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Sensory and Motor Systems

Seeing Your Foot Move Changes Muscle Proprioceptive Feedback

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Abstract

Multisensory effects are found when the input from single senses combines, and this has been well researched in the brain. Presently, we examined in humans the potential impact of visuo-proprioceptive interactions at the peripheral level, using microneurography, and compared it with a similar behavioral task. We used a paradigm where participants had either proprioceptive information only (no vision) or combined visual and proprioceptive signals (vision). We moved the foot to measure changes in the sensitivity of single muscle afferents, which can be altered by the descending fusimotor drive. Visual information interacted with proprioceptive information, where we found that for the same passive movement, the response of muscle afferents increased when the proprioceptive channel was the only source of information, as compared with when visual cues were added, regardless of the attentional level. Behaviorally, when participants looked at their foot moving, they more accurately judged differences between movement amplitudes, than in the absence of visual cues. These results impact our understanding of multisensory interactions throughout the nervous system, where the information from different senses can modify the sensitivity of peripheral receptors. This has clinical implications, where future strategies may modulate such visual signals during sensorimotor rehabilitation.

Key words: fusimotor drive; human; kinesthesia; movement perception; muscle proprioception

Significance Statement

It is well known that multisensory processes occur in the brain, yet we know little about the consequences of multisensory interactions at the spinal level. We recorded from single muscle afferents, while participants either saw or did not see their foot moving. We show that adding visual information reduces muscle afferent firing, probably via descending commands by fusimotor efference. These results impact sensorimotor rehabilitation, where clinical strategies using exercises without visual feedback may promote proprioceptive training.

Introduction

Perception is multimodal by nature and the CNS integrates multiple sensory sources to produce coherent percepts (Kavounoudias, 2017). Combining spatially and temporally congruent multisensory cues is beneficial (Stein and Stanford, 2008), where combined vision and muscle proprioception can improve perceptual or motor

responses (Tardy-Gervet et al., 1986; Rossetti et al., 1995; Van Beers et al., 1999; Sober and Sabes, 2003; Reuschel et al., 2010; Guerraz et al., 2012; Blanchard et al., 2013). These studies have shown that convergent inputs must be integrated properly to assess body configuration and any changes that may occur. Computational modeling, in particular the theoretical Bayesian framework, provides

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such an approach to predict perceptual enhancement due to multisensory integration, by postulating that the multisensory estimate of an event is given by the reliability-weighted average of each single-cue estimate (Ernst and Banks, 2002; Landy et al., 2011). Bayesian predictions have shown the optimal integration of vision and proprioception when evaluating arm movements (Reuschel et al., 2010), positions in space (Van Beers et al., 2002; Holmes and Spence, 2005; Tagliabue and McIntyre, 2013), and in performing pointing motor tasks (Sober and Sabes, 2003).

Interactions between sensory systems are found in the brain, including in the early stages of sensory information processing (Kavounoudias et al., 2008; Cappe et al., 2009; Hagura et al., 2009; Helbig et al., 2012; Klemen and Chambers, 2012). The sensitivity of muscle afferents can be modulated via central efference, which may mean that the periphery is subject to multisensory influences. The fusimotor system sends efferent γ -motoneurons from the spinal cord to the intrafusal fibers of muscle spindles (Awiszus and Schäfer, 1989; Murphy and Martin, 1993; Ellaway et al., 2002, 2015), where the positional sensitivity of muscle afferents is changed by γ -static fusimotor neurons and their velocity sensitivity by γ -dynamic fusimotor neurons (Matthews, 1981).

Since direct recordings of γ efferents are rare in humans (Ribot et al., 1986), the influence of the fusimotor drive is classically assessed by recording the activity of single muscle afferents, whose modulation can likely be indirectly supported by a change in the fusimotor drive. Through this approach, microneurographic studies have shown that the fusimotor drive can influence muscle afferent firing depending on the attentional (Hospod et al., 2007; Ribot-Ciscar et al., 2009) or emotional (Ackerley et al., 2017) context. Hospod et al. (2007) showed a decrease in the dynamic sensitivity of primary muscle afferents when a participant's attention was selectively directed to the recognition of an imposed, complex, two-dimensional movement. Conversely, muscle afferent dynamic sensitivity has been observed to increase when the proprioceptive attention task was specifically oriented towards the movement velocity (Ribot-Ciscar et al., 2009). These studies show an independent static or dynamic fusimotor control of muscle spindle sensitivity in humans, which depends on the behavioral context.

There are few studies on the influence of vision on muscle proprioceptive sensitivity via the fusimotor drive.

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Wessberg and Vallbo (1995) compared muscle afferent activity from the hand during a visual tracking task that consisted of following a target displayed on a screen; during the reproduction of the same movement in the absence of visual control, no difference was reported. In contrast, Jones et al. (2001) showed that muscle afferent activity decreased in a visuo-motor adaptation task, where the displacement of a visual target was shifted, making the visual information incongruent with proprioceptive information from the moving hand. The decrease in proprioceptive sensitivity was interpreted as a strategy for resolving bisensory conflict. More recently, Dimitriou (2016) showed that the muscle spindle firing varied with adaptation state independently of muscle activity, making the γ system a specific contributor to motor learning.

In these previous studies, vision was not directed towards the participant's own moving body, but towards a visual target (displaced by the participant's moving hand). In addition, these studies used active, rather than passive movements. Active movements are more representative of natural body conditions; however, passive movements are ideal to address muscle spindle sensitivity in the absence of concomitant activation of skeletomotor neurons (α - γ coactivation). Presently, we investigated whether seeing your own foot move passively altered muscle proprioceptive feedback and how it might be related to perceptual performance. We designed a behavioral experiment to test whether movement amplitude discrimination was better when participants viewed their foot moving, as compared to only having muscle proprioception when participants kept their eyes closed. Further, we examined changes in muscle spindle sensitivity to similar passively-imposed foot movements, varying both vision and attention, where we hypothesized that muscle afferent firing would be modulated over these conditions.

