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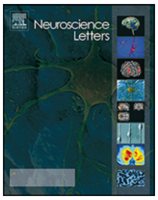


Proprioception: Bilateral inputs first

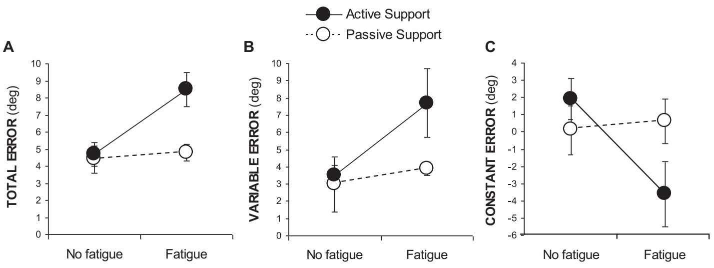
Matthieu P. Boisgontier[a,b,*], Vincent Nougier[a]

[a] UJF-Grenoble 1/CNRS/TIMC-IMAG UMR 5525, Grenoble, F-38041, France
[b] Motor Control Laboratory, Research Center for Movement Control and Neuroplasticity, Group Biomedical Sciences, KU Leuven, Leuven 3000, Belgium

HIGHLIGHTS

- Proprioceptive weighting gives priority to bilateral over unilateral inputs.
- The fatigue effect is stronger in bilateral muscle contractions.
- Effects of muscle fatigue are weaker in passive relative to active joint position sense.

GRAPHICAL ABSTRACT



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ABSTRACT

The present study focused on assessing whether the effects of muscle fatigue on joint position sense are dependent upon the unilateral or bilateral nature of proprioceptive inputs. To this aim, a group of young adults performed an active contralateral concurrent ankle matching task in two conditions of support of the reference limb (active vs. passive) and two conditions of fatigue of the indicator limb (no fatigue vs. fatigue). In the absence of muscle fatigue, results failed to evidence significant difference of matching errors between the active and passive conditions of support. However, in the context of muscle fatigue, increased matching errors were observed in active but not passive condition of support. The deleterious effects of muscle fatigue on joint position sense were therefore dependent upon the laterality of the proprioceptive inputs related to muscle contraction. These results suggested that sensory weighting for proprioception gives priority to inputs available bilaterally over the ones available in a single limb only.

1. Introduction

Proprioception is the perception issued from the central processing of information coming from proprioceptive receptors and motor cortical areas [6]. This perception reports the relative position of body segments in relation to each other and to the environment. The processing of such information in the somato-sensory cortical areas allows perception of body kinematics. More precisely, this perception stems from an afferent component related to information gathered by: (1) muscle spindles which have been assigned a prominent role in proprioception and provide information about muscle stretch [19], (2) Golgi tendon organs especially sensitive to contractile forces [16], (3) skin receptors [9] and (4) joint receptors whose proprioceptive contribution is thought to be minor [25]. Proprioception also stems from efferent signals derived from motor commands of cortical areas involved in planning and executing a motor act. These signals are transmitted to somato-sensory areas involved in processing the resulting sensations.

One of the main methods used to assess proprioception is the contralateral concurrent joint position matching task [5,6]. In this task, a subject's limb is displaced to a reference position. While this reference limb is actively or passively maintained in a reference position, the subject is asked to actively replicate this position with the contralateral limb (i.e., the indicator) on the basis of concurrent

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Abbreviations: TE, total error; VE, variable error; CE, constant error; VAS, visual analogue scale.

* Corresponding author at: Department of Biomedical Kinesiology, Research Center for Movement Control and Neuroplasticity, Katholieke Universiteit Leuven, Tervuurse vest 101, 3000 Leuven, Belgium. Tel.: +32 16329098; fax: +32 16 329197.

E-mail address: Matthieu.Boisgontier@faber.kuleuven.be (M.P. Boisgontier).

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proprioceptive information of the two limbs and without visual feedback.

