Chinese Journal of Physiology 49(1): 22-30, 2006

Contrast of Directional Influence upon Motor Overflow between Submaximal and Maximal Static Exertions

Ing-Shiou Hwang[1, 2], Chih-Feng Lin[3, 4], Yi-Ching Chen[3, 4], Chiung-Yu Cho[1], and Chun-Hou Wang[3, 4]

[1]*School of Physical Therapy*
National Cheng Kung University
Tainan 701
[2]*Institute of Allied Health Sciences*
National Cheng Kung University
Tainan 701
[3]*School of Physical Therapy, College of Medical Technology*
Chung Shan Medical University
Taichung 402
and
[4]*Department of Physical Therapy*
Chung Shan Medical University Rehabilitation Hospital
Taichung 406, Taiwan, R.O.C.

Abstract

This study investigated exertion-dependent motor overflow among healthy adults when they performed isometric tasks with contralateral joints in different task directions. Twenty healthy adults (10 males and 10 females, mean age = 26.2 yrs) were instructed to complete a set of isometric contractions of various force vectors with the shoulder, elbow, and wrist joints, in a total of ten motor tasks at submaximal and maximal intensities (50%, 100% maximal voluntary contractions). The electromyographical activities from eight muscles of the unexercised upper limb were recorded to characterize intensity of motor overflow during sustained isometric contraction. Both occurrence frequency and magnitude of motor overflow in terms of standardized net excitation (SNE) increased with exertion level for all joint movements ($P < 0.001$). Additionally, the motor overflow magnitude depended strongly on the task direction of maximal isometric contraction ($P < 0.05$). Motor overflow was particularly augmented by the contralateral isometric contractions where task directions were opposed to gravity. However, such a directional effect upon SNE was not evident during submaximal contraction ($P > 0.05$). The difference of the net excitation between maximal and submaximal contraction ($DNE_{100\%-50\%MVC}$ data) indicated that the pectoralis major and triceps brachii consistently exhibited a marked recruitment in reaction to change in task direction of isometric contraction. Patterned motor overflow may be physiologically relevant to topological mapping of the ipsilateral pathways and altered effectiveness of use-dependent interhemispherical connectivity. The current observations provide better insight into gain in muscle strength due to contralateral exercise.

Key Words: motor overflow, electromyography, isometric contraction, task direction

Corresponding author: Chun-Hou Wang, Associate Professor, School of Physical Therapy, College of Medical Technology, Chung Shan Medical University, No. 110, 1 Sec., Chieh Kuo N. Rd, Taichung 402, Taiwan, R.O.C. Tel: +886-4-23248181, Fax: +886-4-24730022 ext 11765, E-mail: chwang@csmu.edu.tw
Received: April 7, 2005; Revised: May 17, 2005; Accepted: June 8, 2005.

Introduction

A common feature of vigorous contraction of a target joint is unintended coactivation of the muscles in the opposite limb (1, 35). Extraneous to the target movement, this unintended muscle activation has been documented with different terminologies, such as motor overflow (2), contralateral irradiation (13), or synkinesis (4). Motor overflow is common for healthy subjects during strenuous contraction (1, 24) and also in patients suffering neurological dysfunction (9, 13). For healthy subjects, motor overflow are often considered non-purposive and it interferes with bimanual coordination for loss of limb dexterity (40). When motor overflow arises, it is typically observed in homologous muscles contralateral to those performing the task. The occurrence and magnitude of motor overflow have been shown to be affected by many demographic factors such as limb dominance (2, 34), age (20, 32), and occupation (36). A greater observable level of overflow is associated with use of the non-dominant limb, especially for children and aged people who reveal immaturity or degeneration of the callosal myelination (24, 32).

To gain in strength and function, cross education (14, 38) that based empirically upon motor overflow has long been proposed to facilitate the execution of a feeble movement by performing identical movement on the other stronger side. However, overflow-based facilitation responds on earlier studies addressed motor overflow mainly limited to the reference of the homologous muscle (1, 14). In fact, irradiation may emerge not only the homologous muscle, but also spread globally to other non-homologous muscles (15). As the motor overflow of different muscles may be coupled, it is necessary to characterize contralateral overflow in both homologous and non-homologous muscles that jointly drive associated movements in the unexercised limb (4, 8, 40).

Several lines of evidence point to the fact that motor overflow is task specific (12), and its magnitude related to contraction type (11, 14), joint position (38), and exertion level (27, 35) used during contralateral voluntary contraction. Compared to a normal motor overflow, the greater level of motor overflow may be resulted from intensive force requirement, unfamiliar task, and contraction of eccentric mode at faster speed. In spite of task specificity, the influence of force vector of isometric contraction upon motor overflow has rarely been investigated. The only study concerning force vector was that the occurrence frequency of ipsilateral overflow in knee muscles differed between ipsilateral dorsiflexion and plantarflexion at maximal exertion (15). For irradiation from contralateral movements, whether the motor overflow magnitude is influenced by the force vector of muscle contraction has never been assessed.

The purpose of this study was to characterize, using multiple channel surface electromyography, the motor overflow magnitude of the upper limb during isometric contraction of various task directions at submaximal and maximal exertions. In particular, our interests focus upon 1) the interacting effect of exertion level and task direction upon the degree of specificity for motor overflow, and 2) the relative contribution of each irradiated muscle to directionality of motor overflow with respect to exertion increment. The results could interest clinicians who intend to shape desired movement patterns and gain in strength efficiently with motor overflow based facilitation, and for neuroscientists who are interested in inter-hemispheric connectivity.