Materials and Methods

The present experiments were performed on healthy human volunteers [human subjects were recruited at Aix-Marseille University], where written, informed consent was obtained and a random experimental design was used. The study was approved by the local ethics committee [Comité de protection des personnes Sud-Méditerranée I, Marseilles] and performed in accordance with the Declaration of Helsinki. The study consisted of two series of experiments to investigate the multisensory effects of visual and proprioceptive processing: one using behavioral psychophysics and the other using the *in vivo* technique of microneurography. Fifteen volunteers (two males; 26 years \pm 5 SD) took part in the first behavioral experiment, and 13 (seven males; 26 years \pm 6 SD) different volunteers took part in the second microneurographic experiment.

General experimental set-up

In both experiments, the participants were seated in a semi-reclined armchair with their legs positioned in cushioned grooves, so that a standardized position could be maintained without muscle activity. The knee joint was at a flexion angle of \sim 120–130°. The right foot rested on a stationary plate and the left foot rested and was held on a pedal connected to a computer-controlled robot, allowing

sinusoidal foot plantar flexion/dorsiflexion movements to be imposed. The absence of concomitant muscle activity was monitored throughout the two experiments by recording surface electromyography (EMG). A pair of surface electrodes (Ag–AgCl, interelectrode distance 2 cm) was placed over the tibialis anterior (TA) and another pair on gastrocnemius soleus (GS) muscle bellies during the behavioral experiment. In the microneurographic experiment, pairs of surface electrodes were placed over the TA [corresponding to afferents originating in TA and extensor digitorum longus (EDL) muscles] and peroneus longus (PL; corresponding to afferents originating in PL) muscle bellies. The location of each pair of electrodes was defined by asking the participant to isometrically contract the muscle under consideration and palpation of the muscle belly. The EMGs were band-pass filtered (30–3000 Hz), recorded with a high gain (5000×), and sampled at 10 kHz. Autonomic responses were recorded through electrodermal activity (EDA), using two surface electrodes placed on each side of the left hand (gain: 500×, band-pass: 0.1–100 Hz, sampling frequency: 500 Hz). Physiological data were stored on a digital tape recorder (DTR 1802, Biologic) and processed off-line in Spike2 (Spike2 Software, RRID:SCR_000903). During all experiments, participants wore noise-cancelling headphones (Bose) to prevent extraneous sounds.

Unitary muscle afferent recordings

The *in vivo* technique of microneurography was used to record from the left common peroneal nerve at the popliteal fossa in humans (Hagbarth and Vallbo, 1968; Bergenheim et al., 1999). The nerve was located by palpation. Unitary muscle afferent activity was recorded differentially using an insulated tungsten microelectrode (impedance 0.3–1 MΩ, tip diameter ~5 μm, length ~30 mm; FHC). The recordings were monitored continuously using an oscilloscope and a loudspeaker. Neural activity was amplified (100,000×) and band-pass filtered (300–3000 Hz) to ensure an optimal signal-to-noise ratio and sampled at 20 kHz. Muscle afferents were identified as primary endings on the basis of their irregular spontaneous activity, their high dynamic sensitivity to ramp-and-hold movements, and their silencing during passive muscle shortenings (Edin and Vallbo, 1990). The activity from 24 single muscle spindle endings (21 Type Ia muscle afferents and three Type II) was recorded, but due to a loss of unit stability over time in some recordings, we gained full datasets over all conditions (vision, no vision, attention, no-attention) from 16 units (all Type Ia). These originated in the EDL ($n = 10$), PL ($n = 3$), and TA ($n = 3$) muscles. Microneurographic data were stored via digital tape recorder (DTR 1802, Biologic), along with the physiological data. Data were processed off-line by means of Spike2 Software (RRID:SCR_000903).

Procedure

Behavioral experiment

Participants were required to discriminate the amplitude difference between two imposed movements of their left foot. The robot moved their foot up-and-down twice, which then returned to its initial position (set at 20° and

40° from typical maximal dorsal and plantar flexions, respectively). The velocity was fixed at 5°/s. One of the movements was always the same reference movement, corresponding to an amplitude angle of 6.4° between the foot and the shin bone. Before each movement pair (repeated 15 times), participants were orally instructed to keep their eyes closed (“no vision,” proprioceptive-only information) or have them open (“vision,” combined and congruent visuo-proprioceptive information); vision and no vision trials were randomized. In the vision condition, the participants were required to look at their left foot moving. Each trial included the reference movement at 6.4° (given randomly the first or second movement) and another “test” movement, which consisted of one of seven possible angles (5.1°, 5.6°, 6°, 6.4°, 6.8°, 7.2°, or 7.6°). These angles were chosen on the basis of a previously defined pilot study (performed on four participants not included in the main experiment), in order to identify angle amplitudes that make discrimination against the 6.4° reference very difficult (6° and 6.8°) or rather easy (5.1° and 7.6°) or of intermediate difficulty (5.6° and 7.2°). Participants had to decide whether the first or the second movement was the largest in amplitude. They answered orally “one” or “two,” after the movements had finished, when prompted by the experimenter. Each angle was tested 30 times (15 times with closed eyes and 15 times with opened eyes) and resulted in a total of 210 movement comparisons (30 repetitions × seven angles) per participant. All movement pairs were pseudo randomized. Three-minute breaks were systematically given after every 20 pairs of movement comparisons and the experimenter regularly checked whether the subject needed to take an extra break at any time to prevent fatigue and loss of motivation.

