Title: Human ability to discriminate direction of 3D force stimuli applied to the finger pad

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Abstract

Sensory information from tactile mechanoreceptors located in the glabrous skin of the hand is crucial for skillful object exploration and manipulation. These mechanoreceptors reliably encode the direction of fingertip forces and the brain certainly relies on this information in both sensorimotor and cognitive tasks. In this study we have examined human ability to discriminate the direction of force stimuli applied to the volar surface of the index fingertip on the basis of tactile information only. We show that humans can discriminate 3D force stimuli whose directions differ by an angle as small as 7.1 deg in the plane tangential to the skin surface. Moreover, we found that the discrimination ability was mainly affected by the time-varying phases of the stimulus because adding a static plateau phase to the stimulus improved the discrimination threshold only to a limited extent.

Keywords

Psychophysics, force direction; tactile physiology; human skin; haptics
Introduction

Sensory signals critical for object manipulation and haptic identification are generated by receptors located in the skin and subjacent structures (Vallbo and Johansson 1978; Jones and Lederman 2006). Considerable efforts have been directed to elucidate the signals generated in tactile afferents when the skin is stimulated with controlled forces and various surface curvatures (Birznieks et al. 2001; Johansson and Birznieks 2004; Birznieks et al. 2009; Goodwin et al. 2001; Goodwin and Wheat 1992).

While the human ability to perceive and discriminate direction of force stimuli applied to the fingertips has received little attention in the psychophysics literature it has recently gained interest in the field of virtual environments and teleoperation systems (Robles-De-La-Torre 2006; Barbagli 2006; Panarese et al. 2009). These studies have focused on different skin regions (e.g., hand, finger) and used experimental conditions in which the finger or the hand was free to move, i.e., situations in which both proprioceptive and tactile sensory signals might have contributed to the percept and, accordingly, they shed little light on the specific contribution of the tactile sensory system (Pongrac et al. 2006; Yang et al. 2008; Dorjgotov et al. 2008). When humans, for instance, are asked to reproduce the magnitude and direction of forces applied to their hand through a joystick, the RMS error of their responses was on average ~18 deg (Toffin et al. 2003). Moreover, human ability to perceive direction of force stimuli applied to the hand seems to depend on the direction of the reference stimulus (Elhajj et al. 2006). Studies in which force stimuli were applied to specifically activate tactile afferents have focused on rather small forces (typically <1N) and addressed issues of scaling and discriminating force magnitudes rather than identifying force directions. For example, it has been shown that humans are able to scale the magnitude of force stimuli applied to the fingertip both normally and tangentially with respect to the skin-tangential plane (Goodwin et al. 1992; Parè et al. 2002). We know that human can discriminate normal forces independent of surface curvature (Goodwin and Wheat 1992), and a Weber fraction of 0.16 was found for the discrimination of force stimuli with different magnitude applied tangentially to the skin, independently of the stimulus direction (Wheat et al. 2004). Moreover, humans can scale the magnitude and direction of force stimuli
applied to the hand (Toffin et al. 2003; Pongrac et al. 2006; Yang et al. 2008; Dorigotov et al.
2008), and estimate total force magnitude independently of the size of skin normal and
tangential force components (Paré et al 2002).

Information is still, however, scarce regarding the ability of humans to discriminate force
direction. For instance, when force stimuli in different directions were delivered to the fingertip
through a thimble while the thimble-bearing finger was free to move, humans display
discrimination thresholds of ~30 deg (Barbagli et al. 2006; Tan et al. 2006). The discrimination
threshold in this task was dependent on simultaneous visual information but not on the
direction of the reference force direction.

In this study we have assessed the specific contribution of tactile afferents to the human ability
to discriminate the direction of force stimuli applied to the fingertip. To identify the specific
contribution of glabrous skin mechanoreceptors for encoding force direction and the
dependence of this encoding on dynamic and static stimulus phases we applied forces with a
magnitude (5N) and dynamics (<2Hz) similar to those observed during manipulation to an
immobilized fingertip. We report considerably lower discrimination thresholds than previously
known and conclude that humans rely primarily on the dynamic phases of force stimuli in this
task.