Materials and Methods

Subjects

Twenty healthy right-handed subjects (ten of them men) with no history of neuromuscular disease and a mean age of 26.2 years (range = 20–38) were recruited for this study. None of these subjects were engaged in regular organized physical activities, but all exhibited a normal, full range of motion in the upper extremity. The subjects provided informed consent according to the guidelines set forth by Chung Shan Medical University Rehabilitation Hospital concerning the protection of human subjects.

Test Administration

A Biodex dynamometer (Multi-Joint System 3 Pro, Shirley, NY, USA) was used to perform the exertion protocols for the upper extremity. The subjects, who were not aware of our research interests, performed different modes of isometric contraction with the shoulder, elbow, and wrist joints of the non-dominant limb at two exertion levels (50% and 100% of maximal voluntary contraction [MVC]), randomly ordered across the subjects (Table 1). The determination of the MVC involved the application of a gradual increase in force by the subjects to a maximum level within a period of three seconds, and then sustained for one to two seconds.

There were a total of ten different isometric tasks to be performed at the two exertion levels for the three tested joints. During experiment, a subject remained seated in the dynamometer chair with the hips, knees, and ankles stabilized roughly at positions of 90 degrees of flexion. The positions of the exercised upper limb for the different isometric tasks were standard positions documented in the user manual of

Table 1. Standard testing positions recommended in the Biodex system for voluntary isometric contraction of different directions with joints in the upper extremity. The homologous muscles in this study were defined as the muscles contralateral to prime movers of a target movement. (Bi: biceps brachii, Bra: brachioradialis, ant. Del: anterior portion of the deltoid, mid. Del: middle portion of the deltoid, Ecr: extensor carpi radialis, Fcr: flexor carpi radialis, Lat: latissimus dorsi, Pec: pectoris major, Pro: pronator teres, Tri: triceps brachii)

	Task Vector	Homologous Muscle	Recommended Testing Position in the Upper Extremity (BIODEX)
Shoulder	Abduction	mid. Del	Dynamometer orientation: 0° Dynamometer tilt: 10° Seat orientation: 75° Seatback tilt: 70–85°
	Adduction	Pec	
	Flexion	Bi & ant. Del	Dynamometer orientation: 0° Dynamometer tilt: 0° Seat orientation: 15° Seatback tilt: 70–85°
	Extension	Tri & Lat	
Elbow	Flexion	Bi & Bra	Dynamometer orientation: 30° Dynamometer tilt: 0° Seat orientation: 0° Seatback tilt: 85°
	Extension	Tri	
	Pronation	Pro	Dynamometer orientation: 0° Dynamometer tilt: 5° (shaft down) Seat orientation: 90° Seatback tilt: 85° Elbow flexion: 90°
	Supination	Bi	
Wrist	Flexion	Fcr	Dynamometer orientation: 0° Dynamometer tilt: 0° Seat orientation: 0° Seatback tilt: 85° Elbow flexion: 90°
	Extension	Ecr	

the Biodex system. The target joints were aligned with the axis of the dynamometer with the trunk and lower extremities secured to the testing chair. The investigators verbally encouraged the subjects to perform steady isometric contractions at the desired levels. These contraction forces were determined by matching a line for the true dynamometer torque output with a line representing the required level as displayed on an oscilloscope (Instek GOS-620, Good Will Instrument Co., Taipei County, Taiwan). Submaximal and maximal voluntary contractions brought about unintended coactivation of several muscle groups contralateral to the target joint, although the subjects were instructed to relax the unexercised limb.

Eight preamplified bipolar surface electrodes (Motion Control, Inc., Salt Lake City, UT, USA) (electrode spacing 2.5 cm, diameter 1.1 cm, with a gain of 375 and a common-mode rejection ratio (CMRR) of 102 dB) were used to record electromyographical activities from eight muscle groups in the unexercised limb for periods of five seconds, including the biceps brachii (Bi), brachioradialis (Bra), flexor carpi radialis (Fcr), middle deltoid (Del), triceps brachii (Tri), pronator teres (Pro), extensor carpi radialis (Ecr), and pectoris major (Pec). Surface electromyography (EMG) electrodes were applied over the muscles in parallel with the muscle bellies according to the method described by Cram *et al*. (6). In this study, the term homologous muscle(s) of a target movement refers to the 5 analogous muscle(s) contralateral to the prime mover(s) responsible for the movement, and non-homologous muscles are the irradiated muscles of the unexercised limb other than the homologous one (Table 1).

For both submaximal and maximal exertion levels, each subject performed an isometric task three times with a two-minute rest interval between trials.

During rest intervals, the background activity for homologous and non-homologous muscles in the unexercised limb was recorded for a period of five seconds, for which the subject had been instructed to relax completely. The recorded myosignals were conditioned using analog low-pass filters (cut-off frequencies set at 400 Hz) within a distribution box and then digitized at 1KHz using a specific computer program constructed on a Labview 6.0 platform (National Instruments, Austin, TX, USA).

Data Analyses

Off-line EMG analyses included removal of the linear trend from the raw EMG and possible artifacts using a tenth order digital Butterworth bandpass filter (cut-off frequency = 40–400 Hz) and the calculation of the root mean square (RMS) value from the conditioned EMG results. Mean RMS, which represented magnitude of irradiation due to an isometric task, was determined by averaging the RMS of three separate trials of the task. We defined occurrence frequency of irradiation for a given muscle as the number of subjects whose muscles exhibited a significant level of irradiated activity (i.e., mean EMG RMS > 1.96 × standard error of background activity)(15). In terms of RMS, the net excitation of an irradiated muscle was determined by subtracting the corresponding EMG activity of the irradiated muscle from its background activity at rest, and this calculated value was further normalized to the level of background activity (Fig. 1).

