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The contribution of non-digital afferent signals to grip force adjustments evoked by brisk unloading of the arm or the held object

F. Danion *

UMR 6152 "Mouvement et Perception", Université de la Méditerranée, CNRS, Faculté des Sciences du Sport, 13 288, Marseille, France

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Abstract

Objective: Earlier studies suggest that grip force adjustments evoked by mechanical perturbations result more from cutaneous signals from the fingertips, than from afferent signals from the supporting limb. Generally an increase in tangential load at the fingertips induces an increase in grip force, whereas a decrease in load induces the opposite reaction. Some data suggest that prior knowledge and experience influences the magnitude of grip force adjustments.
Methods: This study examines the relative contribution of digital and arm afferent signals in the context of brisk involuntary upward flexions obtained either by unloading the arm (ARM) or the held object (OBJECT). Following the perturbation, the tangential load at the fingertips increased in ARM, but decreased in OBJECT. A subsidiary goal was to compare the performance of naïve subjects with the performance of trained and informed subjects.
Results: When the perturbation was completely unexpected, grip force increased sharply after OBJECT and ARM unloading. By contrast, when subjects had prior knowledge and experience with the upcoming perturbation, grip responses were clearly differentiated; grip force increased after ARM, but decreased after OBJECT.
Conclusions: These results challenge the view that cutaneous signals of the fingertips are the driving signals of grip force responses. Instead, afferent signals from the flexed arm would account well for the lack of difference between grip force responses in ARM and OBJECT under unpredictable conditions. These data provide clear evidence that prior knowledge and experience influences reactive grip force control, since subjects became able to repress unnecessary grip force modulation in OBJECT.
Significance: These data have implications for understanding the initiation and the modulation of grip force adjustments.

Keywords: Grip force; Reactive control; Human; Mechanical perturbation; Afferent signals; Central set

1. Introduction

Grip force adjustments evoked by mechanical perturbations have been widely studied (Johansson and Westling, 1988; Cole and Abbs, 1988; Winstein et al., 1991; Johansson et al., 1992a,b; Eliasson et al., 1995; Häger-Ross and Johansson, 1996; Harrison et al., 2000; Ohki et al., 2002; Mrotek et al., 2004). Some studies have specifically examined the nature of the afferent signals driving those grip force responses. Converging evidence suggests a massive contribution of fingertips cutaneous signals as compared to afferent signals from the supporting limb. First, it has been demonstrated that grip force responses were substantially reduced when the digital pulp was anesthetized (Cole and Abbs, 1988; Johansson et al., 1992c; Häger-Ross and Johansson, 1996), or when loads were delivered directly to the hand (Cole and Abbs, 1988). Second, to evaluate the contribution of non-digital afferent input, Häger-Ross and Johansson (1996) have compared grip force adjustments induced by perturbing the posture of the upper limb in different conditions of arm and hand support, but grip force responses were not markedly influenced. Last, direct recordings from hand muscle-spindles or tendon-organs

* Tel.: +33 04 91 17 22 78; fax: +33 04 91 17 22 52.
E-mail address: frederic.danion@univmed.fr

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showed that they did not respond to the load forces before the onset of the automatic grip response (Macefield and Johansson, 1996). Despite converging evidence, the contribution of non-cutaneous signals cannot be completely ruled out for the following two reasons. First, grip force responses were not always abolished by digital anaesthesia (Cole and Abbs, 1988; Johansson et al., 1992c; Häger-Ross and Johansson, 1996). Second, the induced movements of the supporting limb were rather small (3 mm in Johansson et al., 1992c; 4 mm in Häger-Ross and Johansson, 1996) thereby limiting the contribution of muscular afferent signals. The goal of the present study is to examine the possible contribution of non-digital signals in the context of larger postural perturbations of the supporting limb.

