side, the amount of irradiation (5.5 ±
5.5%) was still significantly declined when compared with prefatigue values \((P < 0.05)\).

**Bilateral deficit and its lack of relationship with contralateral irradiation**

Our results confirmed that, in either target hand, the MVC force produced when each hand was contracted separately was larger than that obtained when both hands were contracted together (for statistics see Table 1), i.e., there were signs of a small but significant degree of “bilateral deficit.” Neither during the initial series of six unilateral contractions or during the series of bilateral contractions was there any significant correlation between MVC force and the number of preceding MVCs in the same hand. Therefore, it seems unlikely that the smaller forces of the bilateral contractions were simply caused by depressing effects of the preceding unilateral contractions. For all of the prefatigue MVCs together, the average bilateral deficit was \(\sim -5.1 \pm 5.8\%\) MVC \((n = 50)\). No correlation was found between the degree of contralateral irradiation and the degree of bilateral deficit (Fig. 6).

**DISCUSSION**

Our results showed that, also at moderate levels of force and effort, unilateral voluntary contractions of the FDI are frequently associated with “unintended” contractions in the homologous muscle of the contralateral side (contralateral irradiation). Further observations concerning the contralateral irradiation of activity are 1) a gradual increase in MVC-

![FIG. 5](image_url)

**FIG. 5.** Development of contralateral irradiation activity with time during fatigue tests. Contralateral mean force production (A and B) and amount of mean rectified EMG (C and D) during the first (A and C) and second (B and D) endurance tests. Time was normalized in relation to endurance time. All plotted values are mean ± SE \((n = 25; SE\) often of same size or smaller than symbol). A and C: force and EMG values are expressed as percentages of prefatigue MVC measurements. B and D: values are normalized in relation to MVC measurements obtained after the first endurance test \((MVC-F_1)\). Diamonds and solid lines indicate MVC-associated contralateral irradiation values for force (A and B) and for EMG (C and D). For comparison, the MVC-associated data of the first test (A and C) also are shown in the charts for the second test (B and D; here plotted as crosses joined by dotted lines). Hatched areas represent the difference between the MVC-associated values of the two tests. During the initial 60% of the second test, the amount of contralateral activation was significantly lower than that seen in the first test (asterisks, \(P < 0.05\)). The three lower sets of values (dotted lines) represent the mean values of contralateral irradiation force (A and B) and EMG (C and D) during the submaximal holding task (target-side force: 30% MVC), as was calculated for the first (bottom line), middle (middle line), and last (top line) third of each 22-s holding period. For the mean irradiated force and EMG values obtained during submaximal target contraction (22 s), crosses denote the presence of a significant difference between the first and second endurance tests (B and D).

**FIG. 6.** Lack of relationship between bilateral deficit and contralateral irradiation. Plots of the amount of “bilateral deficit” (unilateral MVC–bilateral MVC; % unilateral MVC) vs. the amount of MVC-associated contralateral irradiation force (% MVC) measured before fatigue tests. Data was plotted for all of the individual experiments and for left and right hands together \((n = 50)\). Different symbols represent different subjects.
associated contralateral irradiation during fatigue tests, 2) a postfatigue decrease in the degree of “expressed” contralateral irradiation, and 3) the saw-tooth behavior of contralateral activity during a maintained submaximal contraction.

**Contralateral irradiation**

In accordance with expectations based on earlier qualitative observations, the mean amount of contralateral irradiation increases roughly in parallel with known variations in the level of perceived effort (Dimitrijevic et al. 1992; Mayston et al. 1994; Zijdewind et al. 1998). Therefore, enhancement of contralateral force was observed when the absolute level of voluntary force was increased (Fig. 3B) and also when the same submaximal force was maintained during an increasing degree of fatigue (Figs. 4 and 5). However, factors other than the level of effort must also play a role because, during the course of the fatigue tests, interspersed MVCs also produced a gradually increasing amount of contralateral irradiation; this happened despite the fact that, in accordance with its definition (and the subject’s instructions), each MVC should have represented a truly maximal effort.

Compared with the data of Mayston et al. (1994), our data showed consistently more contralateral activation during maintained contractions. This difference could be caused by differences in task quality (handgrip vs. index finger abduction) and/or task duration. During our endurance tasks, short periods of rest were included, which probably resulted in a longer test duration as compared with the tonic isometric handgrip task of Mayston et al. (1994).

Analysis of earlier data (Zijdewind et al. 1998) showed that, during an initial endurance test of the dominant hand, the amount of contralateral activity in the nonfatigued nondominant hand was slightly larger ($P < 0.05$, paired *t*-test) than was the amount of contralateral activity reported here in the nonfatigued dominant hand (Fig. 5, A and C). Therefore, the testing order between dominant and nondominant hands could not have been an important factor in the prominent decline of contralateral activation in the fatigued nondominant hand (Fig. 5, B and D).

