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RESEARCH ARTICLE | *Sensory Processing*

Human 8- to 10-Hz pulsatile motor output during active exploration of textured surfaces reflects the textures' frictional properties

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Dione M, Wessberg J. Human 8- to 10-Hz pulsatile motor output during active exploration of textured surfaces reflects the textures' frictional properties. *J Neurophysiol* 122: 922–932, 2019. First published June 26, 2019; doi:10.1152/jn.00756.2018.—Active sensing in biological system consists of emitting/receiving a periodic signal to explore the environment. The signal can be emitted toward distant objects, as in echolocation, or in direct contact with the object, for example, whisking in rodents. We explored the hypothesis that a similar mechanism exists in humans. Humans generate periodic signals at ~10 Hz during voluntary finger movements, which reflects a pulsatile motor command in the central nervous system. In the present study, we tested whether the ~10-Hz signal persists during the active exploration of textures and whether the textures' features can modulate the signal. Our results confirm our assumptions. The ~10-Hz signal persisted during active touch, and its amplitude increased with textures of higher friction. These findings support the idea that the ~10-Hz periodic signal generated during voluntary finger movements is part of an active sensing mechanism acting in a pulse-amplitude modulation fashion to convey relevant tactile information to the brain.

NEW & NOTEWORTHY For the first time, we show that pulsatile motor output during voluntary movement of a finger persists during active exploration of a surface. We propose that this is part of an active sensing system in humans, with generation of an ~10-Hz signal during active touch that reinforces extraction of information about features of the touched surface.

movement discontinuities; muscle vibrations; pulsatile motor output; tremor

INTRODUCTION

Active sensing systems emit periodic signals toward the external environment to explore it (Nelson and MacIver 2006). For example, bats and dolphins emit sounds and analyze their echoes to detect preys or obstacles (Au 1993; Simmons et al. 1979), and electric fish similarly emit weak electric signals to detect objects in their close environment (von der Emde 1999). Active sensing systems are not only used to detect distant objects. For example, rodents move their whiskers directly over the objects with a regular frequency of ~10 Hz (Berg and Kleinfeld 2003; Nelson and MacIver 2006) to analyze the properties of the objects touched, such as their texture (Carvell and Simons 1995; Itskov et al. 2011; Welker 1964).

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The hypothesis that a similar active touch sensing system exists in humans when they explore their environment with their fingers has never been tested (Prescott et al. 2011). However, a periodic signal is generated at a frequency of ~10 Hz (between 8 and 10 Hz) when humans execute slow finger movements (Vallbo and Wessberg 1993). It is known that the ~10-Hz signal reflects a pulsatile motor command to the muscles controlling the finger movements initiated at a central level through a cortico-cerebellar loop (Gross et al. 2002; Welsh and Llinás 1997). Several suggestions have been made regarding a potential role for the ~10-Hz signal in motor control. During free finger movements, the ~10-Hz signal could be used to signal the movement speed, since the amplitude of the signal increases with the movement speed (Vallbo and Wessberg 1993; Wessberg and Kakuda 1999), or to signal the presence of movement, since the signal is absent when the finger is held still (Kakuda et al. 1999). The ~10-Hz signal could also play a role in the central organization of the motor output (e.g., by synchronizing the motor units engaged in the motor execution; Kakuda et al. 1999). The ~10-Hz signal could also play a role of common modulation for more distant anatomical structures, such as the eye and the hand when moved in coordination rather than independently (McAuley et al. 1999) or the two index fingers when moved in-phase rather than anti-phase (Evans and Baker 2003; Wessberg 1995). To our knowledge, the hypothesis that the ~10-Hz signal could also play a role in tactile feedback in humans (e.g., to coordinate the motor and the tactile system) has not yet been considered.

In the present study, we tested the hypothesis that the ~10-Hz signal generated during voluntary movements of the fingers in humans is part of an active sensing system for touch. More precisely, we asked participants to execute mediolateral movements of the finger against surfaces to test whether the ~10-Hz signal was present under touch conditions. We also varied the textures according to their level of friction to test whether the amplitude of the ~10-Hz signal was affected by the qualities of the textures touched. The movements were executed at slow or fast speed and with light or stronger force applied to the texture to control whether forces and speeds could have been confounding factors.

METHODS

Participants. Nine naive, healthy individuals (6 men, 3 women; age 25–33 yr) volunteered to participate in the study. They were all

students at the University of Göteborg. All participants were right-handed, but to keep the task comparable to previous experiments (Vallbo and Wessberg 1993), they performed the task with the left hand. All participants provided written informed consent. The study was approved by local ethics board and was conducted according to the Declaration of Helsinki.

Experimental setup. The participant was seated comfortably in a reclining chair, with the left arm resting on a support (see Fig. 1A). To record finger movements, a triaxial accelerometer (Prof. Veikko Jousmäki, Brain Research Unit, Aalto University, Espoo, Finland; 500-Hz bandwidth) was firmly fixed to the nail of the left index finger using double-sided tape. Video tracking of the finger was done using a digital camera (Microsoft LifeCam Studio), and a dot was drawn on the tip of the finger just under the nail to facilitate tracking (Fig. 1A). The skin over the belly of the first dorsal interosseous muscle was scrubbed, Ag-AgCl electromyography (EMG) electrodes were attached, and EMG signals were recorded using a custom-built amplifier for human surface EMG (bandwidth: 1.6 to 800 Hz). In one participant, EMG had to be discarded due to lack of signal stability. One of four natural textures (paper, silk, burlap, or P180 grit sandpaper) that were attached to rectangular plastic plates (77 × 32 mm) was mounted on a 6 degrees of freedom load cell (Nano 43; ATI Industrial Automation, Apex, NC). Accelerometer, force, and EMG data were sampled at 16,000 Hz using Spike2 software (Power 1401; CED, Cambridge, UK). The webcam was controlled with Spike2 and sampled at 25 Hz. A light-emitting diode (LED) was attached to the side of the load cell and used to indicate the start and end of each trial in the video. Tones of either high or low pitch were used to indicate, respectively, the start and end of a trial to the participant. Tones were generated from the Spike2 program.

Procedures and instructions. The participant was asked to explore the textures by executing mediolateral movements of the index finger over the texture presented, alternating between radial and ulnar deviations of the finger, without interruption until the end of the trial. Each trial lasted 20 s. The participant was clearly instructed to move the index finger only, to lightly grab the arm support with the other fingers, and to keep the rest of the hand, the wrist, and the arm as still

as possible (see Fig. 1A). Regarding the movement speeds and forces, the participant was asked to move as slowly as possible in the “slow” condition and significantly faster in the “fast” condition. Similarly, the participant was asked to use very light force in the “light” condition and significantly more force in the “strong” condition. The participant freely chose the speeds and forces to use. The experimenter agreed with the speed and force chosen in such a way as to avoid intermittent movements (especially when movements that were too slow were executed) or mechanical vibrations of the setup (when movements that were too intense were executed). The participant was also instructed to maintain the speeds and force constant within single trials and over the entire test. Before beginning the experimental test, the participant was familiarized to the task: each texture was touched for a few seconds (~5 s) using the four different types of movements (slow/light, slow/strong, fast/light, fast/strong). The tones indicating the start/end of a trial were also displayed for the duration of a trial. The full experimental design comprised four repetitions of the four movement conditions for each texture, for a total of 64 trials. Before each trial, the experimenter instructed the participant of the movement condition orally (e.g., “slow, light”). After each trial, the experimenter changed the texture plate manually. Trials were semirandomized using a Latin square. The same randomization was used for each participant. A 5-min pause was taken after the first 32 trials. The full experimental session lasted ~1.5 h.

