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Sense of effort revisited: Relative contributions of sensory feedback and efferent copy

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HIGHLIGHTS

- Vibration was used to modulate sensory feedback during grip force matching task.
- Matching error exacerbated when right reference hand was vibrated and left matched.
- Matching error unchanged when left reference hand was vibrated and right matched.
- Contribution of sensory feedback significant for left hand/right hemisphere system.
- Contribution of sensory feedback minor for right hand/left hemisphere system.

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ABSTRACT

Although controversial, muscular effort perception is frequently attributed to the efferent copy of the associated motor command. While peripheral/sensory information is thought to be necessary for force modulation/control, it is not involved in initial force production. We recently showed in right-handers, that perception of effort was asymmetric for grasp-force tasks. This asymmetry was related to individual differences in right and left hand strength and an intrinsic component. A difference in gain (input/output magnitude relationship) for each limb/hemisphere system was proposed as the mechanism explaining intrinsic asymmetries. To further investigate the relative contributions of efferent copy and sensory feedback to the sense of effort, vibration was used to distort sensory information from the muscles providing the reference force. Visual feedback (vision) of the reference hand force was also manipulated. The absolute error (AE) was generally larger in the vision than no-vision condition and the influence of reference hand vibration was significant for left hand matching of the right hand reference force. However, this effect was negligible when matching in the reverse condition. These two results may reflect an interaction between two phenomena: (1) visual feedback, which represents the total output force may not be congruent with the internal representation of effort associated with the efferent copy and eventually the proprioceptive feedback; and (2) a vibration-induced larger AE for left than right hand contralateral matching indicates that the contribution of proprioceptive feedback to force matching is significant for the left but not the right hand/hemisphere system. Overall, it may be suggested that in right-handers, the sense of effort associated with the right hand may be primarily based on the efferent copy while the left hand/hemisphere system may use a combination of efferent copy and proprioceptive feedback. However, the weight of each type of information may depend on the association between motor command and representation of the execution of the motor command (visual vs. internal).

1. Introduction

The basis of our ability to judge force and weight has long been debated. The point of contention being whether force perception is based only on the corollary discharge or efferent copy of the descending motor command or the efferent copy modulated by peripheral sensory information. The classical, and still predominant view is that sense of effort is based on efferent copy [6,15,19]. However, the contribution of sensory information from cutaneous receptors, muscle spindles [3,20] and tendon organs [12,14] to the sense of force and force modulation [16,20] cannot be discounted. Carson et al. [6] acknowledged this fact by suggesting that the sense of force and sense of effort might potentially be separable sensory elements serving different sensorimotor functions. Regardless of

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this distinction, an important differentiation between efferent copy and sensory feedback is that the former only provides information about the input to muscles while the latter represents the outcome of muscle actions.

Further, the influence of muscle fatigue on force matching error [11,15] has corroborated the notion that force perception is predominantly modulated by a centrally mediated sense of effort. Specifically, these studies have shown that force/weight is perceived to be greater when an increased motor command is required to produce equivalent force. The reproduction of force by deafferented individuals is either used to dismiss/downplay the role of peripheral information in sense of effort mediation [18,19] or to propose that residual peripheral information [7,9,23] and/or acquired strategies based on any movement information [9,23] contribute to a sense of effort. In a new perspective Luu et al. [20] posit, “peripheral information is integral to the perception of heaviness”. In a contralateral weight matching study these authors found that halving of force production capability by fatigue or neuromuscular blocking resulted in a perceived doubling in weight by deafferented participants while healthy participants judged the force to be similar or lighter. These results were thought to be contrary to that expected of a centrally mediated sense of effort. The difference in perception/matching error between deafferented and healthy persons was interpreted as a modulation of the sense of effort by muscle proprioceptive feedback [20].

Since muscle spindles are extremely sensitive to vibratory stimuli [8,27,28], vibration-induced changes in proprioceptive signals should affect the perception of force associated with the reference hand and in so doing the force matching error. Furthermore, since each hand/hemisphere system is likely specialized in processing specific kinematic parameters [21,35] and utilizing a specific mode of control for motor activities, we can then presume those hand/hemisphere functional differences could be reflected in the utilization of sensory feedback to estimate muscular effort.