Microneurographic experiment

Participants underwent similar passive foot displacements at the level of the ankle, where a series of 30 sinusoidal plantar flexion/dorsiflexion movements (5° amplitude and 5°/s velocity, over ~1 min) were imposed during microneurographic recording. This longer foot movement protocol was chosen for the single unit microneurographic recording because it was important to analyze muscle afferent firing in the absence of muscle activity. A time pause of 30 s was given after each movement.

To investigate the effect of vision, the activity of each muscle afferent was recorded under four conditions presented in a pseudo-randomized order using a 2 × 2 factorial design, with vision (vision, no vision) and attention (attention, no attention) as experimental factors. Visual information was manipulated by asking the participant either to keep their eyes closed (no vision condition), or their eyes open with the instruction to watch the movement of their foot (vision condition). Attention was manipulated by asking the participants either to simply relax and not pay attention to their foot moving (no attention condition) or they were instructed to pay attention to the movement of their foot (attention condition). To make sure that the participants were attentive, the participant was asked to judge whether it felt like the current sinusoidal

Table 1. Data structure for statistical analyses

	Data structure	Type of test	Power
a	Behavioral amplitude discrimination level ($n = 15$ participants)	GzLM	0.5
b	EMG and EDA data tests per condition/variable ($n = 15$ participants) for behavioral experiment	Student's paired t test	0.5
c	Microneurography data for change in muscle afferent firing over conditions ($n = 16$ units)	Repeated measures two-way ANOVA	0.6
d	EMG and EDA data tests per variable ($n = 16$ recordings) for microneurography experiment	Repeated measures two-way ANOVA	0.6

Type and power of the statistical tests carried out in the psychophysics and microneurography experiments. Letters in the left column refer to values within the Results section.

movements were of larger amplitude than the previous ones. In fact, it was always the same passive movement imposed on the participant, to compare the response of muscle afferents to investigate a change in firing properties of the afferent fibers depending on the experimental conditions. Therefore, the same movement amplitude was used over all the four experimental conditions in the microneurographic study. We chose the lowest amplitude (5°) from the range of amplitudes previously tested in the present psychophysical study. Only one amplitude was used to minimize the duration of the experiment, as the longer the microneurographic recording, the higher the risk of losing the unit (e.g., due to electrode displacement) and thus not obtaining data. This is a common risk during microneurography in humans, which was more likely to occur presently due to the long-lasting trials used in this study (30 cycles of 189 ankle movements, repeated). In addition, to avoid any implicit attention task, the no-attention and attention trials were blocked separately, and the no-attention block always preceded the attention block.

Data analysis

Data were analyzed in MATLAB (RRID:SCR_001622) and compared statistically in SPSS (RRID:SCR_002865) with a level of significance set at $p < 0.05$. For all statistical tests, effect sizes were determined using partial η^2 . See the statistical table (Table 1) for further details of the tests carried out.

Behavioral experiment

In order to evaluate and compare participants' performances across the two conditions (vision/no vision), we used an approach classically employed to estimate velocity discriminative thresholds of self-movements (Wichmann and Hill, 2001; Ernst and Banks, 2002; Kingdom and Prins, 2009; Reuschel et al., 2010; Tagliabue and McIntyre, 2013; Chancel et al., 2016a; Landelle et al., 2018). The psychometric data (i.e., the proportion of answers corresponding to movements found to be larger in amplitude than the reference) were fitted by a cumulative Gaussian function:

$$P(x) = \lambda + (1 - 2\lambda) \frac{1}{\sigma_\psi \sqrt{2\pi}} \int_{-\infty}^x e^{-\frac{(y - \mu_\psi)^2}{2\sigma_\psi^2}} dy$$

Here, x represents the movement angle (in degrees); μ_ψ is the mean of the Gaussian, i.e., the point of subjective

equality (PSE), that corresponds to the stimulation intensity leading the participant to perceive no difference between the reference and the test movements; and σ_ψ is the standard deviation (SD) of the curve (discrimination threshold), which is inversely related to the participant's discrimination sensitivity. A smaller σ_ψ value corresponds to higher discrimination sensitivity in the task and was used to measure their discrimination capability. The two indices, PSE and σ_ψ , characterize the participant's performance, and λ accounts for stimulus-independent errors (e.g., due to participant lapses) and was restricted to small values ($0 < \lambda < 0.06$; Wichmann and Hill, 2001). This parameter is not informative about the perceptual decision, thus we disregarded it for the subsequent analyses. Psignifit toolbox, implemented in MATLAB, was used to fit the psychometric curves. In this fitting procedure, bootstrap analysis was performed and the goodness-of-fit of the chosen model (i.e., the Gaussian function) was checked. As a result, the statistical power of the two parameters obtained to describe each participant's perception, mean and variance, was reinforced which leads to a reliable comparison between the different conditions both within and between participants (Wichmann and Hill, 2001). Since the σ_ψ (β) values can be assimilated as positively-skewed continuous variables modeled by a γ distribution, we used a non-parametric generalized linear model for repeated measured (GzLM) to compare these variables between the vision and no vision conditions.