The summation of the individual normalized EMG activity from all recorded muscles resulted in the determination of a standardized net excitation (SNE)(16), which was taken to represent the magnitude of the motor overflow provoked by a particular isometric task. The difference of the net excitation for an irradiated muscle between 100% MVC and 50% MVC was defined as $DNE_{100\%\text{-}50\%MVC}$. $DNE_{100\%\text{-}50\%MVC}$ specifies the amount of change in overflow for an irradiated muscle due to alternation in exertion level from 50% to 100% MVC.

For a given joint of the unexercised limb, repeated measures two-way analysis of variance (ANOVA) was used to examine the effects of task direction and study-specified exertion levels upon SNE. One way ANOVA for repeated measure was used to examine [1] the difference in background activity among eight recorded muscles, and [2] the dependence on task direction of the $DNE_{100\%\text{-}50\%MVC}$ for an irradiated muscle. The level of significance for the determination of difference for the ANOVA and post-hoc testing was selected as being 0.05. Signal processing and statistical analyses were completed using Matlab v. 6.0 (Mathworks Inc. Natick, MA, USA) and the Statistical Package for Social Sciences (SPSS) for Windows v. 10.0 (SPSS Inc. Chicago, IL, USA).

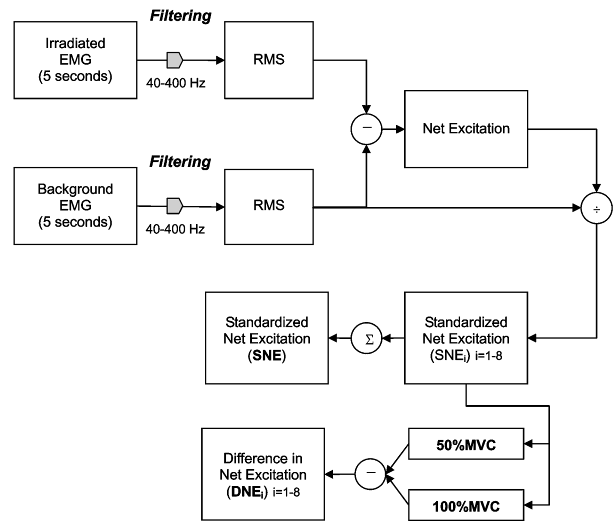

Fig. 1. A schematized diagram showing the obtainment of the SNE and DNE values

Results

Fig. 2(a)-(c) displays typical example of muscle background activity in the relaxed condition and motor overflow activity that spread through the muscles of the unexercised upper limb consequent to 50% and 100% MVC of shoulder abduction. Repeated measure ANOVA indicated that the background EMG activity was well controlled without any significant difference among recorded muscles ($F(7,133) = 1.35$, $P = 0.231$). The consistent background validates the use of SNE and $DNE_{100\%\text{-}50\%MVC}$ in this study. Fig. 3 (a)-(c) shows the occurrence frequency of motor overflow occurring in the non-homologous muscles with the non-dominant shoulder, elbow, and wrist joints at maximal and submaximal voluntary contractions. The non-homologous muscles of the unexercised upper limb were excited during contralateral movements, and their occurrence frequency increased with exertion levels. This widespread excitation among the contralateral muscles validated the use of the SNE value to characterize global irradiation patterns. Fig. 4 schematizes the statistical analysis of the mean values of the SNE resulting from isometric contractions in different task directions for all the involved joints. Repeated measures two-way ANOVA revealed that the SNE value increased significantly with exertion level [shoulder: $F(1,19) = 56.65$; elbow: $F(1,19) = 25.00$; wrist: $(1,19) = 25.41$; $P < 0.001$], and varied dependently with the task direction for the shoulder and elbow joints [shoulder: $F(3,133) = 8.74$, $P < 0.001$; elbow: $F(3,133) = 4.63$, $P = 0.004$]. For