Materials and Methods

Participants and general procedure

Twelve healthy males (age 24-28 years old, all right-handed) gave their informed consent to
participate in the experiment. During the experiment, each subject was seated on an office chair
with the elbow placed on a table. The right upper arm was at ~45 deg with respect to the trunk,
the elbow flexed at ~120 deg with respect to the upper arm, and the palm was in the vertical
plane. The forearm and the ulnar part of the hand rested on a wooden support covered with
soft foam. The index finger of the right hand was splayed and its dorsal aspect was embedded
in plasticine up to the midlevel of the middle phalanx. To stabilize the distal phalanx, the nail
was glued to a plastic rod subsequently sunk into the plasticine (cf., Birznieks et al. 2001). The skin of the distal phalanx did not contact the plasticine. The subject was asked to bend the remaining digits and the thumb around a manipulandum placed at the level of the middle palm and fixated to the wooden support for the forearm and hand (Fig. 1A). Headphones and a wooden flat screen placed between the subject and the computer-controlled stimulator masked all auditory and visual cues.

**Apparatus**

Mechanical stimuli were delivered to the tip of the finger by means of a commercial game 3D controller (Novint Falcon, Novint Technologies Inc., Albuquerque, NM, USA) modified to operate as a precision computer-controlled stimulator allowing control of force and position in three dimensions (Fig. 1; Panarese and Edin 2011). The modified controller was equipped with a six-axis force/torque transducer (F/T Nano17, ATI Industrial Automation, Garner, NC, USA) and to the other end of the transducer a square (17 mm side) flat wooden surface was attached to contact the skin (Fig. 1A). A layer of bi-adhesive tape was used to keep the tip in stable contact with the skin of the fingertip also during experimental phases with zero normal force.

The signals from the F/T transducer were used both to monitor the contact force and for force-feedback control of the tip in three dimensions, the latter realized by a software-based control algorithm. The contact force was measured as three orthogonal components: two in the plane of the contact surface (along the distal-proximal direction and along the radial-ulnar direction of the fingertip) and one normal to the surface (resolution 2.5 mN rms, bandwidth 0-1.2 kHz). The force control loop (0–10 Hz bandwidth) permitted both an accurate and robust delivery of force stimuli with normal and tangential (with respect to the skin-tangential plane) time-varying components. For data aggregated across 12 subjects, the actual force stimulus differed <0.3% from the desired stimulus during static force stimulation, and 2.6% of the peak force value during dynamic force stimulation. These variations were consistent across different directions and across subjects, i.e., the controller compensated for both anisotropic fingertip properties and inter-subject variability. Based on 2,304 trials (12 subjects × 48 directions × 4
repetitions), the r.m.s. value of the standard deviation of the applied force stimulus was 15 mN (range 7.3–21 mN) for static force phases, 74 mN (56–97 mN) for force-increasing phases, and 37 mN (26–65 mN) for force-decreasing phases (Fig. 1B-C).

The Novint Falcon has three built-in encoders, whose recordings were used to implement a position control loop to return the tip into its original position after each force stimulus. The actual position of the stimulator tip after the replacement differed from the desired value by a mean value of 150 µm. To obtain precise measurements of the tip position for monitoring purposes, we placed IR reflective markers on the Falcon end-effector and tracked their displacement by means of REMAC, a video-based motion analyzer (Sandström et al. 1996). The system tracked the markers placed on the surface perpendicular to the plane of the CCD camera and on the sides of the end-effector viewed by the camera through a mirror. The frame rate was ~100 Hz and the positions were measured with a resolution of ~10 µm.

**Force stimuli and subjects’ task**

The stimulation probe was placed centered on the midpoint of a line extending in the proximal-distal direction from the papillary whorl to the distal end of the fingertip, that is, centered on the flat portion of the volar surface of the fingertip. The computer-controlled stimulator was oriented such that the z-axis of the F/T transducer (and of the Falcon coordinate system) was perpendicular to the skin surface at the site of contact. At the beginning of the experiment, the experimenter manually set the tip of the stimulator on the primary contact site and commanded the stimulator to apply a constant normal offset force of 0.5 N. A series of stimulation trials was then presented to the subject. In each trial a sequence of two stimuli was presented. The first stimulus of each sequence was the “reference” and always pointed towards a fixed direction close to the long axis of the index finger. The second stimulus always pointed towards a different direction. Each stimulus consisted of a force protraction phase and a force retraction phase both lasting 250 ms. During these phases the time course of the normal and tangential forces followed a half-sinusoid (sine wave frequency of 2Hz). Thus, for the force protraction phase, the stimulus started at the offset value (0.5N for the normal component and 0N for the tangential) and ending at the peak value. The force stimuli delivered had a total magnitude of
5N (offset + stimulus) and were always delivered at an angle of 20 deg with respect to the direction normal to the skin; the peak normal force was thus ~4.7N and the peak tangential force ~1.7N. In the Plateau sessions a force plateau lasting 500 ms was interposed between the protraction and retraction phases whereas no such plateau was present in the No Plateau sessions. Stimuli were delivered in pairs separated by 500 ms. At the end of the retraction phase, the forces approached the offset values again. Each session lasted for ~25 min and the subjects were allowed to rest for 5-10 min between the sessions that were run in a balanced order across the subjects. Their index finger was stabilized again in the plasticine before the new session started.