Microneurographic experiment

The nerve spikes were inspected carefully for their single unit nature in an expanded time scale and then transformed into an instantaneous frequency curve (bin size = 0.005 s). The mean curve was obtained by averaging the response to 29 sinusoidal movements, where the first movement was excluded because of a dynamic response from the onset of the movement. Occasionally, some EMG activity (i.e., fluctuations in the steady EMG baseline) was found, despite the instruction for the participant to relax. When this occurred, the contaminated movement cycle was removed (Ackerley et al., 2017). This occurred in only 5/64 runs (16 units \times four conditions) and for each case, at least 85% of cycles were included. Measures were extracted from the averaged response, including the maximum and minimum frequency, and the difference between these two measures (" δ "), which was used as an index to characterize a unit's response in each condition

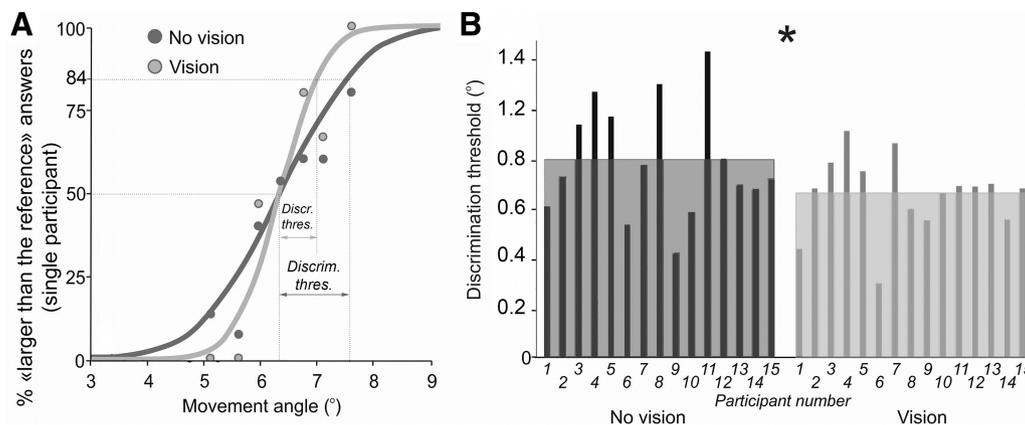


Figure 1. Behavioral effects of visual information on foot movement amplitude discrimination. **A**, An example of the mean psychometric curves for a single participant, where the slope is significantly steeper (lower amplitude discrimination threshold (Discrim.thres.)) when they saw their foot moving. **B**, For the group ($n = 15$ participants, shown in individual bars), there was a significant decrease in the discrimination threshold of movement amplitude when the participant watched their foot moving, as compared to having their eyes closed and only using proprioceptive information ($*p < 0.05$ and the mean discrimination levels are shown as boxes).

Figure Contributions: Marie Chancel performed the experiment. Marie Chancel and Anne Kavounoudias analyzed the data.

(Ackerley et al., 2017). This measure was used to quantify the dynamic response of muscle afferents (Kakuda, 2000).

In line with other microneurographic studies of muscle afferent firing (Dimitriou, 2016), the data were normalized (z-transformed to give z-scores), so as to compare differences across the conditions over the individual afferents. Here, we obtained the δ per afferent/condition, which was then normalized by subtracting the mean δ , and this was divided by the δ SD, for that afferent. This produced the number of SDs by which each condition differed from the mean value for each afferent tested. Statistical analyses were conducted on these normalized data, on the whole population of afferents, where the data were first checked for normality. A repeated measures two-way ANOVA was carried out in SPSS, to determine the effects of visual information and attention, and any interaction between these.

Physiological indexes in both experiments

The EMG and EDA activity were used to investigate whether the participant showed muscular or autonomic activity in the experiments. The direct current offset was removed from the EDA data and the EDA and EMG data were down-sampled to 2.5 kHz. For the psychophysical experiment, these data were separated by visual condition, where data were epoched from the beginning of the movement to the end of a movement, per trial, resulting in 105 total trials for the combined visuo-proprioceptive information condition and 105 for the proprioceptive-only condition. For the microneurographic experiment, EMG (one EMG source was used, which depended on the muscle afferent recorded from) and EDA signals were extracted, per condition per participant, from the duration of the sinusoidal movement. For both signals, areas under the curves were measured to analyze the modulation of physiological signals across conditions. The mean values, per measure, were checked for normality and the visual conditions were compared by Student's paired t tests in the behavioral experiment and the visual/attention condi-

tions using repeated measures two-way ANOVA for the microneurography experiment.

Results

Behavioral measurement of effect of visual information on movement discrimination

Figure 1A shows an example of a participant's ability to discriminate the amplitude of their foot movement. The discrimination improved in the visuo-proprioceptive condition, compared to the proprioception-only condition, as shown by an increased slope of the visuo-proprioceptive psychometric curve. More precisely, the discrimination threshold σ (i.e., the increase in movement amplitude required to induce a perception of movement larger than the reference movement in 84% of the trials with respect to 50% of the trials) was lower in the visuo-proprioceptive condition. The group data revealed that participants were on average able to discriminate the angle of their foot with higher precision in the vision condition, as compared to the no vision condition, as shown by a decrease in the discrimination level (Fig. 1B). The discrimination threshold σ was significantly lower in the vision condition (mean $\sigma = 0.66 \pm 0.04^\circ$ SEM (standard error of the mean)) than in the no vision condition (mean $\sigma = 0.8 \pm 0.06^\circ$ SEM; GzLM analysis slope = 0.242, $t = 3.31$ $p < 0.001$; Fig. 1B, Table 1, row a). No significant differences were found in the physiological measures (EMG, EDA) between the visual conditions (Table 1, row b, Table 2).