Measured variables. The finger displacement was first tracked from the video recordings using Tracker, an open source tracking software (<https://physlets.org/tracker/>). The displacement in the lateral direction was then exported to MATLAB (The MathWorks, Natick, MA). The normal and lateral forces, the lateral acceleration, and the EMG data were exported from Spike2 to MATLAB. EMG was notch filtered at 50 Hz if necessary, rectified, and downsampled to 800 Hz along with the other signals. The signals recorded are illustrated in Fig. 1B for two successive movements.

The distance traveled over the texture (in mm), the movement time (in s), the mean movement speed (in mm/s), the normal force (in N), and the number of movements were measured as descriptors of movement performance. The coefficient of friction was measured as

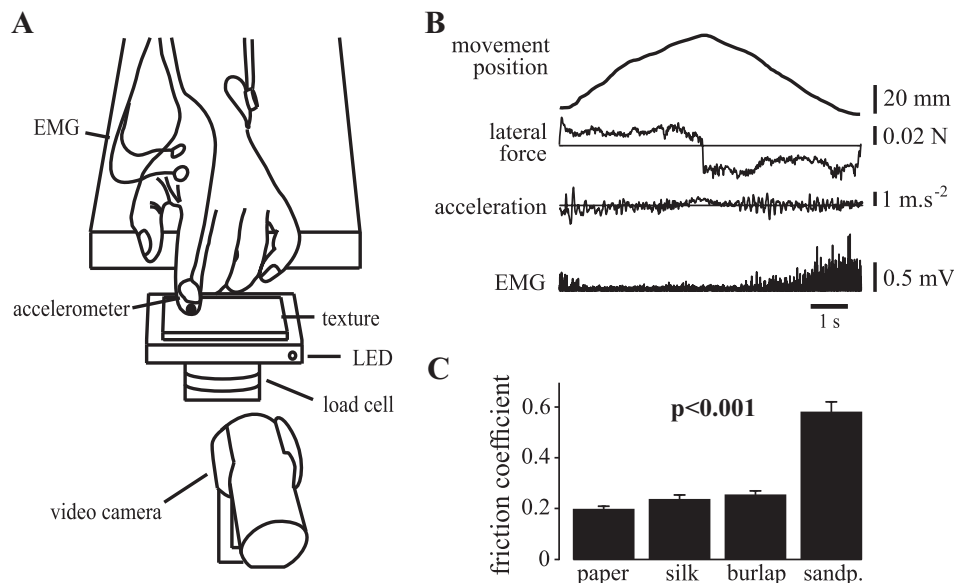


Fig. 1. Design of the experiment. **A:** the participant was seated comfortably in a reclining chair, with the left arm resting on a support. The participant was instructed to move the index finger only (left hand), and finger position was tracked with a webcam. A light-emitting diode (LED) was used to synchronize video and other recorded signals. Forces applied to the texture were recorded with a 6-degrees of freedom load cell under the texture support. Surface electromyography (EMG) from the first dorsal interosseous muscle (1DI) and acceleration were measured to characterize the periodic signals emerging during the active exploration of textures. **B:** signals recorded for a typical movement were position, force, acceleration, and EMG. It is important to note that the muscular activity was measured for the 1DI only, hence reflecting activity in the radial direction only. **C:** coefficient of friction was measured as the ratio of lateral to normal force for each trial. Friction was significantly different between the textures ($P < 0.001$; all pairwise comparisons significant, $P < 0.02$ or better). sandp., Sandpaper.

an indicator of the textures' properties. To calculate these measurements, the movements contained in a trial (20 s of movement) were first separated into single epochs using MATLAB, with each epoch containing a single movement in one direction. The measurements obtained for each movement were then averaged for each participant. The coefficient of friction of the materials was measured as the ratio of the participants' mean lateral and normal forces. For the measures of force and friction, analyses were always restricted to the sliding phase of the movement. The sliding phase was estimated as 40% of the data centered at the midpoint of the movement.

To characterize aberrant movements, *Z* scores were calculated for each movement epoch for the following variables: mean EMG, force, acceleration, movement time, and movement speed. An epoch was rejected as aberrant if the *Z* score exceeded 3.0 for at least two of the variables. On average, 5.5% (SD 2.3%) of the movements were discarded for each participant. Altogether, 18,802 movements were analyzed.

To test whether the ~10-Hz signal persisted during varying touch conditions, we conducted power spectra analyses of the acceleration time series (entire series; i.e., without separation into movement epochs). Standard procedures for continuous processes were followed (Bendat and Piersol 1986; Halliday et al. 1995; Rosenberg et al. 1989). The Fourier transforms of successive 1-s segments of time series were averaged, providing a frequency resolution of 1 Hz. We also conducted power spectra analyses of the EMG time series (same procedure and same resolution as for the acceleration data), coherence analyses between the EMG and acceleration data, and cross-correlation analyses with the main peak upward indicating the delay between the two signals (Rosenberg et al. 1989). Coherence was computed as the normalized cross power spectra. Coherence can be defined as a linear correlation squared between the two signals at a given frequency.

Statistical analyses. When means were compared, statistical analyses were conducted using SPSS software. When the conditions of normality and homogeneity were respected according to the Shapiro-Wilk test and Mauchly's test, respectively ($\alpha > 0.10$), then means were compared using paired *t*-tests (to compare 2 conditions) or using ANOVA for repeated measures (Fisher's test, *F*; to compare more than 2 conditions). Least significant difference (LSD) post hoc tests were used to complete ANOVA analyses when necessary. If the data were not homogeneous, then the Greenhouse-Geisser correction was applied. If the data were not normal, then the nonparametric Friedman test (χ^2) was used as the main test, and if needed, Wilcoxon signed-rank tests (*z*) with Bonferroni correction ($\alpha = 0.05/\text{number of tests}$) were used as post hoc tests. The alpha value was set by default to 0.05.

Correlations analyses were also conducted using SPSS. Pearson's correlations were used. Alpha was set to 0.05.

When frequency-domain analyses were conducted, statistical analyses are presented as confidence limits of estimates (Rosenberg et al. 1989). Comparison of means were also conducted to compare the amplitude of the peaks observed in a given frequency range. In this case, the same procedure was used as that described above.