The participants were asked to report the direction of the second stimulus of each pair with respect to the first stimulus by using their left hand to press one of two buttons on a remote control. The remote control was kept orthogonally with respect to the table plane, such that the positions of the buttons were spatially congruent with the stimuli directions. Specifically, when the participants wanted to express ‘clockwise’, their left thumb moved upward to push the right button on the remote control. Their responses were prompted by a sound delivered 500 ms after the end of the second stimulus. Once the participant had responded, a second sound provided feedback of result. At the same time, the tip of the stimulator was returned to the starting position. The exact re-alignment of the tip between trials could not be guaranteed by the force servo alone because of the nonlinear viscoelasticity of the finger pad (Pataky et al. 2005). Repositioning was achieved by the servo that switched from force control to position control along the skin contact plane while remaining in force control along the normal direction attaining a final force value of 0N. After the realignment phase, which lasted 2 s, the servo switched to force control also in the tangential directions, the 0.5N offset along the normal direction was re-established, and 2 s later a new stimulation cycle commenced.

Data collection and analysis

Force signals were acquired and digitized at 10 kHz (16 bits resolution) using a USB DAQ board (USB-6251, National Instruments Corp., Austin, TX, USA), averaged and sub-sampled at 500 Hz using a custom software application written in MS Visual C++ on a Windows XP
operating system (Microsoft Corp., Redmond, WA, USA). The position of the stimulating tip was acquired via the USB of the Novint Falcon at 500 Hz. Both force and position signals were stored on a notebook PC.

Position signals were acquired by the SC/ZOOM sampling system (Physiology Section, IMB, Umeå University) at 100 Hz and stored on a different PC. Position data from Falcon and REMAC were synchronized offline.

For each trial, the subject’s response was stored along with information about the trial type, the desired force vector components for both the stimuli, the time series of the measured x-y-z forces delivered to the fingertip, the x-y-z position of the stimulator tip, and the time lag between the end of stimulation and the subject’s response.

**Parameter estimations and fitting procedures**

We used an adaptive variant of the method of constant stimuli to estimate the subjects’ discrimination thresholds (Treutwein 1995). This procedure adjusted the direction of the comparison stimulus according to the outcome of an on-line parametric estimation of a psychometric function. The session was divided into blocks and each block consisted of 4 repetitions of 8 trials. During the initial block of trials, the 8 variant stimuli were delivered in random order at [-20, -15, -10, -5, +5, +10, +15, +20] deg with the reference direction being 0 deg.

The subject’s probability to respond ‘clockwise’ was fitted to a normal cumulative distribution function (normal CDF):

\[
P_{ck}(\varphi, \mu, \sigma) = \frac{1}{\sigma \sqrt{2\pi}} \int_{-\infty}^{\varphi} e^{-(x-\mu)^2/2\sigma^2} dx
\]

(eq. 1)

and the \( \varphi \) to be used in the following block was determined on the basis of the estimated distribution. The slope of this curve (e.g., Fig. 2C) depends on both the subject’s responses to direction \( \varphi \) and the estimated \( \sigma \). The stimulus angle corresponding to 50% of the estimated distribution was defined as the ‘point of subjective equality’ (PSE), while the distance from PSE to the stimulus angle corresponding to the 75% of the estimated distribution was defined as the ‘discrimination threshold’. Thus, in the equation above, \( \mu \) corresponded to PSE and \( \sigma \) was
proportional to the discrimination threshold. After the fitting procedure, eight new variant
stimuli were obtained for the subsequent block (4 repetitions of 8 stimuli) corresponding to the
normal CDF values of 22, 30, 38, 46, 54, 62, 70 and 78%, i.e., 4 directions clockwise and 4
counter-clockwise compared to PSE. The procedure thus adaptively adjusted the stimuli
directions such that the new range was centered on the best available estimate of PSE and
encompassed the estimated threshold. From extensive pilot experiments we learned that stable
estimates of PSE and discrimination thresholds were obtained after repeating 6 blocks of trials,
i.e., 192 trials. Outliers were identified by computing the probability that they belonged to the
distribution defined by the remaining values. Two estimates were excluded: the threshold value
of subject 8 during the session Plateau ($P(\text{th}_8 | \mu_{\text{P}}, \sigma_{\text{P}}) = 0.006$) and of subject 7 during the
session No Plateau ($P(\text{th}_7 | \mu_{\text{NoP}}, \sigma_{\text{NoP}}) = 0.029$).