Additionally visual feedback, provided to establish the reference force and which represents the resulting force outcome, was assumed to be poorly associated with the internal representation of effort/force exertion in a simple matching task of short duration [1]. It was argued that visual feedback may be more closely associated with sensory than efferent copy information. Then, a lack of congruence between the two sources of information is presumed.

Therefore, the aims of this study were (1) to determine the extent to which muscle proprioceptive feedback contributes to the sense of effort and whether this sensory component contributes to asymmetry in the sense of effort, and (2) to determine whether force matching performance is influenced by the way in which the reference force level is acquired (with or without the contribution of a visual feedback).

2. Methods

2.1. Participants

Twenty-two (17 females; 5 males, mean age 26.2 ± 4.8 yrs) right-handed individuals with a mean laterality index of 0.83 ± 0.14 (range: 0.6–1), as determined by the Edinburgh Handedness Inventory [24], participated in the experiment. All participants were recruited from the local community and signed an informed consent form approved by the Human Investigation Committee at Wayne State University and Internal Review Board at the University of Michigan.

2.2. Experimental set-up and procedure

The experimental set-up and procedure were used previously [2]. Participants were instructed to match left and right reference grasp forces with the same (ipsilateral remembered – IR) and opposite (contralateral remembered – CR) hand. The only differences are in the use of visual feedback to establish the 20% MVC reference force and/or applying wrist vibration in specific sets of trials. Vibration was applied perpendicularly at a frequency of 60 Hz [8] to the distal tendons of finger flexor muscles of the reference hand (right or left) as illustrated in Fig. 1. Each handle was equipped with stain gauges. Force signals were sampled at 100 Hz.

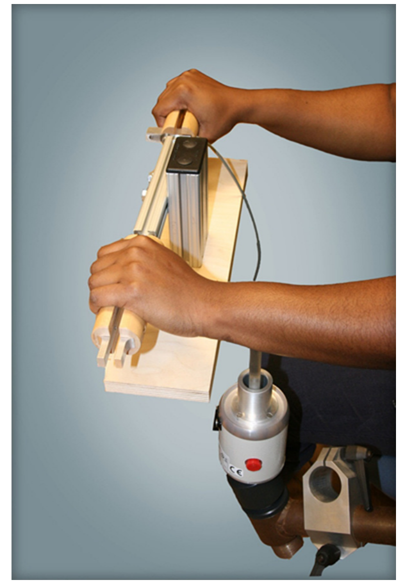

Fig. 1. Custom-designed grasp devices. Composed of a split aluminum force transducer embedded with strain gauges and equipped with semi-circular wooden handles (radius 4.0 cm, length 13 cm). The devices were held horizontally by a coupling support fixed to the table. Right hand flexor muscle vibration case illustrated.

A software-generated visual timer indicated when to provide the verbal commands to establish/release/match the reference force and indicate which hand. Experimental tasks were divided into four blocks using vibration (with, without) by visual feedback (with, without). Ten of the twenty-two participants completed all four experimental blocks; the others completed two blocks without vibration only. Blocks, reference hand and condition (IR, CR) were randomized across participants. However, trials (2 practice + 3 test) pertaining to the same scenario were performed consecutively.

2.2.1. Visual feedback mediation

Visual feedback of the reference force displayed on a screen was provided for 50% of the trials. Visual feedback was only available to establish and stabilize the reference force but never available during the match. For the no-vision scenario, a brief practice session was provided to learn how to establish the reference force with verbal quantitative cues only. Subjects were instructed to grasp the handle and establish the required grasp exertion within 2 s and then sustain the force for an additional 3 s. If variation from the intended grasp force during the holding phase was greater than 5%, an additional trial was requested. Within two–three practice trials, all participants learned to consistently exert the required force level based on effort perception. No matching occurred during this learning practice.

2.2.2. Proprioceptive information modulation

Vibration was applied for 4 s to the limb producing the reference force after the force level exceeded 15% MVC. Ten of the 22 participants completed the trials with vibration. Vibration was never applied to the matching hand since it would have modified the force