RESULTS

Movement speed, force, and other descriptive results. Movement speed was on average 33 mm/s (SD 18 mm/s) in the slow condition and 140 mm/s (SD 56 mm/s) in the fast condition. The difference in movement speed between the slow and fast conditions was significant [$t(8) = -7.6$, $P < 0.001$]. The normal force applied in the normal direction was on average 0.32 N (SD 0.09 N) in the light condition and 1.98 N (SD 0.78 N) in the strong condition. The difference in force between the light and strong conditions was significant [$t(8) = -7.0$, $P < 0.001$]. On average, 12.2 movements (SD 7.8) were made in the slow condition and 54.4 (SD 23.8) in the fast condition.

Movements lasted 2.5 s (SD 1.8 s) in the slow condition and 0.5 s (SD 0.3 s) in the fast condition. For each movement, participants traveled across 52.1 mm (SD 9.8 mm) of texture in the slow condition, and 50.5 mm (SD 8.0 mm) in the fast condition. The coefficient of friction was on average 0.20 for paper, 0.23 for silk, 0.25 for burlap, and 0.58 for sandpaper (see Fig. 1C). The main effect of friction was significant [$F(3,6) = 113.8$, $P < 0.001$]. LSD post hoc tests revealed that all pairwise differences were also significant ($P < 0.02$ for the large difference observed).

Spectral analysis of acceleration and surface EMG. To facilitate comparisons of patterns of acceleration, power spectra were normalized (by dividing by total power) for each movement condition and texture. The results are shown in Fig. 2. In the slow/light condition, we observed systematic and prominent peaks in the 8- to 10-Hz range for all participants. These peaks were still present in the slow/strong condition but with lower amplitude. In the fast conditions, peaks were observed either in the 8- to 10-Hz range or around 6–7 Hz in most participants. Double peaks (6–7 Hz and 8–10 Hz) were observed in five participants in the fast/light condition and in four participants in the fast/strong condition. Extra peaks were observed near 40 Hz in the slow/light and fast/light conditions in one participant and near 17 Hz in the slow/strong condition in two participants. These observations suggest that peaks in acceleration were present in all conditions in the 6- to 10-Hz range.

Power spectra of surface EMG were computed in the same manner as for acceleration. Peaks in the low frequency range were in general less prominent than the acceleration peaks (see Fig. 3).

Figure 3 shows acceleration spectra, EMG spectra, the coherence between EMG and acceleration, and the cross-correlation between EMG and acceleration in detail for one participant. Coherence between acceleration and surface EMG was significant ($P < 0.01$) in the 8- to 10-Hz range for all participants and conditions, except for two participants in the fast/strong condition only. Coherence was also significant in the 6- to 7-Hz range when these peaks were present, that is, for 6 of 8 participants in the fast conditions. In addition, a broadband increase in the coherence around 20 and 40 Hz was found for three of eight participants in the slow/light condition, for five participants in the slow/strong condition, and for two participants in the fast/strong condition.

When the coherence was significant, the delay between the EMG and the acceleration could be estimated from the cross-correlation between the two signals (see Fig. 3, *bottom*), and was on average 6.9 ms (SD 2.4 ms). Delays were always in the direction of surface EMG to acceleration, confirming that the periodic signals recorded in the surface EMG preceded the periodic signals measured with the accelerometer.

Power spectra of acceleration for each texture: main results. For an extended analysis of acceleration, nonnormalized spectral analyses, which preserved the power of the peaks in the spectrum, were done for each texture separately. This is illustrated in Fig. 4A. Peaks in the 8- to 10-Hz range were observed for each texture, and the amplitude of the peak of acceleration increased with the increase in friction of the materials. This was particularly noticeable in the slow/light condition. In the 6- to 7-Hz range, peaks were also revealed for each texture.

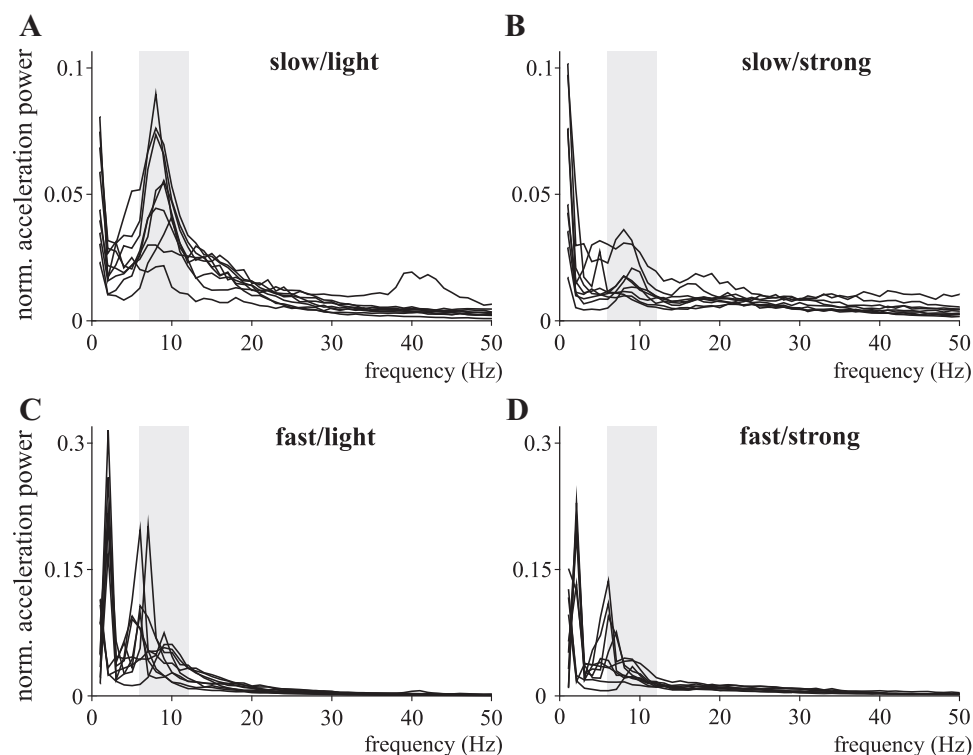


Fig. 2. Power spectra of acceleration. Normalized power spectra of acceleration are shown for all participants in the slow/light (A), slow/strong (B), fast/light (C), and fast/strong conditions (D). Low-frequency peaks are especially prominent in the slow/light condition. The area at 6–12 Hz is highlighted with shading. norm., Normalized.

However, the amplitude of these peaks did not vary with the friction of the material.

To test whether there was a significant effect of the character of textures on the amplitude of the peak of acceleration, statistical analyses were conducted at the group level. Analyses were conducted separately for the 8- to 10-Hz range and for the 6- to 7-Hz range. The peak of acceleration was computed as the maximal value of acceleration observed between 8 and 10 Hz or 6–7 Hz. In the 8- to 10-Hz range, analyses were conducted for all conditions. In the 6- to 7-Hz range, analyses were conducted in the fast conditions only, because these peaks were not observed in the slow conditions. Results are shown in Fig. 4B.