To perceive the position of both limbs when performing the contralateral concurrent matching task, the brain computes the weighted sum of all available information related to this perception [29]. Two possible strategies could then be considered: (1) to weight the proprioceptive inputs (muscle spindles, Golgi tendon organs, skin and joint receptors, efferent signal) regardless of the unilateral or bilateral nature of these inputs or (2) to weight the proprioceptive inputs according to their laterality nature.

No previous study aimed at assessing whether the brain was using one or the other strategy. One possibility to unmask this strategy is to assess the proprioceptive system in the context of muscle fatigue. Most of the previous studies using the contralateral concurrent matching task to assess proprioception showed a deleterious effect of muscle fatigue on joint position sense [2–4,10–13,21,26–28] but some others failed to demonstrate such an effect [7,12,24,27,28]. We suggested that the discrepancy reported in these previous studies using active matching tasks could be related to the active or passive condition of support of the reference limb which are associated to differences in laterality of the proprioceptive information (unilateral vs. bilateral). Indeed, most of the results demonstrating an effect of muscle fatigue were observed when the reference limb was active [2,4,10,11,13,21,27,28]. Conversely, all the results that failed to evidence an effect of muscle fatigue were observed when the reference limb was passive [7,12,24,27,28]. Nevertheless, the only experiments that could be linked to an effect of support on joint position sense in a single sample of participants were performed at the elbow [3,27]. Unfortunately, these latter results did not lead to any conclusion. Indeed, one of these studies did not report any effect of limb support [3] whereas the other one showed an effect of support with greater constant errors after fatigue of the elbow muscles when the reference forearm was active but not when it was passive [27].

The present study proposed to test whether the effects of muscle fatigue on joint position sense were dependent upon the unilateral or bilateral nature of the proprioceptive inputs. To this aim, participants performed a contralateral concurrent ankle matching task in two conditions of support of the reference limb (active vs. passive) and two conditions of fatigue of the indicator limb (fatigue vs. no fatigue). It was hypothesized that (1) laterality of the available proprioceptive information (unilateral vs. bilateral) would have no significant effect on ankle joint position sense in the absence of muscle fatigue of the indicator limb but that (2) addition of muscle fatigue would reveal a sensory weighting strategy based on the laterality nature of the inputs.

2. Materials and methods

2.1. Participants

Fourteen young healthy adults (age: 22 ± 2 years; weight: 54 ± 2 kg; height: 162 ± 8 cm; mean ± SD) participated in the study. Leg dominance was an inclusion criterion. To identify the dominant leg, participants were asked their preference for kicking a ball towards a target [18]. All participants indicated their right leg as their dominant leg. All participants gave written informed consent before undertaking the experiment which was conformed to the declaration of Helsinki (1964).

2.2. Apparatus and materials

Joint position sense performance was measured with an apparatus and a setup previously described [5,6]. To explain it briefly, participants were seated barefoot with the feet secured onto two rotating lightweight paddles. Two precision linear potentiometers attached to each paddle provided analogue voltage signals which were converted into angular displacements proportional to ankle angles. Participants held a switch in the dominant hand to record the trial.

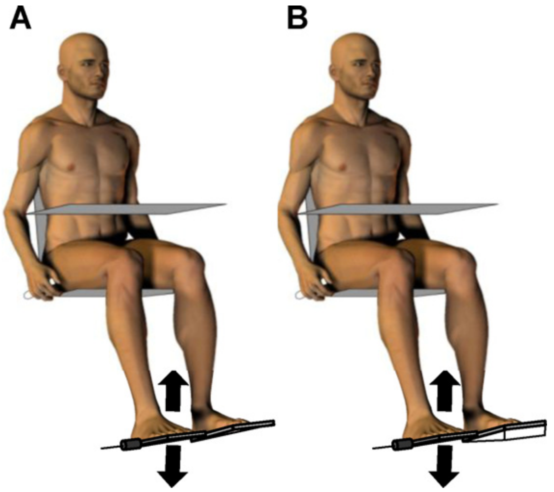

Fig. 1. Setup for the contralateral concurrent ankle joint position matching task in active (A) and passive (B) conditions of support of the reference. Black arrows stand for the possible motion of the indicator foot.