In order to elicit noteworthy changes in muscular arm afferent signals, we got inspiration from a well established behaviour: unexpected unloading of the elbow joint results in a brisk deflection of the arm (Asatryan and Feldman, 1965; Crago et al., 1976; Forget and Lamarre, 1995; Biryukova et al., 1999; Diedrichsen et al., 2003). Practically, our subjects were asked to hold an object, while a brisk deflection of the arm was elicited in two different ways. A first type of unloading consisted in releasing a substantial load suspended under the grasped object (OBJECT), whereas the second one consisted in releasing a substantial load suspended under the forearm (ARM). In ARM, the brisk upward movement resulted in sharp increase in load. In OBJECT, the movement related load-component also increased, but the overall change was an abrupt decrease in load due to the substantial drop in the object mass. Consequently the resulting profile of shear forces at the digital pulp was different depending on the unloading condition: increasing in ARM, and decreasing in OBJECT. Considering that digital cutaneous signals convey unambiguous information about shear forces (Paré et al., 2002), and that grip force responses mediated by those signals are usually selective with respect to increase and decrease in shear forces (Winstein et al., 1991; Häger-Ross et al., 1996; Mrotek et al., 2004), we assumed that subjects should respond selectively to OBJECT and ARM perturbations if digital signals remains critical in the context of brisk elbow flexion. By contrast, if grip force reactive control starts to rely predominantly on afferent signals from the supporting limb, we hypothesized that subjects should exhibit similar grip force responses in OBJECT and ARM conditions.

A subsidiary goal of the present study was to investigate the influence of prior knowledge and experience on grip force responses. A recurrent observation in studies investigating motor adjustments induced by mechanical perturbations is that subject's responses are largely dependent upon prior knowledge about the forthcoming perturbation (Latash et al., 1993; Winstein et al., 2000; Shimura et al., 2001; Ohki et al., 2002; Blouin et al., 2003; Vallis and Patla, 2004). This phenomenon, referred as a "central set effect" (Evarts et al., 1984), enables descending commands to preset aspects of response in advance of a stimulus. Although the influence of central set has been largely documented for reactive postural control (Horak et al., 1989; Horak and Diener, 1994), only two studies addressed specifically this issue on grip force reactive control (Winstein et al., 1991, 2000). These studies showed that grip force responses were somewhat larger when the magnitude of the upcoming load was unpredictable (Winstein et al., 2000), or when the subjects were instructed to "resist" as compared to "let go" (Winstein et al., 1991). However the differences were statistically marginal, and clearer evidence of a central set effect on grip force responses remains to be found. To investigate further the possibility of a central set effect, grip forces responses induced by OBJECT and ARM unloading were investigated in a group of naïve and untrained subjects and compared to another group of subjects that received prior knowledge and experience with each perturbation type.

2. Method

2.1. Subjects

Two experiments were successively performed. Each of these experiments was performed by a group of eleven unpaid healthy volunteers. In the first experiment (UNPREDICT), the group of subjects was composed of eight males and three females (33.7 ± 9.3 year of age); the mean body height and mass were, respectively, 1.73 ± 0.06 m and 67.5 ± 8.4 kg. In the second experiment (PREDICT), the group was composed of nine males and two females (29.6 ± 6.1 year of age); the mean body height and mass were, respectively, 1.76 ± 0.08 m and 68.5 ± 8.2 kg. All of them were right-handed according to their preferential use of the right hand during writing and eating (excepted one subject who was ambidextrous). The subjects had no previous history of neuropathies or trauma to the upper extremities. All the subjects gave informed consent according to the procedures approved by the Mediterranean University. Studies were approved by the local ethical committee.

2.2. Apparatus

Five unidirectional sensors (ELPM-T1M-25N, Entran) were used for finger force measurement. Each sensor measured the normal force component (i.e., force perpendicular to the sensor's surface). The sensors were mounted on an aluminum handle (see Fig. 1A). The configuration of the sensors was identical for all subjects, with the thumb (one side) in opposition to the remaining four fingers (other side). Sensors were distributed 25 mm apart in the direction of finger adduction–abduction. This configuration felt comfortable for all the subjects. The surface of each transducer was covered with sandpaper (80 grain/cm^2). Another force sensor (ELPM-T1M-50N, Entran) was mounted underneath the grip apparatus. On the lower part of this sensor, an electromagnet (5.11.05, Mecalectro, 35N) was used to suspend an extra load. A manual switch connected to the electromagnet allowed the experimenter to release