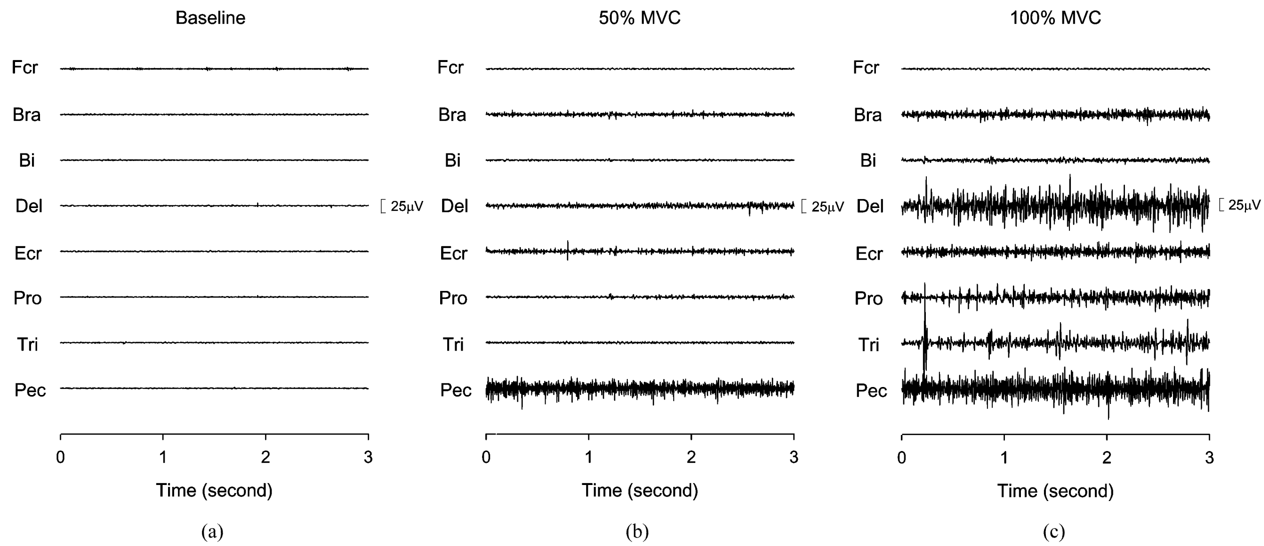

Fig. 2. A typical example of motor overflow associated with contralateral isometric shoulder abduction. (a) relaxed baseline activity, (b) 50% MVC, (c) 100% MVC.

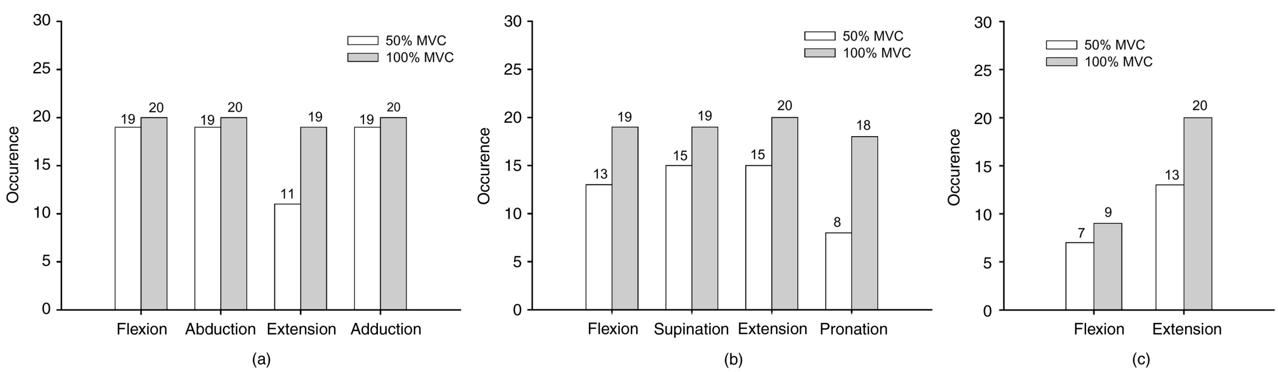

Fig. 3. Occurrence frequency of significant irradiation for non-homologous muscles at submaximal and maximal exertion levels. The numbers above each bar indicate the number of subjects who presented significant irradiated activity. (a) shoulder; (b) elbow; (c) wrist.

SNE of the wrist movements, there was a significant interaction between exertion level and task direction [F(1,57) = 4.08, P = 0.048]. Post hoc comparison was performed to further contrasting SNE values for different task directions of an involved joint at maximal and submaximal contractions. In particular, SNE was considerably affected by task direction only at maximal contraction [shoulder: F(3,96) = 3.26, P = 0.025; elbow: F(3,96) = 3.163, P = 0.028; wrist: F(1,58) = 4.56, P = 0.037], whereas the SNE level at submaximal contraction was not significantly affected by task direction [shoulder: F(3,96) = 0.48, P = 0.694; elbow: F(3,96) = 0.20, P = 0.896; wrist: F(1,58) = 0.10, P = 0.747]. For shoulder movements at maximal-contraction level, the SNE level was significantly larger for shoulder flexion and abduction than it was for shoulder extension and adduction (P < 0.05; Fig. 4(a)). For the elbow movements, the SNE value corresponding to elbow flexion and extension at maximal contraction was significantly larger than the corresponding value for elbow pronation (P < 0.05; Fig. 4(b)). A significantly larger SNE value was caused by maximal wrist extension than by maximal wrist flexion (P < 0.05; Fig. 4(c)).

Fig. 5 shows the directional effect on the difference in the net excitation level between maximal and submaximal contraction ($DNE_{100\%\text{-}50\%MVC}$) for eight primary muscles. The examination of the $DNE_{100\%\text{-}50\%MVC}$ of a given muscle among different task directions helps to determine whether irradiation of the muscle contributes to directional specificity of motor overflow. Fig. 5(a) shows that the $DNE_{100\%\text{-}50\%MVC}$ for the Pec, Tri, Del, and Bi changed significantly with task direction of the shoulder joint, based on ANOVA statistics (P < 0.05). The $DNE_{100\%\text{-}50\%MVC}$ for the Pec, Tri, and Del was dependent on the task direction of the elbow joint (Fig. 5(b);