2.3. Procedure

To assess the ankle joint position sense, participants performed a contralateral concurrent matching task. Before each condition of this matching task, both ankles were conditioned with a voluntary contraction of ankle plantarflexors and dorsiflexors to control for muscle history effects [14]. For this conditioning, participants placed both feet between the floor and a fixed horizontal block and were asked to push downwards onto the floor for 2 s with an half-maximal contraction, to relax for 2 s and to push upwards onto the block for 2 s. Participants were then asked to relax their lower limbs. The initial feet position was 40 ± 0.1° under horizontal. Next, one experimenter positioned the reference foot at a 10 ± 0.1° position above horizontal, corresponding approximately to a 10° plantarflexion target position. This reference position was chosen to minimize the potential proprioceptive feedbacks issued from skin and joint receptors [8]. A verbal "ready" command alerting participants of the trial's beginning came immediately after the positioning of the reference limb. After a 2 s delay and the verbal command "go", the participants had to actively estimate the reference position with the indicator foot at a self-paced speed. Participants were instructed to indicate that they had reached a satisfactory matching by pressing the switch registering the performance. After each trial, the indicator foot returned to the initial position whereas the reference foot remained in position for the five trials of the considered condition. Reference and indicator feet were the non-dominant and dominant, respectively. This procedure was performed in two conditions of support and two conditions of fatigue of the indicator limb (active + no fatigue; active + fatigue; passive + no fatigue; passive + fatigue). In the condition of active support (Fig. 1A), the reference ankle was actively maintained in position by the participant. In the condition of passive support (Fig. 1B), the reference ankle was passively maintained on a block and participants were instructed to maintain this foot relaxed throughout the duration of the trial. To ensure that participants remained relaxed during and after positioning of their reference ankle, a physical therapist experimenter continuously checked visually the absence of muscle contraction in the reference muscles and provided feedback to the participants when they were not relaxed. The main motors of dorsiflexion and plantarfelxion were the muscle tibialis anterior and the gravity, respectively. Therefore the main muscle to be controlled was the tibialis anterior which is under the skin on a large area. During pre-tests coupling visual control of muscle inactivity and electromyography, the visual control appeared to be sensitive enough to control for muscle inactivity. The no fatigue conditions were performed first to ensure the absence of fatigue; the conditions of support were counterbalanced. Before the experiment, participants received specific instructions on how to perform the experimental tasks and performed a 5 min familiarization session. For each condition, five trials were recorded for a total of 20 trials per participant.

2.4. *The fatiguing exercise*

The effects of muscle fatigue on joint position sense have shown to be independent of the fatigued muscle group, i.e., agonist or antagonist [20]. Therefore, to avoid positioning errors arising from the muscles' inability to reach the reference position due to insufficient torque, fatigue of plantarflexor muscles was preferred to fatigue of dorsiflexors. To induce unilateral ankle proprioceptive alteration through plantarflexors muscle fatigue at the indicator limb, participants performed the single leg standing heel rise test [17] to the point of volitional failure. In this test, participants stand straight to rise and lower on the toes of their dominant foot as many times as possible following the beat of a metronome (40 beats/min). Verbal encouragement was given to ensure that participants worked maximally. The exercise stopped when participants were no longer able to stand on the toes, demonstrating actual fatigue of contractile force (after 103 s on average). Immediately after each exercise, participants were instructed to estimate their degree of calf fatigue and to rate their estimate using a visual analogue scale (VAS) [1]. Muscle fatigue was assessed after each exercise session by recording the VAS cursor placement. Participants were not informed about their VAS scores. The fatigue task was repeated prior to each matching trial in the two conditions of fatigue (i.e., 10 times).