In the 8- to 10-Hz range, the difference between the amplitude of the peaks measured for each texture was significant in the slow/light [$\chi^2(3) = 17.4$, $P < 0.001$], slow/strong [$\chi^2(3) = 15.3$, $P < 0.005$], and fast/strong conditions [$\chi^2(3) = 20.3$, $P < 0.001$]. No differences were revealed in the fast/light condition [$\chi^2(3) = 5.0$]. When a main effect of friction was obtained, the amplitude of the peak was always larger for textures of higher friction. Post hoc tests confirmed that pairwise differences were significant at least between the sandpaper and the paper in all conditions showing an effect.

In the 6- to 7-Hz range, no significant differences between the amplitude of the peaks of acceleration measured for the four distinct textures were observed in either the fast/light [$\chi^2(3) = 7.0$] or fast/strong conditions [$\chi^2(3) = 0.6$; see Fig. 4B].

Origin of the 6- to 7-Hz peaks in the acceleration power spectra. Several potential mechanisms were considered for the origin of the 6- to 7-Hz peak in the acceleration during fast movements. In principle, this could be caused by unintentional increased movements of the arm. The arm and wrist have lower biomechanical resonant frequencies compared with the fingers,

and a 5- to 8-Hz peak in the acceleration has been observed during muscle contraction and steady position holding of the forearm (Kakuda et al. 1999). To investigate this possibility, we extended the video analysis to track a marker placed on the dorsum of the wrist in five participants. We found that there were larger movements at the wrist in the lateral direction in fast/strong (mean amplitude 2.0 mm, SD 0.21 mm) compared with slow/light movements (0.87 mm, SD 0.23 mm; Wilcoxon $z = -2.0$, $P < 0.05$), but not in the palmar-dorsal direction (slow/light: 0.63 mm, SD 0.24 mm; fast/strong: 0.63 mm, SD 0.24 mm; Wilcoxon $z = -0.4$, not significant). However, the magnitude of movements at the wrist markers was negatively correlated with the size of the 6- to 7-Hz acceleration peak at the finger in the fast/strong condition (Pearson's $r = -0.89$, $P < 0.05$). Hence, there was no indication that increased movement at the wrist was transmitted to the fingers to produce the observed 6- to 7-Hz peak in the acceleration.

A detailed inspection of the raw records of the fast movements revealed a pattern of a pair of prominent acceleration-deceleration peaks just at the onset of each movement. This was consistently seen in all participants that exhibited the previously described double peaks at 6–7 and 8–10 Hz in the acceleration spectrum. It is illustrated for a sequence of fast movements in one subject in Fig. 5A. The average latency from the first acceleration peak to the first deceleration negative peak was computed for each participant in which they were present ($n = 5$ in the fast/light condition, $n = 4$ in the fast/strong condition) and for both movement directions (Fig. 5B). The group average was 0.081 s, corresponding to a frequency of 6.2 Hz (the time from the positive peak to the negative peak is a half cycle; 2×0.081 s = 0.162 s). This was confirmed by focusing the spectral analysis of the acceleration to the onset

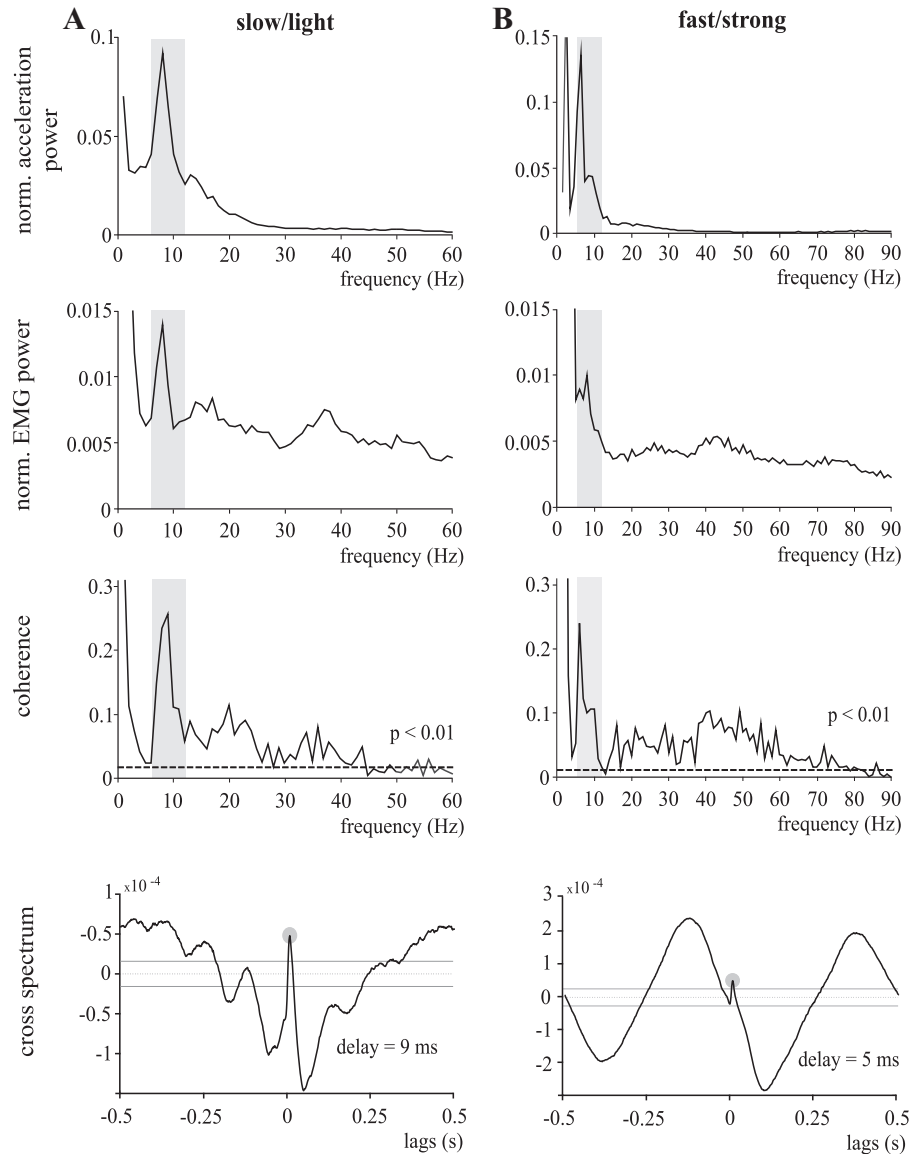


Fig. 3. Coherence analysis between surface electromyography (EMG) and acceleration. A power spectrum of acceleration, power spectrum of EMG, coherence between acceleration and EMG, and cross-correlation between acceleration and EMG are shown for 1 participant (from *top to bottom*, respectively) in the slow/light (A) and fast/strong conditions (B). Coherence was significant ($P < 0.01$), and average delay from EMG to acceleration was 6.9 ms, confirming that EMG was leading acceleration. The area at 6–12 Hz is highlighted with shading. norm., Normalized.

of the fast movements (Fig. 5C, *left*), which showed a peak at 6–7 Hz.