The increasing amount of contralateral MVC irradiation might have been a consequence of an increase in excitability in cortical pathways related to the nontarget muscle. Signs of a general and progressive increase in cortical excitability also have been seen during maintained MVC contractions, as was investigated using transcranial magnetic stimulation (TMS) (Taylor et al. 1996, 1999). Furthermore, TMS studies have shown that, while voluntary contractions are being performed, excitability changes occur in central pathways associated with target muscles as well as in those directed toward contralateral homologous muscles (Hess et al. 1986, 1987; Muellbacher et al. 2000; Stedman et al. 1998; Zwarts 1992). The actual coactivation of the contralateral homologous muscle, as seen in our experiments, is likely to be a consequence of such a central “spreading-out” of facilitation. It is possible that this “irradiated” facilitation occurred at cortical and/or subcortical levels.

Beside the facilitating effects of fatigue on the amount of contralateral force, we also observed that the irradiation phenomenon itself may become depressed by fatigue. During the second fatigue test, the initial amounts of contralateral nontarget force and EMG was significantly lower than was seen in the first test (Fig. 5, B and D, hatched area), even after normalization for the fatigue-induced changes in force and EMG data. Similarly, after the completion of the second fatigue test, the most recently fatigued muscle (dominant side) expressed less MVC irradiation during target contractions of the nontarget side. Therefore, postfatigue depression of contralateral irradiation took place independently of whether the irradiation was directed to the dominant or the nontarget hand. TMS has shown that, after a fatigue contraction, there is a decline in excitability at supraspinal levels (Brasil-Neto et al. 1993; McKay et al. 1995). However, in the present study, the depression of contralateral irradiation was still evident after correction for fatigue-related changes in MVC and EMG reactions. These findings might be explained as being caused by marked fatigue-associated changes that took place in physiological structures that are of critical importance for contralateral irradiation but are less important for voluntary force production.

An important question for further research concerns the anatomical substrates that are involved in the irradiation of activity. Several options are briefly discussed in the following three paragraphs.

**IRRADIATION TO THE OTHER HEMISPHERE.** During the voluntary activation of a muscle, imaging techniques and magnetoencephalography have shown increased activity both in the contra- and in the ipsilateral motor cortices (Cramer et al. 1999; Dettmers et al. 1996; Kim et al. 1993; Kristeva et al. 1991). Also, contractions of contralateral muscles result in the facilitation of TMS-evoked responses of the contralateral as well as of the ipsilateral homologous muscles (Hess et al. 1986, 1987; Meyer et al. 1995; Muellbacher et al. 2000; Stedman et al. 1998; Zwarts 1992). These results suggest increased excitability of the motor cortex ipsilateral to the target muscle, which results in a higher probability of the nontarget muscle being activated. The increased excitability of the ipsilateral hemisphere could be caused by direct input to the ipsilateral cortex (e.g., from premotor areas) or by interhemispheric facilitation (Ugawa et al. 1993).

**IRRADIATION WITHIN THE TARGET HEMISPHERE.** Transcranial stimulation has shown that the motor cortex is involved in the control of ipsilateral finger movements (Chen et al. 1997; Wassermann et al. 1994; Ziemann et al. 1999); this has also been shown to be true in a subject lacking a corpus callosum (Ziemann et al. 1999). Intrahemispheric irradiation of the activity from neurons that activate the “normal” crossed target–muscle pathways to neurons activating uncrossed pathways might result in contralateral activity of nontarget-side muscles. An increase of such intrahemispheric irradiation during more demanding tasks (e.g., higher force or more fatigue) might result in an increase in the activity of nontarget-side muscles.

**SUBCORTICAL INTERACTION.** Subcortical midline regions (e.g., brain stem, spinal cord) are also possible sites for interaction between commands emanating from the two hemispheres. A strong indication for such subcortical bilateral interactions is provided by the experiments of Meyer et al. (1995). They found that TMS-evoked responses from the cortex to the contralateral hand were facilitated by voluntary contractions of the other hand, even in subjects lacking a corpus callosum.

During unilateral voluntary contractions of hand muscles, increased frequencies of F-reponses have been noted to appear in homologous muscles on the nontarget side (Muellbacher et
al. 2000). Also, small bilateral increases of excitability were observed using electrical test stimulation of the spinal cord (Stedman et al. 1998). Such signs of increased excitability in nontarget-side motoneurons might have been caused by irradiation at a cortical, brain stem, and/or spinal level (e.g., via intraspinal axons crossing the midline).

Because the pathways for contralateral irradiation are still uncertain, it is also unclear which mechanisms are responsible for the decline in contralateral irradiation after fatigue. However, the fact that contralateral irradiation may be depressed by a preceding period of voluntary “targeted” activation of the same muscles (Fig. 5, B and D, hatched areas) implies that, to some extent, projecting neurons and synapses are shared between irradiated and targeted motor pathways. Furthermore, the results suggest that this bilaterally accessible portion of the motor pathways might be more sensitive to fatigue than is the portion that is used only for “normal” targeted motor activation.

Bilateral deficit

In accordance with the only other study of the bilateral deficit in intrinsic hand muscles (adductor pollicis; Herbert and Gandevia 1996), the bilateral deficit for FDI was relatively small (5–6%). We found no evidence for a relation between the degree of bilateral deficit and the degree of contralateral coactivation (irradiation) (Fig. 6). This suggests that these two forms of bilateral interaction depend on non-overlapping sections of circuitry within the brain.

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