2.5. *Data analysis*

Three dependent variables were used to assess the matching performance: the total variability also called total error (TE), the variable error (VE) and the constant error (CE) [22]. The absolute error (AE) and TE are dependent variables which are both used to measure the overall performance. However, AE is a complex combination of response variability and bias that makes difficult the determination of the relative contribution of each component [23]. Since TE is always an exact combination of the response variability and bias (namely, $\mathrm{TE}^2 = \mathrm{VE}^2 + \mathrm{CE}^2$) [15], this type of error was preferred to AE to measure the overall performance in the present study. TE's formula is $\sqrt{\left(\sum (x_i - T)^2/n\right)}$, with x_i the score on trial i, T the reference and n the number of trials the participant performed. VE was used to measure the spread about participant's own average, i.e., the intra-individual variability. Its formula is $\sqrt{\left(\sum (x_i - M)^2/n\right)}$, with M the participant's average score. CE was used to measure the response bias. Its formula is $\sum (x_i - T)/n$. Negative CE indicated that the indicator foot undershot the reference position whereas positive CE indicated that the indicator foot overshot the reference position.

2.6. *Statistical analysis*

For the analysis of errors in the fatigued and non fatigued young adults, two support (active vs. passive) × two fatigue (no fatigue vs. fatigue) analyses of variance (ANOVAs) with repeated measures on both factors were applied to the three types of matching errors (TE, VE and CE). For all ANOVAs, post hoc pairwise testing (Tukey Honestly Significant Difference) was used whenever necessary. The level of significance was set to $P < 0.05$. The purpose of these ANOVAs was to determine if joint position sense was differently altered by muscle fatigue depending on the condition of support.

3. Results

A Kolmogorov–Smirnov test of equality of variances first showed that the distributions used for the analysis did not depart from normality ($P > 0.05$).

Analysis of TE showed significant main effects of support ($F_{1,13} = 8.93$, $P = 0.010$) and fatigue ($F_{1,13} = 5.36$, $P = 0.038$). The interaction of support × fatigue was also significant ($F_{1,13} = 10.93$, $P = 0.010$). The decomposition of the interaction into its simple main effects demonstrated that participants exhibited a greater TE in the condition associating active support of the reference and muscle fatigue of the indicator as compared to the other conditions ($P < 0.01$) (Fig. 2A).

Analysis of VE failed to demonstrate significant main effect of support ($F_{1,13} = 3.23$, $P = 0.095$) but showed a significant main effect of fatigue ($F_{1,13} = 6.01$, $P = 0.029$) with greater VE in the context of muscle fatigue. The interaction of support × fatigue ($F_{1,13} = 2.75$, $P = 0.121$) was not significant (Fig. 2B).

Analysis of CE showed no significant main effects of support ($F_{1,13} = 0.43$, $P = 0.525$) and fatigue ($F_{1,13} = 2.60$, $P = 0.131$). However, the interaction of support × fatigue was significant ($F_{1,13} = 6.66$, $P = 0.023$). The decomposition of the interaction into its simple main effects showed that participants exhibited a greater CE in the fatigue condition when the reference was active relative to passive ($P < 0.05$) (Fig. 2C).

Participants rated their muscle fatigue as "extremely strong" with VAS ratings of 9.0 ± 0.7 and 8.9 ± 0.5 out of 10.0 for the active and passive support conditions, respectively.

4. Discussion

The present study proposed to test whether the sensory weighting process of proprioception gives inputs priority on the basis of their laterality nature (unilateral vs. bilateral). To this aim, a group of young adults performed a contralateral concurrent ankle matching task in two conditions of support of the reference limb (active vs. passive) and two conditions of fatigue of the indicator limb (fatigue vs. no fatigue). The results failed to demonstrate any difference of joint position sense between the active and passive conditions of support when participants were not fatigued. However, in the context of muscle fatigue, increased matching errors were observed in the active but not the passive condition of support.

4.1. *Active reference – active indicator*

When the reference limb was actively maintained, all proprioceptive inputs were available for both limbs (muscle, skin and joint information). The fatigue effect observed in the active condition of support confirmed all previous studies assessing the effect of muscle fatigue on joint position sense at the lower [3,10,11,13] and upper limbs [2–4,21,27,28] in this condition of support.