A similar pattern was seen in the lateral force; this increased rapidly at the beginning of each movement and decreased slightly at onset of the sliding phase (Fig. 5A, *bottom*). Power spectral analysis of the lateral force also revealed a component at 6–7 Hz for the fast movements (Fig. 5C, *middle*), and there was strong and significant coherence between acceleration and lateral force (Fig. 5C, *right*). This could, in principle, reflect either that the acceleration-deceleration pattern was part of the motor command generated by the participant, also affecting the force trajectory, or that the finger was transiently stuck due to increased friction at the onset of the fast movements, thus generating the observed 6- to 7-Hz acceleration-deceleration pattern at movement onset (André et al. 2011; Delhaye et al. 2014). We investigated this by calculating the ratio of lateral to normal force when the lateral force reached its maximal value during the loading phase of the movement (i.e., the static coefficient of friction) for each condition. Overall,

there was no correlation between the static coefficient of friction and the amplitude of the 6- to 7-Hz peak of acceleration, in either the fast/light ($R = -0.01$) or fast/strong conditions ($R = 0.12$). Hence, any changes in the force dynamics occurring in the fast conditions could not explain the acceleration-deceleration phenomenon observed in the 6- to 7-Hz range.

The biphasic acceleration-deceleration pattern at onset of fast movements was also reflected by a modulation of the surface EMG (Fig. 5A, *top*). The biphasic onset of the fast movements resembles the previously described patterns for execution of fast “ballistic” movements (Zehr and Sale 1994). Such movements are made with high velocity and acceleration, reflecting strong muscular force, and with a stereotypical activation of agonist and antagonist muscles in rapid succession. Ballistic movements are usually observed for movement durations shorter than 400 ms. To evaluate if the acceleration-deceleration pattern we observed could reflect a ballistic mode of movement execution for the fastest movements, we calculated the correlation between the amplitude of the 6- to 7-Hz

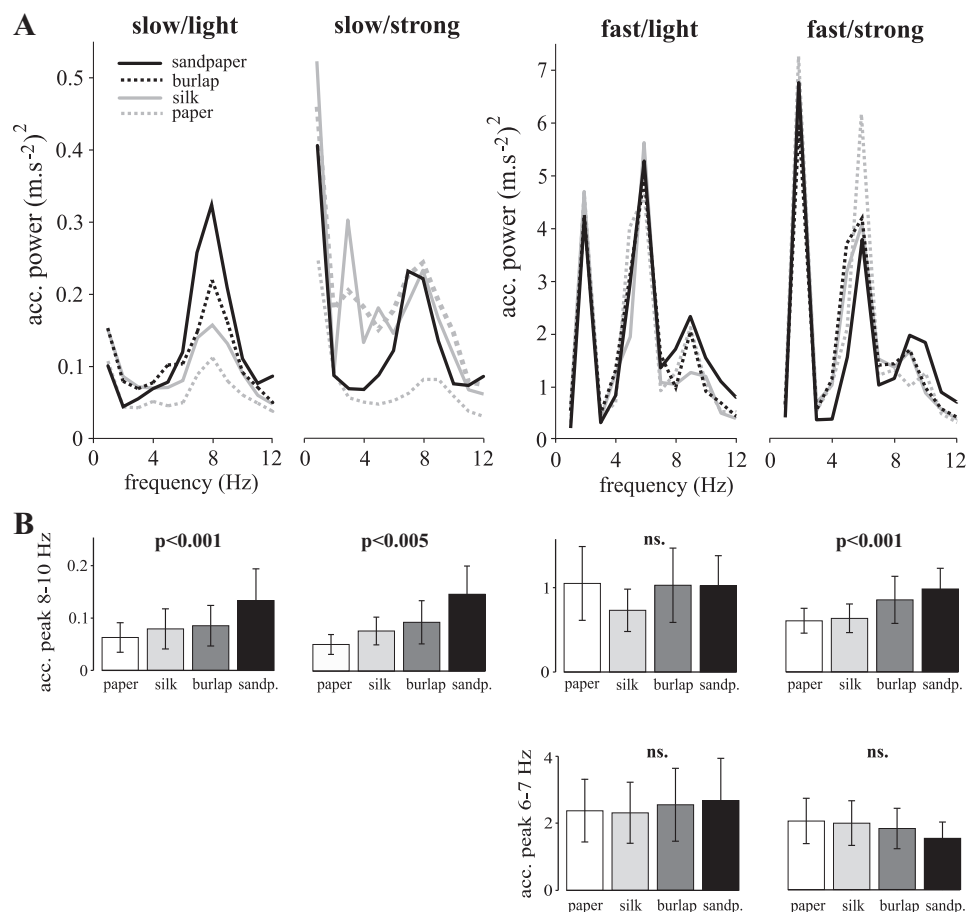


Fig. 4. Power spectra for different textures. **A**: in non-normalized power spectra, the amplitude of the peak of acceleration at ~ 10 Hz increases with textures of higher friction. In the fast conditions, additional peaks are observed in the 6- to 7-Hz range, but these are not affected by the friction of the textures. **B**: acceleration in the 8- to 10-Hz range or in the 6- to 7-Hz range was computed for each participant and separately for each texture and movement condition. Significant differences are observed in the 8- to 10-Hz range in the slow/light ($P < 0.001$), slow/strong ($P < 0.005$), and fast/strong ($P < 0.001$) conditions. acc., Acceleration; ns., no significant difference; sandp., sandpaper.

peak in the acceleration spectrum and movement duration. This revealed a significant negative correlation, shown in Fig. 5D (Pearson's R for the fast/light condition: -0.73 , $P < 0.05$; fast/strong: $R = -0.78$, $P < 0.05$). The same analysis was repeated for the time taken for the lateral force to reach its maximum value during loading; again, a significant correlation was found (fast/light: $R = -0.71$, $P < 0.05$; fast strong: $R = -0.77$, $P < 0.05$). Hence, the shorter the overall movement duration and the shorter the time taken for the lateral force to reach its maximal value, the larger the amplitude of the 6- to 7-Hz acceleration peak observed in the fast conditions. We conclude that the oscillations observed in the 6- to 7-Hz range in the fast movements in the present study reflect a ballistic mode of movement execution.