Microneurography measurement of effect of visual information on movement encoding

A total of 16 primary Ia muscle afferents were tested over the conditions where the participant viewed their foot moving (vision) or had their eyes closed (no vision), during a further task of paying attention to the movement (attention) or not (no attention). Figure 2 shows examples of unitary recordings from a muscle afferent over the conditions (Fig. 2A), with the mean extracted change in instan-

Table 2. Mean values and statistics for the physiological measures during microneurography experiment

	EMG (mean \pm SEM)	EDA (mean \pm SEM)
No vision, relax	14,105 \pm 2927	45,857 \pm 1537
No vision, attention	14,073 \pm 2925	45,828 \pm 1502
Vision, relax	14,105 \pm 2899	45,820 \pm 1555
Vision, attention	14,093 \pm 2897	45,723 \pm 1556
ANOVA main effect vision	$F_{(1,15)} = 3.45, p = 0.081,$ partial $\eta^2 = 0.20$	$F_{(1,15)} = 0.31, p = 0.568,$ partial $\eta^2 = 0.02$
ANOVA main effect attention	$F_{(1,15)} = 0.34, p = 0.857,$ partial $\eta^2 = 0.01$	$F_{(1,15)} = 0.18, p = 0.679,$ partial $\eta^2 = 0.01$
ANOVA interaction vision \times attention	$F_{(1,15)} = 0.17, p = 0.683,$ partial $\eta^2 = 0.01$	$F_{(1,15)} = 0.12, p = 0.739,$ partial $\eta^2 = 0.01$

The mean values for the EMG and EDA, with the SEM, as shown for the microneurography experiment. The EMG and electrodermal responses are shown in arbitrary units (area under the curve) for the duration of the sinusoidal cycles per condition. There was no significant effect of vision, attention, or the interaction of these, as shown in the ANOVAs, where the partial η^2 shows the size effects.

taneous firing (δ) over the sinusoidal movement cycles per condition (Fig. 2B). It can be seen in, both the individual cycles and in the unit's means, that there was a clear difference between the vision conditions, where the mean instantaneous firing frequency was lower with visual information, in both attention and no attention conditions.

The same result was found in the group data (Fig. 3). A repeated measures ANOVA on the δ z-scores showed a significant main effect of vision ($F_{(1,15)} = 20.36, p < 0.001$, partial $\eta^2 = 0.58$; Fig. 3), but no significant effect of attention ($F_{(1,15)} = 0.19, p = 0.672$, partial $\eta^2 = 0.01$), nor an interaction between visual information and attention ($F_{(1,15)} = 0.64, p = 0.435$, partial $\eta^2 = 0.04$; Table 1, row c). Therefore, a significant increase in δ was found when visual information was removed, but paying attention to the movement did not make a difference in the muscle afferent firing in this paradigm.

The physiological data (EMG, EDA) showed no significant differences between the conditions (Table 1, row d, Table 3). Here, for both EMG and EDA data, we found no significant effect of having visual information, or not, and neither was there an effect of whether the participant paid attention to the movement or simply relaxed, nor an interaction of these factors.

Discussion

Presently, we investigated the effect of congruent visual and/or proprioceptive signals on the processing of ankle movement. We found that visual information interacted with proprioceptive information, as seen in behavioral measures and in the responses of single muscle afferents. When participants saw their moving foot, they were more accurate in judging movement amplitude. Further, we found that the response from single muscle afferents was increased when the proprioceptive channel was the only source of sensory information, as compared to when the participant had the congruent visual input.

Enhancement of visuo-proprioceptive perception

Our behavioral results confirmed that combining visuo-proprioceptive information relating to self-body movements provided a perceptual enhancement, as there was a significant decrease in the threshold for discrimination when additional visual information was available. This corresponds well with many studies showing that com-

binning congruent visuo-proprioceptive stimulation enhances the resulting perception, suggesting that both visual and proprioceptive cues are co-processed for kinesthetic purposes (Tardy-Gervet et al., 1986; Rossetti et al., 1995; Van Beers et al., 1999; Reuschel et al., 2010; Guerraz et al., 2012; Blanchard et al., 2013). For example, using the classical mirror paradigm, Guerraz et al. (2012) reported that when participants looked at the reflection of their moving left arm in a mirror, they felt an illusion of a concomitant displacement of their stationary, hidden right arm. When a congruent muscle vibration was added on the resting right arm, i.e., simulating a movement in the same direction as that of the visual moving arm, the velocity of the resulting illusion increased, showing the beneficial impact of multisensory inputs.

Vision and muscle proprioception may combine in movement perception, but it does not mean that the weights allocated to each of these sensory cues are equal. For example, under artificial conflicting visuo-proprioceptive conditions, where visual cues of the participants were deviated using prisms and participants had to place an unseen finger in the same position as their seen finger, visual information has been shown to override muscle proprioceptive information under full-light conditions. In contrast, proprioception dominates when vision input is severely reduced to a small light-emitting diode on the end of their finger, viewed in darkness (Plooy et al., 1998). Therefore, the exact behavioral context must be taken into account. According to the theoretical Bayesian framework, the CNS allocates relative weights to each sensory cue on its relative reliability to encode the perceptual event in a given context and their weighted combination can optimize the resulting perception (Ernst and Banks, 2002; Landy et al., 2011). Although our present experiment was not designed to test the optimality hypothesis, one may hypothesize that the discriminative enhancement we found in the bisensory condition may be explained by a weighted combination of both visual and proprioceptive information, as reported in other perceptual tasks (Van Beers et al., 1999; Reuschel et al., 2010).