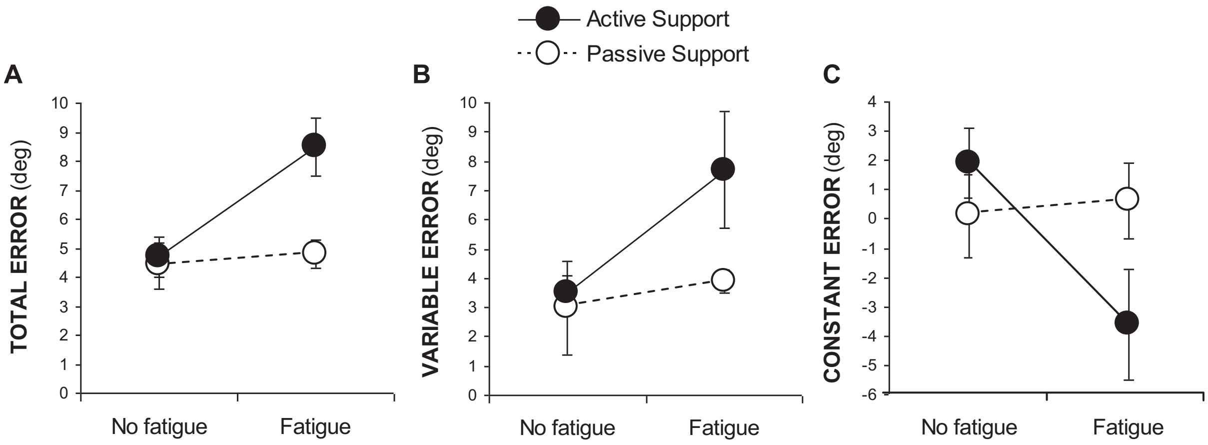

Fig. 2. Total error (A), variable error (B) and constant error (C) in active (black circles) and passive (white circles) conditions of support as a function of fatigue conditions (no fatigue vs. fatigue) (mean ± standard error of the mean).

4.2. *Passive reference – active indicator*

In the passive condition of support, the proprioceptive information related to the muscle contraction issued from the Golgi tendon organs and the motor areas was missing for the reference limb. The absence of significant effects of muscle fatigue in this passive condition of support was consistent with most of the previous studies assessing the effects of muscle fatigue on joint position sense in this condition of support [7,12,24,27,28]. In a passive support condition, Fortier et al. [12] failed to evidence an effect of muscle fatigue after isometric and eccentric exercises but did show an effect after a concentric exercise. This latter result could be explained by the active positioning of the reference elbow. Indeed, this active positioning provided proprioceptive information related to the level of muscle contraction required to reach the reference position. As discussed in the last section, this information could have altered the sensory weighting of proprioceptive information. The study of Vuillerme et al. [26] also showed a fatigue effect with passive support of the reference limb but did not check whether the reference was actually passively maintained.

4.3. *Active vs. passive support of the reference limb*

Results of the present study showed that joint position sense at the lower limbs was more sensitive to an effect of muscle fatigue in the indicator limb when both limbs were active. This result was consistent with the study of Walsh et al. [27] assessing elbow joint position sense. In this study, fatigue of elbow flexors induced greater constant errors when the reference forearm was actively maintained but not when it was passively maintained. In addition, the results of Allen et al. [3] in an elbow matching task also showed a tendency in the direction of greater constant errors in active relative to passive condition of support.

Despite a similar trend in the effect of support on TE and VE (Fig. 2A and B), a significant fatigue × support interaction was observed for TE, only. The absence of significant interaction for VE could be explained by the presence of two distinct behaviours in the condition of active support. Indeed, as illustrated in Fig. 3, participants could be divided into two subgroups: A consistent subgroup ($n = 10$) with participants showing similar performances in no fatigue and fatigue conditions (Fig. 3A) and an inconsistent subgroup ($n = 4$) demonstrating a strong increase in VE from the no fatigue to the fatigue condition (Fig. 3B). These different behaviours could reflect different levels of confidence across participants as empirically reported at the end of the experiment: The lower confidence reported in the matching performance, the greater the intra-individual variability.