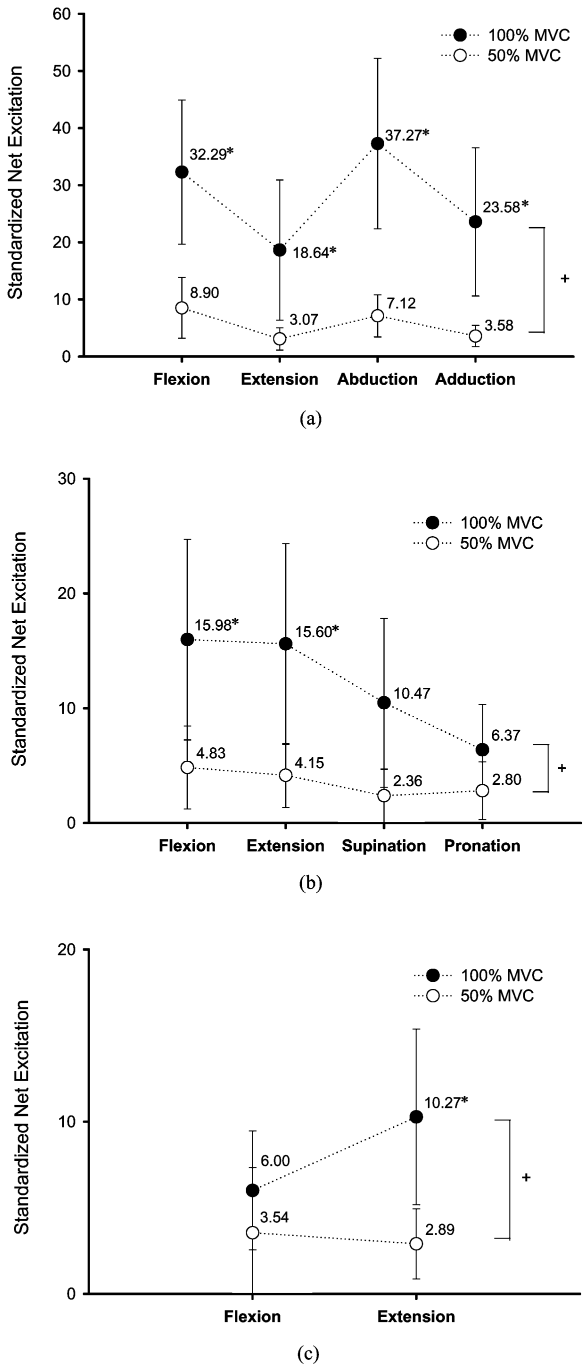

Fig. 4. A graphic summary of the standardized net excitation (SNE) resulting from isometric tasks in different directions. (a) shoulder; (b) elbow; (c) wrist. (100% MVC: -•-, 50% MVC: -◦-). (†: main effect of exertion level, $P < 0.001$; *: post-hoc analysis indicated a significant difference in SNE between maximal and submaximal conditions for a given task direction, $P < 0.05$)

$P < 0.05$). The contrast of the $DNE_{100\%\text{-}50\%MVC}$ for wrist flexion and extension showed that additional irradiation of the Pec, Tri and Pro from 50% to 100% MVC responded differently to force vector of the wrist joint (Fig. 5(c); $P < 0.05$). It would be safe to say that the directional effect on magnitude of motor overflow could be ascribed primarily to the muscles that presented directional-dependent $DNE_{100\%\text{-}50\%MVC}$. Briefly, the Pec and Tri were the most important ones for all joint movements, and distal muscles of the unexercised limb contributed little to the directional specificity on magnitude of motor overflow.

Discussion

Directional Modulation of Motor Overflow at Maximal Exertion

In consideration of the global irradiation of several non-homologous muscles, we found that magnitude of motor overflow increased proportionally with exertion level, and a marked directional specificity upon magnitude of motor overflow presented merely at maximal contraction. The magnitude of motor overflow was exertion-related, with greater exertion resulting in greater magnitude of motor overflow, conforming to the rule of perceived effort (32, 35). In addition to exertion level, magnitude of motor overflow was also subjected to force vector of isometric task, with greater overflow associated with task direction against gravity. However, directional specificity on motor overflow cannot be explained simply by application of the rule of perceived effort. The SNE value at 100% MVC changed specifically with task direction but was independent of the torque developed in that direction. Cahalan *et al*. (1991) reported that the torque generated by shoulder adduction and extension was larger than the torque generated by shoulder abduction and flexion (5). However, the magnitude of SNE in this study revealed the opposite outcome, with a greater motor overflow triggered in a limb by contralateral shoulder flexion and abduction (Fig. 4(a)).

Based upon the peak torque of an isometric contraction as reported by Delp *et al*. (7), likewise, such an incompatible torque-overflow relationship was true for the movements of the elbow and wrist joints (Fig. 4(b), (c)). Collectively, since the directional specificity on motor overflow was evident during maximal exertion level rather during submaximal exertion level, we argue that there are two interacting dimensionality, exertion level and task direction, involving with contralateral irradiation as a result of isometric contraction. As magnitude of motor overflow became directionally dependent merely at maximal exertion, it is of interests to realize what muscles contributed to the overflow directionality. The $DNE_{100\%\text{-}50\%MVC}$ is informative to judge the contribution of an irradiated muscle to directional specificity when exertion level increases