**Finding variables putatively involved in the decision process**

The force trajectories differed consistently between stimuli in different directions but so did the
movement and velocity of the probe as well as the peak force rate. All of these physical
variables were of course correlated with the stimulus direction and presumably also with the
afferent discharges upon which the subjects decided between ‘clockwise’ and ‘counter-
clockwise’. We were interested in determining which ones were most likely to be related to the
subjects’ decision processes. In particular, we focused on the force and probe position along the
ulnar-radial direction of the fingertip, and their respective first time derivatives. Due to the
anisotropic properties of the human fingertip (Nakazawa et al. 2000), the relationship between
force and position differs depending on the stimulus direction, i.e., the position and velocity of
the probe depends on both the stimulus force and stimulus direction. Accordingly, it was
meaningful to investigate both force and position with respect to the subjects’ responses.

For each subject, we considered six variables (termed ‘x’ hereinafter): peak force, peak position,
and during both the protaction and retraction phases, the peak velocity and peak force-rate. We
categorized the above variables as a function of the stimulus direction, $\phi$, as follows: we (1)
low-pass filtered both the reference, $x_r(t)$, and the test stimulus curve, $x_t(\phi, t)$, (2) time aligned
the curves and calculated their difference $\Delta x(\phi, t) = x_t(\phi, t) - x_r(t)$, and (3) estimated the means,
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\( \mu_{x_{\Delta}}(\phi_i) \), and standard deviations, \( \sigma_{x_{\Delta}}(\phi_i) \), across repetitions, of the peak value, \( \Delta x_{\text{peak}} \), assumed by

the variable \( \Delta x(\phi, t) \) during stimulus phases which differ according to the chosen variable \( x \). For

position and force curves, peak values were estimated during the entire stimulus time window; for velocity and force-rate, peak values were estimated during either protraction only or retraction only. Peak values could assume either positive or negative values. We conducted two parallel analyses which differed by the cutoff frequency used for the low pass filter, i.e. 5 Hz and 50 Hz. Our purpose was to analyze how the decision process was complementarily affected by slowly and fast adapting afferents. In fact, low-pass filtering at 5 Hz drastically reduces frequency components to which FA afferents are sensitive, thus leaving SA afferents mainly contributing to the decision process.

For each variable \( x \), the decision process-related variable \( \Delta x_{\text{peak}} \) was normally distributed with mean \( \mu_{x_{\Delta}}(\phi_i) \) and standard deviation \( \sigma_{x_{\Delta}}(\phi_i) \) for each applied stimulus direction. We then computed the probability that the stimulus direction was ‘clockwise’ with respect to the reference as follows:

\[
P_{\text{clockwise}}(\phi_i) = \frac{1}{\sigma_{x_{\Delta}}(\phi_i) \sqrt{2\pi}} e^{-\frac{(s - \mu_{x_{\Delta}}(\phi_i))^2}{2\sigma_{x_{\Delta}}^2(\phi_i)}} dx.
\]  

(eq. 2)

Probability values at different stimulus directions \( \phi_i \) were then fitted by a normal cumulative distribution (eq. 1). This distribution represented the ‘decision function’ based on the variable \( x \) and was thus analogous to the subjects’ psychometric functions.