Dynamic muscle spindle sensitivity increases in absence of vision

It is generally assumed that multisensory integrative mechanisms take place in the brain, but the present

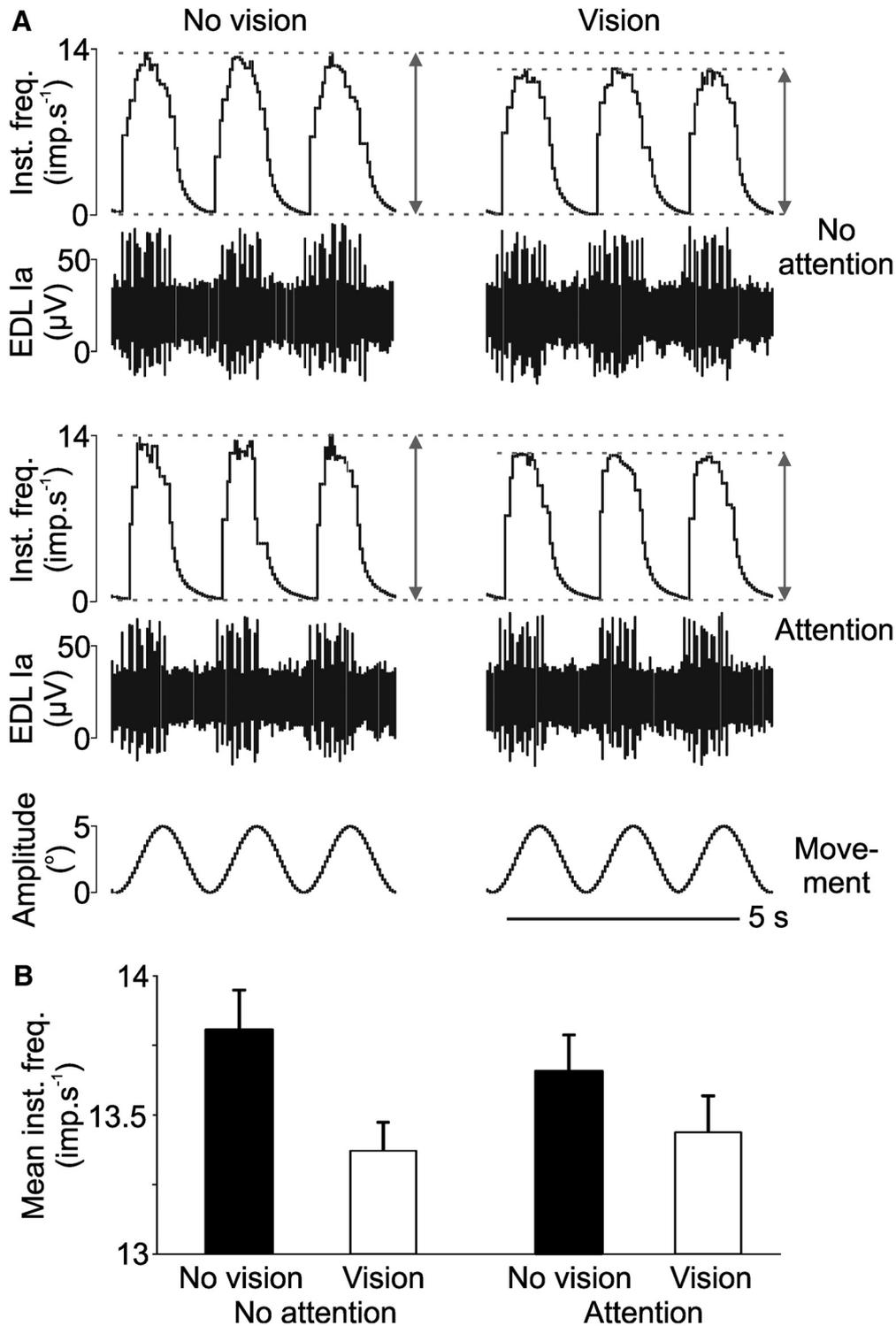


Figure 2. An example of muscle afferent firing, physiological measures, and the differences between conditions in a single participant. **A**, An example of three consecutive sinusoid movement cycles applied during each of the four visual/attention conditions. The minimum and maximum firing rates were extracted (gray arrows at the end of each example) and this mean firing rate change (δ) was used to quantify the dynamic response of the muscle afferent, for each condition. In this example, a microneurographic recording was made from a primary muscle afferent (Ia) arising from extensor digitorum longus (EDL) muscle. **B**, For this muscle afferent, a clear difference in the δ can be seen between when the participant had visual or no visual information (Histograms are mean values and bars are standard deviations per condition), regardless of the attention condition. Inst. freq: instantaneous frequency; imp.: impulses.

Figure Contributions: Rochelle Ackerley, Edith Ribot-Ciscar and Jean-Marc Aimonetti performed the experiments. Rochelle Ackerley, Edith Ribot-Ciscar and Anne Kavounoudias analyzed the data.

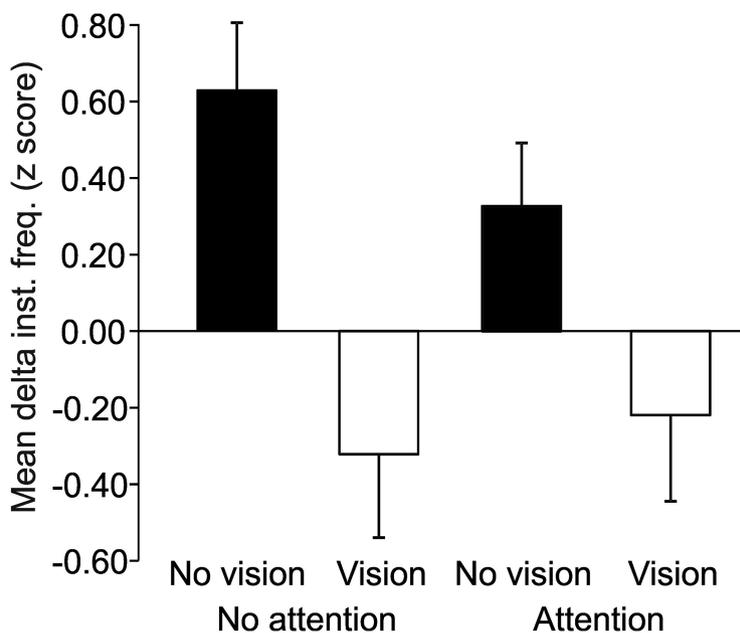


Figure 3. The mean effect of visual information and attention on muscle afferent movement encoding. The group data of Ia muscle afferents ($n = 16$) show a significant difference in the dynamic response of muscle afferents, as measured by the change in the minimum-to-maximum firing rates (δ), which was normalized via z-transform (means and SEMs are shown). A main effect was found for having visual information, where the δ was significantly lower with visual information, but no significant difference was found in the response between attention conditions, nor the interaction between vision and attention. Inst. freq. : instantaneous frequency. *Figure Contributions:* Rochelle Ackerley, Edith Ribot-Ciscar and Jean-Marc Aimonetti performed the experiments. Rochelle Ackerley, Edith Ribot-Ciscar and Anne Kavounoudias analyzed the data.