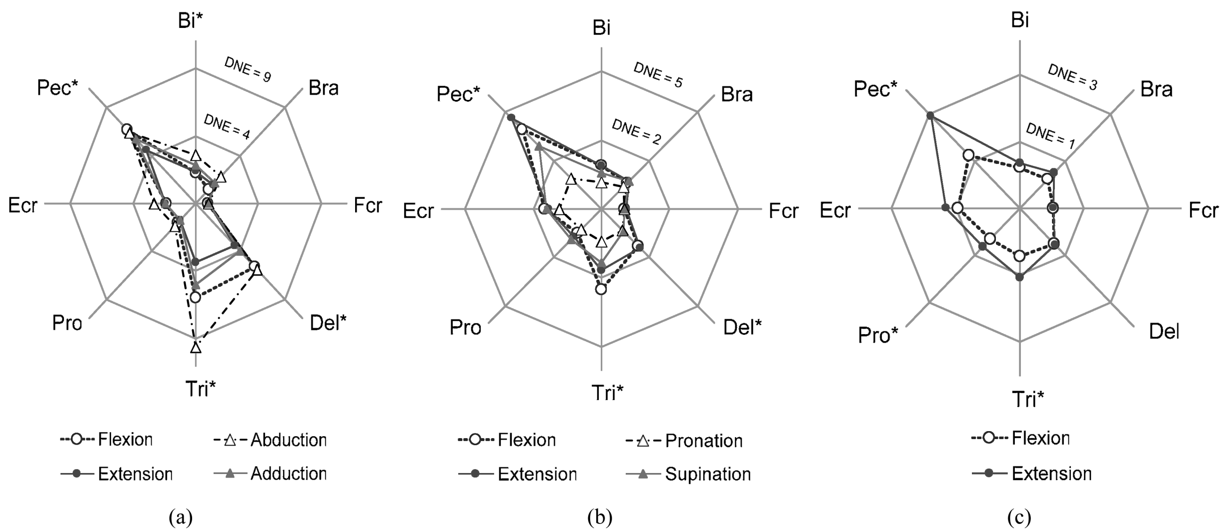

Fig. 5. A graphic summary of the difference in net excitation between maximal and submaximal contractions ($DNE_{100\%-50\%MVC}$) with respect to task direction for all recorded muscles. (a) shoulder ; (b) elbow; (c) wrist. A significant difference in $DNE_{100\%-50\%MVC}$ for an irradiated muscle among different task directions was labeled with a ‘*’. ($P < 0.05$).

from 50% to 100% MVC. If the $DNE_{100\%-50\%MVC}$ of a muscle is statistically different among task directions, irradiation of the muscle adds to directional specificity of overflow. In effect, not all investigated muscles were related to directional specificity of overflow, only the muscles in the proximal upper limb, especially for the Pec, Tri, and Del, were responsive to change in task direction.

The neural mechanisms underlying the patterned EMG presence due to contralateral movement is not completely clear. Modern imaging techniques have shown that motor overflow involves bilateral excitation of the motor cortex by transcallosal connectivity (19, 37). Motor overflow may come from the contralateral corticospinal pathway of the irradiated hemisphere, or from the ipsilateral corticospinal pathway of the working hemisphere. Although there are two possibilities of overflow transfer, our data appear to favor the latter hypothesis. When exertion level increased, prevailing irradiations of axial or proximal muscles of the upper limb, such as the Pec, Tri, or Del, are compatible with anatomical observations. The ipsilateral corticospinal fibers have a richer supply to proximal muscles than to distal muscles (22, 23). In addition, the trunk and proximal limbs of the motor cortex are supplied with a denser level of callosal fibers, while transcallosal projection to the area of distal limbs is comparatively sparse (10, 18, 22, 30). Preferential irradiation of the proximal muscles might be functionally important for postural stabilization against inertial reactance due to different directions of the contralateral movement (8, 15) by stiffening the axial and proximal parts of the body.

There are increasing evidences in support of association between the amount of motor overflow and efficacy of interhemispheric connectivity. When a subject performs target strenuous contraction, a drastic reduction in transcallosal inhibition (3, 21) and the extent of exertion-related overflow depends on the amount of inhibitory projection across hemispheres. It is likely that one hemisphere reduces its inhibitory influence via transcallosal fibers on the working hemisphere (25, 26, 33), and overflow is conveyed by the ipsilateral descending tract, composed of approximately 10% corticospinal fibers for humans, to numerous muscles of the unexercised limb. On the other hand, despite of lacking direct neuroanatomical data, directional modulation of motor overflow might be related to use-dependent interhemispheric connection (29). Several lines of evidence indicate that intensive joint-exertion practice multiplies the size of the corpus callosum and changes its effectiveness in suppressing cortical excitability in the opposite hemisphere (29, 31). Such reduced interhemispherical inhibition is believed to result in a lower bilateral deficit (27), a reduction in muscle strength when simultaneously activating the homologous muscles of the contralateral limb.

Like magnitude of motor overflow, the decline in bilateral deficit was also related to the task direction of a joint. For instance, bilateral deficit in elbow flexors is more manifest than in elbow extensors, and elbow flexors are known to be used against gravity more frequently than extensors (17, 28). Furthermore, we found that movements that tended to produce relatively pronounced levels of motor overflow involved shoulder flexors/abductors, elbow flexors, and wrist extensors that act functionally against gravity in daily life (Fig.4(a)-(c)). Since magnitude of motor overflow is enhanced by contralateral movements driven by these physiological antigravity muscles, such a directional specificity upon magnitude of motor overflow conceptually supports the "cortical activation theory" proposed by Todor and Lazarus (36). According to the theory, preferential use of the muscles for supportive purposes leads to cortical adaptation and, in turn, potentiates magnitude of motor overflow in the opposite limb.

Methodological Issues

An important methodological concern of this study is normalization of the EMG. In this study, we did not measure the maximal EMG value in the muscles performing the target task. Therefore, we expressed irradiated activity in terms of SNE instead of a percentage of MVC value, although the latter seems to be a more popular approach for EMG standardization. Under meticulous control of consistent background activity across muscles, we preferred to express irradiated activity with the SNE value rather than as a percentage of maximal voluntary EMG. The reason for such a choice is apparent. The maximal torque development of a target movement, such as elbow flexion, can hardly be achieved by a single muscle, requiring instead coactivation of several functional synergists. Therefore, the measurement of 100% MVC of the biceps brachii for normalization with elbow flexion paradigm may not be physiologically appropriate. In addition, reliable measurement of EMG at 100% MVC for all investigated muscles is time-consuming and will likely elicit an additional "fatigue" effect upon motor overflow development (39).