Power spectra of acceleration for each texture: other peaks. When the power spectra for each texture was observed, three other phenomena were revealed. First, there was a broadband increase in acceleration power at all frequencies in all participants for the sandpaper in the slow conditions, in three of nine participants in the fast/light conditions, and in six participants in the fast/strong conditions. The same effect was found for the burlap in two participants and for all textures in two participants in the slow/strong condition. Second, in the fast/strong condition, a broadband increase in acceleration power was also seen at around 25 Hz for the sandpaper in five participants and also for the burlap in two of these participants. Third, a peak of large amplitude was found around 15 Hz in the slow/strong condition in one participant and in the fast/strong condition in

another participant. Illustrations of these three phenomena are shown in Fig. 6, A–C, left.

To analyze whether the periodic phenomena described above were also actively generated by muscle activity, we again calculated coherence between surface EMG and the acceleration. In neither of the participants was there any significant coherence between the EMG and the acceleration data for these cases (see Fig. 6, A–C, right).

Variations in movement speed and force as a function of texture friction. Previous studies have reported that the amplitude of the peak of acceleration increases with the movement speed (Vallbo and Wessberg 1993; Wessberg and Kakuda 1999) or with the amount of force used (Vaillancourt et al. 2003). In the present study, to test for confounding effects (i.e., that the change in the acceleration peak may be due to changes in the movement speed or force applied to each separate texture), we computed the movement speed and forces of each texture. Statistical analyses revealed the existence of variations in movement speed as a function of the texture in the fast conditions only [fast/light: $t(9) = 3.1$, $P < 0.05$; fast/strong: $t(9) = 3.1$, $P < 0.01$]. Variations in normal force as a function of the texture were significant for all conditions ($P < 0.05$). However, the movement speeds and the normal forces were in general smaller with textures of higher friction and often similar between the three textures of lower friction (see Fig. 7), which suggests that the effect found regarding the amplitude of the peaks of acceleration is not mediated by local variations in speeds or forces.

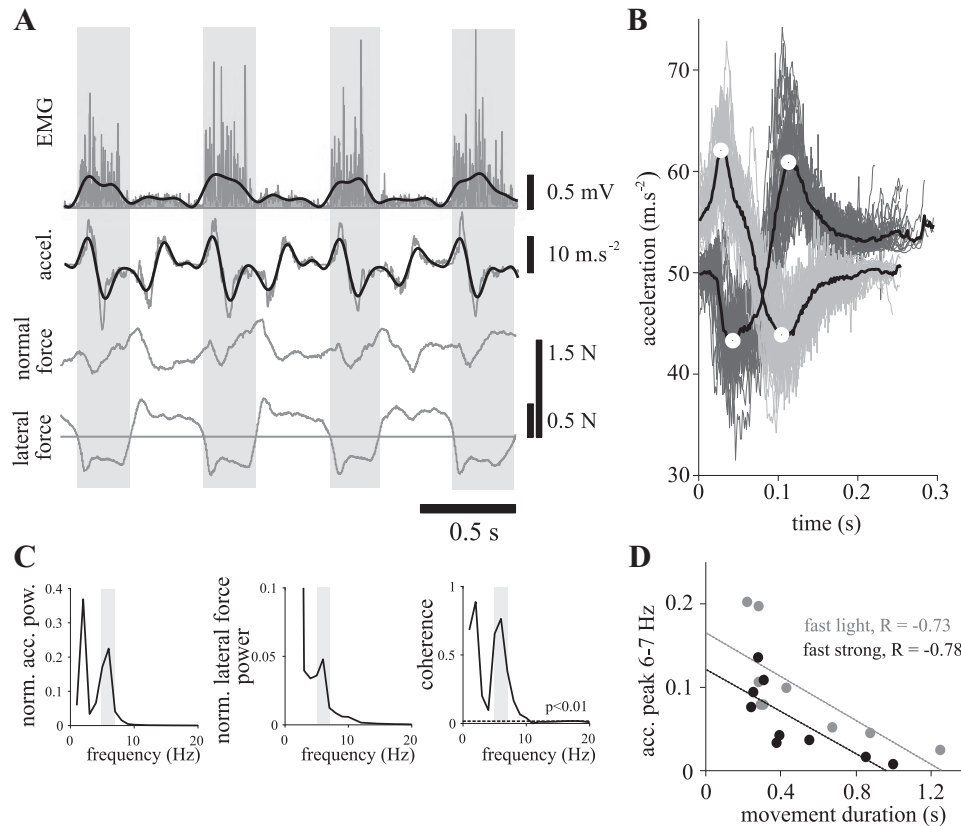


Fig. 5. Origin of the peaks of acceleration in the 6- to 7-Hz range. *A*: electromyography (EMG), acceleration, normal force, and lateral force signals are presented for the participant showing the largest peak in the 6- to 7-Hz range (the same as Fig. 3*B*) in the fast/strong condition. Low-pass-filtered signals of 12 Hz are superimposed on the raw records. Timing of movements in the radial direction is highlighted with shading. *B*: measurement of latency from first acceleration to first deceleration peak (i.e., half of a full cycle). Acceleration records from onset of all fast movements of a trial from the same participant as in *A* are superimposed. Bold black line shows the average. Open circles indicate locations of peaks. The group-average half-cycle duration was 0.081 s, which corresponds to a full cycle of 0.162 s, or 6.2 Hz. *C*: power spectra of the 12-Hz low-pass-filtered records of acceleration (*left*) and lateral force (*middle*) for all fast movements for the same participant. The peak at 6–7 Hz reflects the acceleration-deceleration pattern at onset of movements, shown in *A* and *B*. The peak at lower frequency (1–2 Hz) reflects the overall tempo of execution of the fast movements. Coherence between acceleration and lateral force for fast movements is shown (*right*). *D*: significant negative correlation between the amplitude of the 6- to 7-Hz peak in the acceleration spectrum and movement duration in the fast/light ($R = -0.73$, $P < 0.05$) and fast/strong conditions ($R = -0.78$, $P < 0.05$). acc. or accel., Acceleration; norm., normalized; pow., power.

DISCUSSION

We report that the ~10-Hz modulation of motor output that is generated during execution of finger movements persists when the finger is touching a surface. In addition, the ~10-Hz modulation is affected by the frictional properties of the texture of the touched surface. We suggest that these findings strongly support the hypothesis that ~10-Hz modulation of motor output is engaged in an active touch sensing system.

The ~10-Hz signal persists during touch and reflects the textures' features. In the slow conditions in the present study, peaks were observed within the 8- to 10-Hz range. This confirms the results from previous studies, where acceleration was measured in a freely moving finger or wrist (Vallbo and Wessberg 1993; Wessberg and Kakuda 1999). In the fast conditions, double peaks were often observed with a first peak being observed in the 6- to 7-Hz range and a second one in the 8- to 10-Hz range. Analysis of the coherence between surface EMG of one of the prime movers (the first dorsal interosseous; radial deviation) and the acceleration signals confirmed that the acceleration signal had a muscular origin both in the 6- to 7-Hz range and in the 8- to 10-Hz range.