We were interested to find which one of measured variable best explained the subjects’ psychometric functions: if the decision function based on the variable \( \Delta x_{\text{peak}} \) best matched the subjects’ psychometric functions, \( x \) should be considered the best candidate for explaining the behavioral results. The estimated \( \sigma_{x_{\Delta}}(\phi_i) \) were not, however, representative of the noise affecting the neural representation of the signal \( x \), based on which the subjects took decisions. As expected, none of the decision functions estimated using eq. 2 resembled the subject’s psychometric function as all of them were considerably steeper simply because the stimuli conveyed to the subject were highly repeatable and the signals acquired by the sensors were corrupted by very little noise.
We therefore considered the measured $\Delta x(\phi)$ to be known but $\sigma_{\Delta x}$ to be unknown and looked for the values of this latter parameter which would yield the decision curve that best matched the subject’s psychometric curve. To solve this nonlinear optimization problem, we applied a standard algorithm based on the simplex search method (Lagarias et al. 1998). Prior to the optimization $\Delta x(\phi)$ was offset so that $\phi = 0$ corresponded to $\mu_{\Delta x}$ at the stimulus direction of PSE. It must be noted that the parameter $\sigma_{\Delta x}$ by itself could not be varied in order to make a perfect fit between any variable based decision function and the subject’s psychometric curve. In fact, the basis function used for the non-linear optimization seeks to find the minimum of a scalar function defined as the sum of the squared differences between the subject’s probability to respond ‘clockwise’, $P_{CK}(\phi)$ and the probability that the stimulus direction was ‘clockwise’ with respect to the reference, $P_{CK}^{rin}(\phi)$. Therefore, the optimum $\sigma_{\Delta x}$ represented the noise value which yielded the best matching between these two series of probabilities, and not between the subject’s psychometric curve and the $x$-based decision function. If, for example, the subject’s discrimination ability was similar in both ulnar and radial directions but $x$ changed much less with stimuli in ulnar direction (or vice versa), the matching between the two series of probabilities would necessarily be poor.

Since the transfer functions that described the neural signals as a function of the measured variables were unknown, we tested both linear and non-linear (power functions and logarithms) transformations of the variables and both constant and proportional noise (i.e., with and without ‘signal-dependent noise’).

The quality of the fits were quantified as the mean absolute difference between the fitted decision function and the estimated psychometric function for each subject and stimulus type ($Plateau$ and $No Plateau$) and analyzed by means of a repeated measure ANOVA (2 cutoff frequencies $\times$ 2 session types $\times$ 6 variables). The statistical significance level was set to $p<0.05$.

### Results

The subjects’ task was to identify the direction of a force stimulus delivered subsequently to a reference stimulus to the fingertip of the index finger (i.e., a two alternative forced choice paradigm).
Figure 2 summarize the results from a single subject for the Plateau session. We estimated the cumulative probability function of responding ‘clockwise’ as a function of the stimulus direction, $\phi$, from the measured responses to a number of specific stimulus directions (Fig. 2C). The discrimination threshold for this subject was estimated to be 7.9 deg (4.9–12 deg; 95% confidence interval) and the point of subjective equality (PSE) was estimated to be -1.1 deg (-3.2–1.1 deg), values that were close to the mean values obtained across all subjects (Fig. 3).

Figure 3 shows the individual discrimination thresholds and PSEs for all participants. The average discrimination threshold during the Plateau sessions was 7.1 deg (range 4.3-12 deg), while the value for the sessions with dynamic phases only, i.e., the No plateau sessions was 10 deg (7-14 deg). This difference in performance between sessions was statistically significant (Wilcoxon Matched Pairs Test, $T_{10}=2$; $p=0.0093$) and did not depend on the order in which the sessions were presented, i.e., if a subject first experienced the Plateau session and then the No Plateau session or vice versa (Mann-Whitney U-test, $p>0.15$).

The mean PSE was close to zero during both Plateau and No Plateau sessions (Wilcoxon Matched Pairs Test, $T_{10}=24$; $p=0.72$): -0.8 deg (-4.6 – 2.2 deg) during the Plateau session and -0.6 deg (-7.8 – 5.2 deg) during the No Plateau session. Notably, the directions of the PSEs were not consistent within participants across sessions. The PSEs and discriminations thresholds were not correlated during either type of session ($r^2 \leq 0.006$, $p \geq 0.8$).

Trials with clockwise or counter-clockwise test stimuli generated different compression patterns not necessarily leaving the fingertip in identical final mechanical states. This means that, although the stimulator was carefully repositioned before each new stimulus pair, the initial skin conditions might have varied between trials. To assess any effect of previous stimuli on the subjects’ performances, we estimated PSE separately for stimulus pairs preceded by clockwise and counter-clockwise stimulations. A $2 \times 2$ repeated measures ANOVA with the factors session type (Plateau and No plateau) and preceding test stimulus direction (clockwise and counter-clockwise) revealed a significant but small main effect of session type (a difference of 0.5 deg; $F_{1,9}=13.5$, $p=0.005$) and a significant interaction effect ($F_{1,9}=7.2$, $p=0.025$). The estimated PSE for the Plateau sessions but not for the No Plateau sessions were biased towards clockwise directions.
when the previous stimulus was counter-clockwise and vice versa. Similar analyses on the effect of history on the estimated threshold yielded no significant results.