To compensate for these technical concerns, we standardized the EMG of the irradiated muscle with its background activity at rest for convenience. To be addressed, SNE and $DNE_{100\%\text{-}50\%MVC}$ is unlikely to be affected by background activity that did not differ among muscles ($P > 0.05$). However, the interpretation of results based on SNE and $DNE_{100\%\text{-}50\%MVC}$ still should be cautious. To be noticed, SNE and $DNE_{100\%\text{-}50\%MVC}$ were normalized with respect to a consistent level of background activity, rather than normalized with genuine EMG of 100% MVC. Therefore, SNE and $DNE_{100\%\text{-}50\%MVC}$ cannot provide sufficient information for comparison of the excitation level among different muscles. However, our major findings is not likely be overturned by adopting this alternative approach. This is because we compared only the difference of SNE and $DNE_{100\%\text{-}50\%MVC}$ among task direction and exertion level rather than among muscle, so that differences in motor overflow dimensions were featured under the same electrode-tissue impedance, skin thickness that might affect EMG recording across trials.

Functional Implications and Conclusion

Based physiologically on motor overflow, a number of studies in regard to cross education have claimed that the exercise of one limb causes an increase in the strength of the contralateral unexercised limb (32, 38). Having been considered clinically meaningful for neurological patients, cross education is a unilateral intervention while producing roughly 20%-80% force transfer (14). Although most previous studies reported unilateral muscular activity can be observed in the contralateral homologous muscle, for all force vectors of an isometric contraction, our EMG data clearly suggested the exertion-related motor overflow was not specific to contralateral homologous muscle. Moreover, when subjects exercised contralateral joints at maximal exertion against gravity, the magnitude of overflow tended to be larger compared to that in other directions. The directional specificity of overflow, attributed primarily to the pectoralis major and triceps brachii, was not evident for submaximal contraction.

As a matter of fact, a better strength gain by means of chronic adaptations to unilateral exercise, especially in proximal muscle of the upper limb, can be expected through contraction of large contralateral antigravity muscles. However, exact neural mechanisms for interaction between task direction and exertion level on magnitude of motor overflow are not fully clear. Using available neurophysiological evidence, we argue that the patterned motor overflow response was relevant to use-dependent interhemispherical modulation and the topological density of transcallosal connectivity.

Acknowledgments

The authors are grateful to Miss Hsiu-Ching Chiu for her assistance with data collection. This research was, in part, supported by a grant from the National Science Council, R.O.C., under Grant no. NSC 93-2614-B-006-002, and NSC 92-2314-B040-005.

References

1. Armatas, C.A., Summers, J.J. and Bradshaw, J.L. Mirror movements in normal adult subjects. *J. Clin. Exp. Neuropsychol.* 16: 405-413, 1994.
2. Armatas, C.A. and Summers, J.J. The influence of task characteristics on the intermanual asymmetry of motor overflow. *J. Clin. Exp. Neuropsychol*. 23: 557-567, 2001.
3. Aranyi, Z. and Rosler, K.M. Effort-induced mirror movements. A study of transcallosal inhibition in humans. *Exp. Brain Res.* 145: 76-