In the study of Kakuda et al. (1999), peaks were reported in the 6- to 12-Hz range for wrist movements. Other studies have

reported double peaks coexisting in the 3- to 6-Hz range to the 8- to 10-Hz range for long and strong contractions of the hand (wrist raised and extended) or fingers (Gottlieb and Lippold 1983; Stiles 1976), with added loads on the contracted fingers (Brown et al. 1982), or when the inertia of the forearm was larger compared with the finger (Jacks et al. 1988; Prochazka and Trend 1988). In the present study, wrist movements were minimized by the experimenter's instructions to move the index finger only and to lightly grab the arm support with the other fingers. Close inspection of the videos confirmed the absence of wrist movement. However, with more muscular tension in the high-force conditions, contraction of the forearm was clearly visible in the fast conditions compared with the slow conditions. Quantifying the extent of forearm movement by tracking a marker at the dorsum of the wrist confirmed that there was more movement in the fast conditions, but there was no correlation between forearm movement and the amplitude of the 6- to 7-Hz acceleration peak in the finger.

The videos also showed a tendency for the thumb to move together with the index finger during the fast conditions. As a control, one participant was asked to voluntarily move the thumb and the index together while touching a textured surface, and to move the index only, the thumb only, and to move

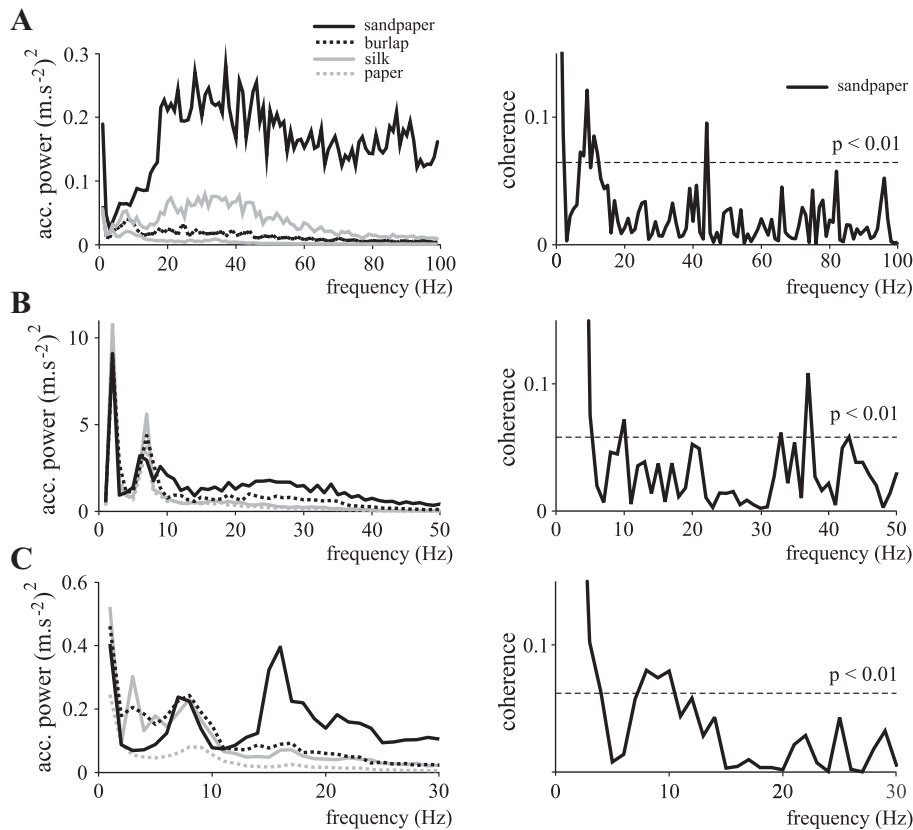


Fig. 6. Other periodicities. A–C, *left*: power spectra of acceleration data are shown for each texture in 3 special cases: a broadband increase in acceleration power was found for sandpaper at all frequencies (A), a broadband increase in acceleration power was found for sandpaper around 30 Hz (B), and a peak of large amplitude was found for sandpaper around 15 Hz (C). *Right*: coherence between the acceleration and electromyography data is shown for sandpaper. The signals are coherent around 10 Hz only ($P < 0.01$), suggesting that these phenomena were not actively generated by the motor output but were mechanical contaminants. acc., Acceleration.

at diverse speeds. We did not observe any acceleration peaks at 6–7 Hz when the thumb was engaged.

In the participants showing the double peaks in the 6- to 7-Hz and in the 8- to 10-Hz ranges, the acceleration signal was dominated by large oscillations, an acceleration-deceleration pattern, which occurred systematically at movement onset. A similar pattern was seen in the lateral force, with an initial peak and reduced force during the sliding phase of the movement. Although transient, all these oscillations had a frequency of 6–7 Hz. We explored the hypothesis that this pattern reflected the dynamics of finger/texture interaction during the fast conditions, potentially leading to the skin being transiently stuck to the texture [see André et al. (2011) and Delhayé et al. (2014) for a description of the force dynamics occurring during texture exploration]. However, no correlation was found between the static coefficient of friction in the fast conditions and the amplitude of the 6- to 7-Hz peaks. Instead, we propose that the biphasic acceleration-deceleration pattern reflects a ballistic motor output during the fastest movements (Cooke and Brown

1990; Zehr and Sale 1994). Such movements are characterized by high velocity and acceleration, and are usually observed for movement durations inferior to 400 ms (Brown and Gilleard 1991). A short and strong burst of activity in the agonist is rapidly followed by activity in the antagonist muscle (Marsden et al. 1983; Osterig et al. 1986; Tyler and Hutton 1986); a final second agonist phase serves to terminate the execution (Wierzbicka et al. 1986). In the present study, the amplitude of the 6- to 7-Hz peak in the acceleration spectrum was significantly negatively correlated with both movement duration and the time for the lateral force to reach its maximal value, with the strongest 6- to 7-Hz peaks observed for movements of duration shorter than 400 ms. Altogether, these results suggest that the 6- to 7-Hz oscillations reflected the mode of movement execution used by some participants in the fast conditions, i.e., ballistic execution of the fastest movements.

In the present study, it is interesting to note that the 8- to 10-Hz periodic signal reflected the textures' features, with the amplitude increasing the higher the friction of the texture (Fig.

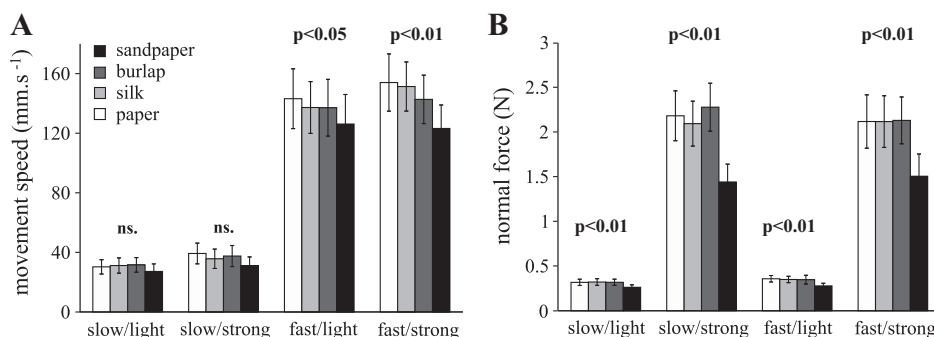


Fig. 7. Variations in movement speed and in normal force used to explore each texture. The movement speed (A) and normal force (B) decrease with the increase in friction. The results are significant in the fast conditions only for movement speed (light: $P < 0.05$; strong: $P < 0.01$) and in all conditions for normal force ($P < 0.01$). These results confirm that the changes observed in the ~10-Hz peak of acceleration are not explained by the relative changes in speed or force applied to each texture.