In a substantial number of cases the 95% confidence intervals of the estimated PSE values did not cross 0 deg (Fig. 3A). The experimental protocol itself did not promote such biases. The previous analysis revealed an ‘after-effect’ of previous stimulations on PSE (cf., Fig 2B), but this could not account for this bias since the previous stimulation direction was completely balanced in all sessions.

Next we addressed which measured variables best explained the subjects’ psychometric functions. For several reasons we could not expect that the recorded signals as such would illuminate this issue. First, the transfer functions that describe the relationship between the afferent signals and the mechanical variables are complex and may not only be non-linear (e.g., resembling power functions) but also display signal-dependent noise. Moreover, decisions based on the recorded signals would have been much more accurate than those of the subjects given the high repeatability of the stimuli and the low noise of the sensor (e.g., the force recordings in Fig. 4A). We reasoned that if the decision function based on a transformed variable – e.g., linear or power function of the variable with or without signal-dependent noise – resembled the subject’s psychometric function, the corresponding variable should be considered candidate for explaining the behavioral results. Unexpectedly, the best fits were invariably found with the simplest possible transformations, i.e., linear transformations with fixed noise (i.e., $\sigma$

We explored six apparently pertinent variables – the maximum deviation in position and force and the maximum velocity and force rates during the protraction and retraction phases – in a 2×2×6 repeated measure ANOVA (2 cutoff frequencies (5 and 50 Hz) × 2 session types (Plateau and No Plateau) × 6 variables). The quality of the fits depended on the cutoff frequency of the low-pass filtering ($F_{1,9}$=95, $p<10^{-5}$) but also on the variable used for fitting ($F_{5,45}$=22, $p<10^{-6}$). The mean residual errors showed a consistent pattern across cutoff frequency and session type, i.e., the best fits were obtained with force, peak force rate during the retraction phase, and the position ($p<2\cdot10^{-5}$; Fig. 4B). Moreover, with the 0-50Hz filtering, the residual
errors of the fits obtained with force and peak force during the retraction phases were similar but both were significantly smaller than that of position (p<0.04). To illustrate representative data, we show data from a single subject for the No Plateau condition (Fig. 4C, D). Of the six variables explored, the way the force varied with stimuli directions in this subject provided the best explanation to this subject’s psychometric function. We reasoned that if a variable was able to 'explain' the subjects’ behavior, $P_C^\phi(\phi)$ plotted against the mean of the variable at each stimuli directions $\phi$, would be represented by a smooth monotonously increasing curve. Indeed, the force and the peak force-rate during the retraction phase seemed to be tightly coupled to this subject’s decision process (Fig. 4D; for comparison the leftmost panel shows $P_C^\phi(\phi)$ plotted against the actual test directions).

We were also interested in the cognitive strategies reported by the subjects. Unfortunately, statistical tests of the effects lacked power because the strategies varied widely. 3/12 subjects reported creating mental images of the finger and the stimuli, and using these to compare the stimuli of each pair. They specifically reported trying to visualize the area of the finger or the position on the finger where the stimulator was pushing toward. The rest of the subjects (9/12) reported relying only on tactile cues when discriminating between the stimuli: 4/9 specifically reported to use tactile information from the nail, 2/9 to use position information about the tip of the stimulator, 1/9 to use skin stretching information, while the remaining 2/9 were unable to specify their strategy. Two subjects reported to be biased to respond counter-clockwise when they felt uncertain: subject #2 only for the Plateau sessions and subject #9 for both sessions.