Fatiguing the dorsiflexor (agonist) rather than the plantarflexor (antagonist) muscles could have yielded a fatigue effect in the passive condition as well. However, the results of Allen et al. [3] that also fatigued the agonist muscles suggested that the effect of muscle fatigue would still have been greater in the active condition.

4.4. *Brain's strategy to match limb positions*

The sensory weighting model proposed that a perception results from the weighted sum of all available information related to this perception [29]. Within this context, we considered two

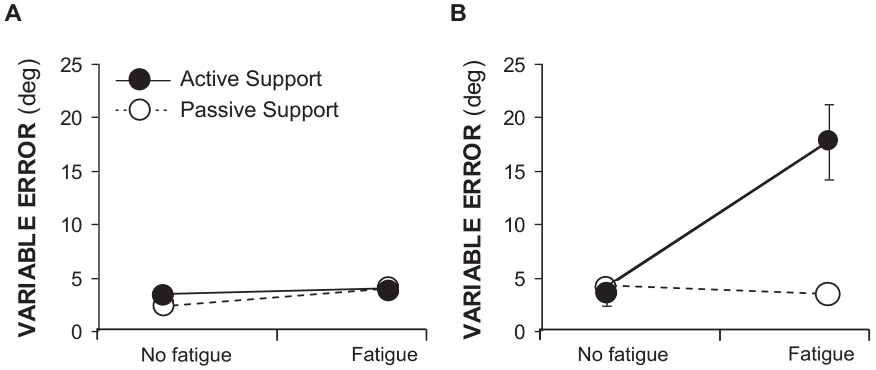

Fig. 3. Variable error for the consistent ($n = 10$) and inconsistent ($n = 4$) subgroups in active (black circles) and passive (white circles) conditions of support as a function of fatigue conditions (no fatigue vs. fatigue) (mean ± standard error of the mean).

hypotheses regarding the strategy the brain could use to weight the proprioceptive inputs in a contralateral concurrent matching task: (1) to weight the proprioceptive inputs (muscle spindles, Golgi tendon organs, skin and joint receptors, efferent signal) regardless of the unilateral or bilateral nature of these inputs or (2) to weight the proprioceptive inputs according to their laterality nature.

Considering the first hypothesis, the estimated position of the fatigued indicator limb would likely be degraded in the same way regardless to the support condition of the reference limb. In addition, removing proprioceptive information related to the muscle contraction of the reference limb (passive condition) would likely degrade its position estimate. However, the results of the present study did not show any degradation of proprioceptive performance in the passive as compared to the active condition of support. On the contrary, in the fatigue condition, the results showed decreased errors when the reference was passively maintained. Therefore, the strategy described in this first hypothesis was likely not the one the brain chose to perform the contralateral concurrent matching task.

The proprioceptive inputs related to the contraction state are critical with regards to the second hypothesis. Indeed, these inputs are bilateral in the active condition of support (contraction vs. contraction) and unilateral in the passive condition of support (contraction vs. no contraction). If greater weight was allocated to unilateral inputs, the matching would have been degraded in the passive condition, which was not the case. Indeed, the better performance observed in the passive condition of support suggested that the weighting process of proprioception gives priority to bilateral inputs. Therefore, together with the upper-limbs study of Walsh et al. [27], results of the present study at the lower limbs supported a weighting strategy which gives priority to bilateral proprioceptive inputs. The facts that all the results that failed to show an effect of muscle fatigue were observed when the reference limb was passively maintained [7,12,24,27,28] and that most of the results showing an effect of fatigue were observed when the reference limb was actively maintained [2,4,10,11,13,21,27,28] also support the second hypothesis.

To conclude, together with the literature, the results of the present study suggested that when intending to position one limb in the same position as the other one, the brain uses sensory weighting that gives priority to proprioceptive inputs available bilaterally over the ones available in a single limb only.

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