findings show spinal effects, where visual signals were associated with decreases in the responses of the muscle afferents. We found that there was a decrease in the depth of modulation (δ) to repeated sinusoidal movements, when the participants viewed their foot moving. We verified that this change in muscle spindle sensitivity was not due to involuntary muscle activity, as the leg EMG activity recorded showed no significant differences across conditions. The effect of vision occurred independently of the attentional state of the participants, as manipulated via direct instructions to attend or not, where attention did not affect the δ . Similarly, there was no significant interaction between vision and attention. Therefore, we postulate that in the present experimental manipulation, attentional effects do not account for the changes in muscle spindle sensitivity in the different visual conditions. However, our manipulation of attention was explicit (i.e., we asked the participants to attend or not), which was in part constrained by the microneurography conditions where the participants are required to remain

relaxed, and we were not able to confirm their attentional load. It may have been the case that participants may have simply disregarded the instruction to either attend or not attend; however, participants often reported the difficulty of the task, since the movements were actually all the same, which suggested that they really followed the instructions and executed the attentional task.

The absence of a change in muscle afferent activity with attention may appear contradictory with the results of previous studies, where it has been observed that a fusimotor-induced sensitization of muscle spindles occurs during proprioceptive attention tasks (Hospod et al., 2007; Ribot-Ciscar et al., 2009). However, the previous experiments were specifically designed to address the effect of attention, while here it was only a controlled parameter, and a difference between the difficulties of the present and previous tasks likely accounts for this. The present task was a simple comparison of movement amplitude at the end of the sinusoidal movements between attention conditions, which is far easier than the recogni-

Table 3. Mean values and statistics for the physiological measures during behavioral experiment

	EMG TA (mean \pm SEM)	EMG GS (mean \pm SEM)	EDA (mean \pm SEM)
Vision	9330 \pm 1146	8478 \pm 1766	8217 \pm 1595
No vision	9237 \pm 1076	8343 \pm 1076	7827 \pm 1237
Paired t test vision vs no vision	$t_{(13)} = 0.92, p = 0.385,$ partial $\eta^2 = 0.06$	$t_{(13)} = 1.82, p = 0.092,$ partial $\eta^2 = 0.20$	$t_{(13)} = 0.64, p = 0.531,$ partial $\eta^2 = 0.03$

The mean values for the EMG and EDA, with the SEM, as shown for the behavioral experiment. The EMG and electrodermal responses are shown in arbitrary units (area under the curve) for the total number of trials per condition. There was no significant effect of vision, as shown in the ANOVAs, where the partial η^2 shows the size effects.

tion of writing movements (Hospod et al., 2007) or classifying different movement amplitudes or velocities (Ribot-Ciscar et al., 2009).

We postulate that during the visual conditions, where the participant viewed their foot moving, the proprioceptive information, coupled with congruent visual signals, aids signal processing. In line with the Bayesian framework, a relative weighting of each visual and proprioceptive cue may account for the perceptual enhancement observed in our visuo-proprioceptive condition. The model predicts that if one sensory source becomes less reliable, the weight of the other one increases (Ernst and Banks, 2002). In the current study, when only proprioceptive information was available, the participant relied on one sensory source, where we found an increased sensitivity in firing of the muscle afferents. Conversely, when congruent visual information was present, the relative visual weight increased, while that of the proprioception decreased. Vision plays a dominant role in spatial tasks, as reported in studies using the mirror paradigm, where seeing the reflection of one's moving arm in a mirror is sufficient to induce an illusion of a concomitant displacement of the other stationary, hidden arm (Guerraz et al. 2012). Furthermore, Chancel et al. (2016b) reported that illusions induced using the mirror paradigm can survive despite a marked visual impoverishment (obtained by covering between 0% and 100% of the mirror); the mirror illusion was significantly degraded only when the visual degradation was >84%, suggesting that even restricted visual information is sufficient to provide relevant kinesthetic cues. Future studies may be conducted to explore whether changing the reliability of the visual feedback by progressively degrading visual information results in an increase of muscle spindle sensitivity.

Previous microneurographic studies exploring the effect of vision on muscle proprioceptive information used external visual targets (Wessberg and Vallbo, 1995; Jones et al., 2001; Dimitriou, 2016), in contrast to our experiment where the participant viewed their own passive movement. Jones et al. (2001) described a decrease in muscle afferent firing rate during incongruent muscle afferent and visual feedback, which was interpreted as a strategy for resolving bisensory conflict. Conversely, an increase in muscle afferent firing was more recently observed during a similar visuomotor task specifically during an imposed adaptation phase, making the fusimotor control a means of adjusting the human proprioceptive system to motor learning (Dimitriou, 2016). Interestingly, the latter study also observed a decrease in muscle spindle dynamic sensitivity in the washout stage, when visual feedback was again congruent with muscle feedback. In line with Dimitriou (2016), we found that the fusimotor drive selectively decreased muscle spindle sensitivity when muscle afferent feedback was accompanied by congruent visual cues. Although at first glance they might seem disparate, taken together, these recent studies and our present one accounted for a fusimotor control of muscle spindle sensitivity independent of the concurrent muscle activity, which has long been debated (Vallbo et al., 1979). They all suggest that muscle spindle sensitivity may change ac-

ording to its relevance to the context and, in particular, the presence or not of relevant visual cues.