Analysis of response latencies failed to reveal statistical difference between the two types of sessions, although the response latencies during the Plateau session on average were slightly shorter than during the No Plateau session (844 vs 932 ms; 932-Wilcoxon Matched Pairs Test, $T_{12}=16; P = 0.07$). Moreover, the estimated discrimination thresholds were not correlated with mean response latencies for either type of sessions ($r^2 \leq 0.02$, $p \geq 0.72$).
We have shown that subjects can discriminate the direction of 3D force stimuli applied to the volar surface of the fingertip with a discrimination threshold of $\sim 10$ deg for dynamic stimuli and slightly better ($\sim 7$ deg) for stimuli incorporating an additional plateau phase. Information about the direction of force stimuli are encoded by human tactile afferents whether by a firing-rate-based or time-based code (Birznieks et al. 2001; Johansson and Birznieks 2004). The dynamic phases of force stimuli are known to be particularly well encoded by FAI afferents whereas SAI afferents encode both dynamic and sustained force stimuli (Macefield et al. 1996). SAII afferent and in particular the so-called SAII nail units may also have contributed to the subjects’ decision processes (Birznieks et al. 2009). Our results suggest that a main part of the sensory inputs that allowed subjects to discriminate force direction occurred during the dynamic stimulus phases because adding a static plateau phase to the stimulus reduced the discrimination threshold only to a limited extent. This fits well with the conclusions from a recent study of the information conveyed by tactile afferent neurons in response to stimuli similar to those used in the present study (Saal et al, 2009): very little additional information about force direction is provided by the FAI and SAI afferents after the latter part of the dynamic protraction phase. Therefore, we suggest that the improvement in performance when the trials included a plateau phase may not be attributable to the afferent inputs per se but to more refined processing that the nervous system applies to immediately preceding afferent inputs during the short-lasting static phase.

Barbagli et al. (2006; Tan et al. 2006) recently reported an averaged force-direction discrimination threshold of $>25$ deg and that the threshold dependent on whether or not concomitant visual information was congruent with the force stimuli. The thresholds they report differ substantially from the threshold in our study but so did the experimental conditions. They used a precision device that delivered controlled force stimuli to the tip of the index finger that was fitted into a thimble and therefore free to move. In contrast to the present study in which the discrimination task exclusively depended on tactile inputs, their subjects were forced to integrate multimodal sensory information from muscles, joints and skin. Accordingly,
our conclusion is that the representation of force direction with respect to the finger is substantially better than the representation of the orientation of the finger itself. Accordingly, the tactile inputs are likely not the limiting factor in natural force discrimination tasks that involve multimodal integration of inputs, i.e. tasks that involve inputs not only from skin afferents but also other sensory systems.

It is obvious that direction per se is not encoded by tactile afferents. Due to the anisotropic mechanical properties of the fingertip, there is no simple relationship between the direction of the stimulus and the deformation of the fingertip, nor between the forces applied and the deformation of the fingertip. Moreover, the effect of the stimuli on the tactile receptors is not necessarily captured by the measures available to us, i.e., the force applied by the probe and its movement. Nevertheless, it seemed of interest to investigate to what extent force and position and their first time derivatives during protraction and retraction phases were related to the subjects’ decision processes. The subjects were instructed to compare the reference stimuli with the test stimuli but not how to do it. They may have focused their attention on the peak values, or the protraction and retraction phases, or perhaps taken all of them into account. Nevertheless, the peak force and the force rate during the retraction phase allowed particularly good fits with the subjects’ psychometric functions irrespective of how the signals were filtered (i.e., whether the signals would be primarily represented by slow or both slowly and fast adapting afferents) or if the stimuli included a plateau phase, whereas position provided similarly good fits when the physical signals were low-passed filter at 5Hz.

We know that tactile stimuli are represented by human afferents in a non-linear fashion (Knibestöl, 1973; Knibestöl, 1975; Knibestöl and Vallbo, 1980), with firing rates showing saturation effects at high stimulus intensities. Moreover, recent studies strongly argue for signal-dependent noise, i.e. that neural representations are corrupted by noise whose variance increases with the intensity of the sensory signals (Harris and Wolpert, 1998). Based on these considerations, we expected that non-linear transformations of the physical variables (power functions or logarithms) and signal-dependent noise (variance of the transformed physical variable proportional to the mean stimulus value) would be necessary to obtain good fits
between the corresponding decision function and the subjects’ psychometric function. Yet, this was not the case. Instead we obtained excellent fits using linear transformations and fixed ‘noise’. This implies that the neural processes involved in this specific perceptual task somehow were able to linearize the inherently non-linear afferent representations, as previous neurophysiological studies seem to confirm (Knibestöhl and Vallbo, 1980).