4A, left, and Fig. 4B). In the 6- to 7-Hz range, the peak amplitude tended to decrease with higher friction (cf. Fig. 4A, right), which was also seen for the more general movement descriptors, movement speed and normal force (Fig. 7). This supports the interpretation that the 6- to 7-Hz phenomenon reflects the mode of movement execution rather than the pulsatile modulation of the motor command at ~10 Hz, which would originate from a separate oscillatory brain mechanism. This finding suggests a specificity of the ~10-Hz signal to modulate tactile afferent signaling from the fingertip and to convey relevant information about the textures' features (see below).

The coherence analyses also revealed strong coherence around 20 and 40 Hz in some participants. This result was also found in a previous study (McAuley et al. 1997) in which slow movements of the finger were executed against an elastic band to render the periodic signals more visible in the high frequencies. This finding further confirms the similarities between the ~10-Hz phenomenon reported in the present and in previous studies.

The possibility that the amplitude of the ~10-Hz peak could depend on the more general movement kinematics was also evaluated in the present study. Indeed, previous motor control studies have reported an increase in the amplitude of the ~10-Hz peak with increasing speeds and forces (Vaillancourt et al. 2003; Vallbo and Wessberg 1993; Wessberg and Kakuda 1999). Hence, the increase in amplitude with textures of higher friction reported for the ~10-Hz peak could reflect variations in the speeds and forces used to touch each specific texture, with, for example, faster speeds and stronger force used to explore textures of higher friction. To evaluate this hypothesis, the speeds and forces used to explore the textures were computed separately for each texture and condition (see Fig. 7). In general, the movement speeds and forces decreased with textures of higher friction. This result contrasts with the effect obtained for the amplitude of acceleration in the ~10-Hz range, which is found to increase with texture of higher friction (see Fig. 4B). This suggests that the movement kinematics did not directly impact the amplitude of the ~10-Hz peak relative to each texture in the present study. The results obtained for the speed and forces replicates the results of a previous study (Tanaka et al. 2014) in which the effect was interpreted as reflecting a motor strategy to reduce the aversiveness and the abrasiveness of those textures. The same strategy may have occurred in the present study, parallel to the other phenomena reported. Taken together, these results suggest that the ~10-Hz active sensing mechanism may have served a distinct function than the active modulation of the movement kinematics and exploration forces, i.e., informing the brain about the texture's frictional properties in the former case, while reducing the sensations elicited by the textures of higher friction in the latter case.

Predicted impact of an ~10-Hz active touch sensing mechanism on sensory feedback. If the ~10-Hz signal generated during the execution of movements of the finger is part of a more general active sensing mechanism, then one can expect that the ~10-Hz modulation of motor output will in turn modulate the activity of the different classes of low-threshold mechanoreceptors in the skin touching the texture. SAI type (Merkel) afferent units are directly sensitive to low-frequency vibrations (Freeman and Johnson 1982; Johansson et al. 1982)

and are probably the best candidates to directly signal the ~10-Hz periodicity back to the central nervous system. However, the skin of the fingertip is laterally stretched during these movements, eliciting firing in SAI (Ruffini) units, which can be modulated by the ~10-Hz signal. In addition, it is likely that changes in acceleration due to the pulsatile output are accompanied of high-frequency vibrations when the fingertip is sliding on the surface with periodic variation in velocity. This would strongly excite FAI (Meissner) and FAII (Pacini) units, with periodic burst responses or periodic variation of the ongoing activity elicited by the surface features of the textures. Hence, any of the four types of skin mechanoreceptors could respond to the ~10-Hz stimulation depending on the exact way the skin is stimulated by the ~10-Hz signal. The assumption of the existence of an active sensing mechanism for touch also balances the current view that smooth textures are only coded temporally, via FAII units, with afferent activity reflecting high-frequency vibrations generated during the finger/texture interaction (Weber et al. 2013). We suggest that other mechanisms may be engaged in natural active touch, compared with the passive stimulus conditions that have mainly been employed for the study of tactile signaling of surface texture.

Relevance of a ~10-Hz active touch sensing mechanism to the neural processing of touch. The existence of an ~10-Hz active sensing mechanism for touch in humans would have several implications and advantages in terms of neural processing. Regarding information processing, the mechanism resembles pulse-amplitude modulation, the advantage of which is to render a signal more distinct in terms of signal-to-noise ratio and less sensitive to interference (Haykin 1988; Shanmugam 1979; Wessberg 1995). Pulse-amplitude modulation is also used in communication engineering to transmit a signal over longer distances. Accordingly, transferring information through pulse-amplitude modulation could help sensory information to be preserved in the ascending signal pathways to the brain. The fact that sensory information appears at the same frequency as the motor signaling, but with a constant delay (or phase shift) with respect to the motor information, could also be a way to "label" the sensory information as the consequences of the action of the agent, an idea suggested by Diamond and Arabzadeh (2013). Based on the finding that coherence is also found between visual and motor channels during visuomotor tracking (McAuley et al. 1999), one could also think that the generation of a ~10-Hz signal could be a way to identify multisensory sources of information (visual, tactile, auditory) as belonging to the same context.

Conclusion and Future Directions

In the present study, we proposed the idea that an active touch sensing system exists in humans. The mechanism shows similarities to the one described in rodents, i.e., with a periodic signal being emitted in direct contact to the object to analyze. We found that the ~10-Hz signal generated during the execution of slow movements of the fingers in humans persisted during active touch conditions and that the signal was affected by the intrinsic qualities of the textures that were being touched. We intend to use microneurography to record from single afferents from the fingertip to examine if and to what extent the skin mechanoreceptors are affected by the ~10-Hz signal in active touch. With the use of magnetoencephalogra-

phy or electroencephalography, it also should be possible to further analyze whether activity in somatosensory cortical areas during active touch reflects the ~10-Hz modulation of central motor output, with a phase lag corresponding to delay through the motor and sensory pathways.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

M.D. and J.W. conceived and designed research; M.D. performed experiments; M.D. and J.W. analyzed data; M.D. and J.W. interpreted results of experiments; M.D. prepared figures; M.D. drafted manuscript; M.D. and J.W. edited and revised manuscript; M.D. and J.W. approved final version of manuscript.

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