The reweighting of proprioceptive information in the absence of visual signals can be related to the modulation observed in the primary somatosensory cortex depending on concomitant visual signals (Blakemore et al., 2005; Helbig et al., 2012). Using a design inspired by the Bayesian framework, Helbig et al. (2012) showed that during a task of shape identification, activation of the primary somatosensory cortex was modulated by the reliability of visual information within congruent visuo-tactile inputs. The less reliable the visual information, the more activity in the primary somatosensory cortex increased. In line with the modality appropriateness model (Welch and Warren, 1986) and the Bayesian framework (Ernst and Banks, 2002), one can assume that crossmodal processing is more likely to occur within the sensory pathway corresponding to the most accurate signal regarding the task, since this sensory signal is supposed to get a greater weight compared to the other less reliable signals.

Descending fusimotor influences from relevant visual cues may reduce the sensitivity of muscle afferents, reflecting a decrease in the proprioceptive contribution to encode the actual movement. Indeed, watching a video of one's own hand in movement is sufficient to elicit an illusory movement of participant's resting hand. By recording brain activity during this pure visually-induced kinesthetic illusion, Kaneko et al. (2015) found that the lateral premotor (PM) cortex and the supplementary motor area (SMA) were specifically activated together with the posterior parietal cortices and the insula. It is well known that the SMA and lateral PM are part of the motor system, with direct connections to M1, and descending output to the spinal cord (Dum and Strick, 1991; He et al., 1995; Picard and Strick, 1996, 2001; Maier, 2002). Further, the SMA and the lateral PM were not activated when participants viewed a video of someone else's own hand. Only relevant kinesthetic visual cues may therefore influence proprioceptive sensitivity through descending motor commands that can modulate spinal fusimotor efference.

Functional significance of the fusimotor modulation

One may consider that the observed fusimotor effect is small, as compared to in animals; however, it has been repeatedly observed in humans (Burg et al., 1975; Vallbo and Hulliger, 1981; Vallbo and Al-Falahe, 1990; Gandevia et al., 1994; Ribot-Ciscar et al., 2000, 2009; Jones et al., 2001; Hospod et al., 2007; Dimitriou, 2016; Ackerley et al., 2017) and has been considered as intriguing when compared to animal data, where muscle spindle firing rates are ten times higher than in humans, as are the fusimotor-induced changes (Matthews, 1981). Whatever its amount, the observed effect was sufficient to significantly alter activity of muscle afferents and hence may have a functional impact on the resulting perception.

Moreover, the fact that our two experiments have been done with two different populations of participants may at first appear as a limitation of the present study. However,

it is worth noting that there is commonly a high variability in the firing of muscle afferents, depending on the nature and number of intrafusal muscle fibers that are included, the fusimotor innervation received by the intrafusal fibers, and the location of the muscle spindle inside the muscle, where a receptor near the ankle joint will be more affected by the movement than another located more proximally in the EDL or TA muscles. Therefore, one can consider that the variability introduced by the use of different participants does not overly influence the outcome, with respect to the intra-subject variability, due to the technical challenge of recordings made in the same subject.

Our finding that afferent proprioceptive signals from ankle could be modulated by visual cues may be important for controlling postural balance (Burke and Eklund, 1977; Massion, 1992; Kavounoudias et al., 2001). High ankle proprioceptive acuity has been observed to be predictive of sport performance level in elite athletes such as dancers (Han et al., 2015b) and in balance performance of the elderly (Goble et al., 2011). Similarly, better ankle proprioception is correlated with reduced ankle injuries (Han et al., 2015a), while after a complete loss of somatosensory afferents, deafferented patients present severe deficits in postural and motor tasks (Forget and Lamarre, 1995). The central processing of ankle proprioceptive information with other sensory information enables optimal integration for balance control. When a source of information is used for other purposes, for example, if vision is used to track a target in the environment, the CNS uses a reweighting strategy relying on the most reliable sources of information to optimize balance control. We presently show that a relative reweighting of visual signals may occur by a recalibration at more peripheral levels of ankle proprioceptive inputs, via a direct setting of muscle receptor sensitivity by the CNS.

The present results may have further clinical impact on sensorimotor rehabilitation. Different interventions are used to improve ankle proprioception and balance control, particularly after ankle injury. While passive interventions, such as taping or compressing, do not seem to particularly improve proprioception, active interventions with task-specific paradigms are efficient, suggesting central processing modifications (Han et al., 2015b). The present results suggest that removing visual information may optimize the intervention, by providing the brain with increased proprioceptive information that may favor a better recovery of balance control.

In conclusion, we show that muscle afferent sensitivity can be altered in a context-dependent way via descending influences. Specifically, we show that when proprioceptive signals from a foot movement are coupled with congruent visual information, a decrease in muscle afferent firing was found. This decrease in the bisensory condition may reflect a re-weighting of the two sensory cues in favor of the visual source. Our study shows that the mechanisms of sensory reweighting are not limited to higher-level neural control in the brain, but that there are also spinal effects of multisensory processing between visual signals and proprioceptive coding. This opens up the opportunity for the study of other multisensory

effects below the level of the brain and impacts on our understanding of multisensory interactions throughout the CNS, which may also provide clinical therapeutic strategies for ameliorating visuo-sensorimotor disturbances.

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