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References


Legends to figures and tables

**Figure 1.** *Experimental apparatus.*

A: The index finger of the right hand was splayed and its dorsal aspect was embedded in plasticine. Reflective markers were placed on the custom end-effector attached to the Novint Falcon and recorded via the REMAC video-based motion analyser. The displacement on the axis orthogonal to the desk plane was captured by means of a reflective mirror placed at 45 deg with respect to this plane, which tracked the light reflected by a marker placed in a lateral face of the wooden cube (not shown). The index finger of the right hand was splayed and its dorsal aspect was embedded in plasticine up to the midlevel of the middle phalanx. B: Superimposed traces (n=8) collected in four different directions from a single subject (black lines). The initial force was 0.5 N, orthogonally directed to the fingerpad surface. The grey line represents the desired force stimulus. C: 2,304 (12 subjects x 48 directions x 4 repetitions) superimposed force traces. The actual force stimulus on average differed <0.3% from the desired stimulus during static force stimulation, and 2.6% of the peak force value during dynamic force stimulation. The r.m.s. value of the standard deviation of the applied force stimulus was 15 mN (range 7.3-21 mN) for static force phases, 74 mN (56-97 mN) for force-increasing phases, and 37 mN (26-65 mN) for force-decreasing phases.

**Figure 2.** *Sample data from a single subject.*

A: One pair of force stimulations during the Plateau session from Subject #1. In each trial two stimuli were applied, the reference stimulus along the axis of the finger and the test stimulus (in this case 20 deg clockwise). The 3D force vectors are represented by the normal component and the component tangential to the skin. B: The tangential force and displacements trajectories during the stimuli shown in A; the reference stimulus is shown with gray lines and test stimulus with black lines. Note that that force was controlled by the system whereas the displacements emerged as a result of viscoelastic properties of the fingertip and that the displacements were drawn ~12 times larger than the scale of the fingertip. C: The proportion of response ‘clockwise’ of Subject #1 as a function of test stimulus direction, \( \varphi \). The solid line represents the estimated probability function and the dashed line the 95% confidence interval of the function.
PSE was defined as the $\phi$ of 50% level of the probability functions (left vertical error) and the discrimination threshold as the distance from PSE to the $\phi$ corresponding to the 75% level (the horizontal error).

**Figure 3. Performance across all subjects.**

_A_: Estimated point of subjective equality (PSE) and discrimination threshold across all subjects. The bars correspond to the 95% confidence intervals. _B_: Normal cumulative functions to respond *clockwise* as a function of the direction of the test force stimulus for all subjects; for individual subjects the thin black and gray lines represent for *Plateau* and *No Plateau* sessions, respectively, and thick lines the corresponding average probability functions.

**Figure 4. Dependence of the subjects' psychometric function on the measured kinetic and kinematic variables.**

_A_: Force along the ulnar-radial axis recorded during *Plateau* sessions of subject #2. Force values are positive along the radial direction. All the 48 different stimulation directions each repeated four times are shown. These curves illustrate the high repeatability of the stimuli and the low noise of the sensor. _B_: The residual errors when decision functions based on peak position, peak velocity, peak force, and peak force rate were fitted to match the subjects’ psychometric function. Empty black (grey) circles and filled black (grey) squares represent the results for *Plateau* and *No Plateau* sessions, respectively, obtained with a 50 Hz (5 Hz) cutoff frequency. Peak force and peak force rate during the retraction phase yielded the best results during both the sessions and with different cutoff frequencies, whereas peak position yielded a comparable good fits only with a 5 Hz cutoff. _C_: Comparison between different optimal decision functions and psychometric function of subject #2 during *No Plateau* sessions (thick gray line). The solid, the dotted and the dashed black curves correspond to decision functions based on measured peak force, peak position and peak velocity during the protraction phase, respectively, illustrating that, for this subject, the best fit was obtained with the decision function based on peak force. _D_: For each stimulus direction $\phi$, the mean of the six analyzed variables (0-50Hz) were plotted against the psychometric function, $p(\text{clockwise} | \phi)$, of subject #2 during *No Plateau*
session. For comparison, the leftmost panel shows the stimulus direction plotted against the subject's psychometric function.
Figure 1

A

Novint Falcon
Custom end-effector with force sensor
Plasticine
Supporting handle

B

Normal force, N

C

Tangential force, N

AB C

Supporting handle

Novint Falcon
Custom end-effector with force sensor
Plasticine
Figure 2
Figure 3

A

PSE, degr

Subject: 1 2 3 4 5 6 7 8 9 10 11 12

Discrimination threshold, degr

B

P_{clockwise}

Direction of test stimulus, degr

Plateau sessions

No Plateau sessions
Figure 4

A. Force vs. Stimulus direction (φ) and Position.

B. Psychometric function showing Plateau and No Plateau for different Stimulus directions.

C. Protraction velocity vs. Position and Force rate.

D. Data from subject #2 showing p(clockwise|φ) for different Stimulus directions.