82, 2002.
4. Boissy, P., Bourbonnais, D., Kaegi, C., Gravel, D. and Arsenault, B. A. Characterization of global synkineses during hand grip in hemiparetic patients. *Arch. Phys. Med. Rehabil.* 78: 1117-1124, 1997.
5. Cahalan, T.D., Johnson, M.E. and Chao, E.Y. Shoulder strength analysis using the Cybex II isokinetic dynamometer. *Clin. Orthop.* 271: 249-257, 1991.
6. Cram, J.R., Holtz, J. and Kasman, G.S. Introduction to surface electromyography. Gaithersburg: Aspen Publishers, 1998, pp. 237-326.
7. Delp, S.L., Grierson, A.E. and Buchanan, T.S. Maximum isometric moments generated by the wrist muscles in flexion-extension and radial-ulnar deviation. *J. Biomech*. 29: 1371-1375, 1996.
8. Devine, K.L., LeVeau, B.F. and Yack, H.J. Electromyographic activity recorded from an unexercised muscle during maximal isometric exercise of the contralateral agonists and antagonists. *Phys. Ther.* 61: 898-903, 1981.
9. Dickstein, R., Pillar, T. and Abulaffio, N. Electromyographic activity of the biceps brachii muscles and elbow flexion during associated reactions in hemiparetic patients. *Am. J. Phys. Med. Rehabil*. 74: 427-431, 1995.
10. Ebner, F.F. and Myers, R.E. Distribution of corpus callosum and anterior commissure in cat and raccoon. *J. Comp. Neurol.* 124: 353-366, 1965.
11. Farthing, J.P. and Chilibeck, P.D. The effect of eccentric training at different velocities on cross-education. *Eur. J. Appl. Physiol.* 89: 570-577, 2003.
12. Hermsdorfer, J., Danek, A., Winter, T., Marquardt, C. and Mai, N. Persistent mirror movements: force and timing of "mirroring" are task-dependent. *Exp. Brain Res.* 104: 126-134, 1995.
13. Hopf, H.C., Schlegel, H.J. and Lowitzsch, K. Irradiation of voluntary activity to the contralateral side in movements of normal subjects and patients with central motor disturbances. *Eur. Neurol*. 12: 142-147, 1974.
14. Hortobagyi, T. Cross education and the human central nervous system. *IEEE Eng. Med. Biol. Mag*. 24: 22-8, 2005.
15. Hwang, I.S. and Abraham, L.D. Quantitative EMG analysis to investigate synergistic coactivation of ankle and knee muscles during isokinetic ankle movement. Part 1: time amplitude analysis. *J. Electromyogr. Kinesiol*. 11: 319-325, 2001.
16. Hwang, I.S., Tung, L.C., Yang, J.F., Chen, Y.C., Yeh, C.Y. and Wang, C.H. Electromyographic analyses of global synkinesis in the paretic upper limb after stroke. *Phys. Ther.* 85: 755-765, 2005.
17. Jakobi, J.M. and Cafarelli E. Neuromuscular drive and force production are not altered during bilateral contractions. *J. Appl. Physiol.* 84: 200-206, 1998.
18. Killackey, H.P., Gould, H.J., 3rd, Cusick, C.G., Pons, T.P. and Kaas, J.H. The relation of corpus callosum connections to architectonic fields and body surface maps in sensorimotor cortex of new and old world monkeys. *J. Comp. Neurol*. 219: 384-419, 1983.
19. Kristeva, R., Cheyne, D. and Deecke, L. Neuromagnetic fields accompanying unilateral and bilateral voluntary movements: topography and analysis of cortical sources. *Electroencephalogr. Clin. Neurophysiol*. 81: 284-298, 1991.
20. Lazarus, J.A. and Todor, J.I. Age differences in the magnitude of associated movement. *Dev. Med. Child. Neurol.* 29: 726-733, 1987.
21. Lorenzano, C., Gilio, F., Inghilleri, M., Conte, A., Fofi, L., Manfredi, M. and Berardelli, A. Spread of electrical activity at cortical level after repetitive magnetic stimulation in normal subjects. *Exp. Brain Res*. 147: 186-192, 2002.
22. Matsunami, K. and Hamada, I. Effects of stimulation of corpus callosum on precentral neuron activity in the awake monkey. *J. Neurophysiol*. 52: 676-691, 1984.
23. Matsunami, K. and Hamada, I. Characteristics of the ipsilateral movement-related neuron in the motor cortex of the monkey. *Brain Res*. 204: 29-42, 1981.
24. Mayston, M.J., Harrison, L.M., and Stephens, J.A. A neurophysiological study of mirror movements in adults and children. *Ann. Neurol*. 45: 583-594. 1999.
25. Meyer, B.U., Roricht, S., Grafin von Einsiedel, H., Kruggel, F. and Weindl, A. Inhibitory and excitatory interhemispheric transfers between motor cortical areas in normal humans and patients with abnormalities of the corpus callosum. *Brain* 118: 429-440, 1995.
26. Nordstrom, M.A. and Butler, S.L. Reduced intracortical inhibition and facilitation of corticospinal neurons in musicians. *Exp. Brain Res*. 144: 336-342, 2002.
27. Oda, S. and Moritani, T. Maximal isometric force and neural activity during bilateral and unilateral elbow flexion in humans. *Eur. J. Appl. Physiol. Occup. Physiol*. 69: 240-243, 1994.
28. Ohtsuki, T. Decrease in human voluntary isometric arm strength induced by simultaneous bilateral exertion. *Behav. Brain Res*. 7: 165-178, 1983.
29. Ridding, M.C., Brouwer, B. and Nordstrom, M.A. Reduced interhemispheric inhibition in musicians. *Exp. Brain Res*. 133: 249-253, 2000.
30. Rouiller, E.M., Babalian, A., Kazennikov, O., Moret, V., Yu, X.H. and Wiesendanger, M. Transcallosal connections of the distal forelimb representations of the primary and supplementary motor cortical areas in macaque monkeys. *Exp. Brain Res.* 102: 227-243. 1994.
31. Schlaug, G., Jancke, L., Huang, Y., Staiger, J.F. and Steinmetz, H. Increased corpus callosum size in musicians. *Neuropsychologia* 33: 1047-1055, 1995.
32. Shinohara, M., Keenan, K.G. and Enoka, R.M. Contralateral activity in a homologous hand muscle during voluntary contractions is greater in old adults. *J. Appl. Physiol*. 94: 966-974, 2003.
33. Stinear, C.M., Walker, K.S. and Byblow, W.D. Symmetric facilitation between motor cortices during contraction of ipsilateral hand muscles. *Exp. Brain Res.* 139: 101-105, 2001.
34. Todor, J.I., Kyprie, P.M. and Price, H.L. Lateral asymmetries in arm, wrist and finger movements. *Cortex* 18: 515-523, 1982.
35. Todor, J.I. and Lazarus, J.A. Exertion level and the intensity of associated movements. *Dev. Med. Child. Neurol.* 28: 205-212, 1986a.
36. Todor ,J.I. and Lazarus, J.A. Inhibitory influence on the emergence of motor competence in childhood. In: The psychology of motor behavior: Development, control, learning, and performance, edited by Zaichkowsky, L.D. and Fuchs, C.Z., New York: Movement Publication, 1986b.
37. Wassermann, E.M., Pascual-Leone, A. and Hallett M. Cortical motor representation of the ipsilateral hand and arm. *Exp. Brain Res*. 100: 121-132, 1994.
38. Weir, J.P., Housh, T.J. and Weir, L.L. Electromyographic evaluation of joint angle specificity and cross-training after isometric training. *J. Appl. Physiol.* 77: 197-201, 1994.
39. Zijdewind, I. and Kernell, D. Bilateral interactions during contractions of intrinsic hand muscles. *J. Neurophysiol.* 85: 1907-1913, 2001.
40. Zülch, K.J. and Müller, N. Associated movements in man. In: Handbook of Clinical Neurology Vol. 1, edited by Uniken, P.J. and Bruyn, G.W. New York: John Wiley & Sons, 1969.