Human Ability to Discriminate Direction of Three-Dimensional Force Stimuli Applied to the Finger Pad

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Panarese A, Edin BB. Human ability to discriminate direction of 3D force stimuli applied to the finger pad. J Neurophysiol 105: 541–547, 2011. First published November 24, 2010; doi:10.1152/jn.00322.2010. 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 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 three-dimensional (3D) force stimuli whose directions differ by an angle as small as 7.1° 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.

INTRODUCTION

Sensory signals critical for object manipulation and haptic identification are generated by receptors located in the skin and subjacent structures (Jones and Lederman 2006; Vallbo and Johansson 1978). 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, 2009; Johansson and Birznieks 2004).

Although 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 (Barbagli et al. 2006; Panarese et al. 2009; Robles-De-La-Torre 2006). 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 (Dorjgotov et al. 2008; Pongrac et al. 2006; Yang 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° (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 <1 N) 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 and Wheat 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 (Dorjgotov et al. 2008; Pongrac et al. 2006; Toffin et al. 2003; Yang et al. 2008), and estimate total force magnitude independently of the size of skin normal and tangential force components (Parè 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° (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 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 (5 N) and dynamics (<2 Hz) 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.

METHODS

Participants and general procedure

Twelve healthy males (age 24–28 yr 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° with respect to the trunk, the elbow flexed at ~120° 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 phalanges. To stabilize the distal phalanges, the nail was glued to a plastic rod subsequently sunk into the plasticine (cf., Birznieks et al. 2001). The skin of the distal phalanges 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 three-dimensional (3D) controller (Novint Falcon, Novint Technologies, Albuquerque, NM) 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) 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 RMS value of the SD of the applied force stimulus was 15 mN (range, 7.3–21 mN) for static force phases, 74 mN (range, 56–97 mN) for force-increasing phases, and 37 mN (range, 26–65 mN) for force-decreasing phases. (Fig. 1, B and 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 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 toward a fixed direction close to the long axis of the index finger. The second stimulus always pointed toward 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 2 Hz). Thus for the force protraction phase, the stimulus started at the offset value (0.5 N for the normal component and 0 N for the tangential) and ended at the peak value. The force stimuli delivered had a total magnitude of 5 N (offset + stimulus) and were always delivered at an angle of 20° with respect to the direction normal to the skin; the peak normal force was thus ~4.7 N and the peak tangential force was ~1.7 N. 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 orthogonal 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 realignment 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 0 N. After the realignment phase, which lasted 2 s, the servo switched to force control also in the tangential directions, the 0.5 N offset along the normal direction was re-established, and 2 s later, a new stimulation cycle started.

Data collection and analysis

Force signals were acquired and digitized at 10 kHz (16-bit resolution) using a USB DAQ board (USB-6251, National Instruments, Austin, TX), averaged, and subsampled at 500 Hz using a custom software application written in MS Visual C++ on a Windows XP operating system (Microsoft, Redmond, WA). 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 off-line.

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 (Treuwelten 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 four repetitions of eight trials. During the initial block of trials, the eight variant stimuli were delivered in random order at [−20, −15, −10, −5, +5, +10, +15, +20°] with the reference direction being 0°.

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

\[ P_{\text{CK}}(\varphi, \mu, \sigma) = \frac{1}{\sigma \sqrt{2\pi}} \int_{-\infty}^{\varphi} e^{-\frac{(x-\mu)^2}{2\sigma^2}} dx \] (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 (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), whereas 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., four directions clockwise and four counterclockwise with 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 six 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 \( [P(t_{\text{th8}}|\text{PSE})] \) and subject 7 during the session No Plateau \( [P(t_{\text{th7}}|\text{NoPSE})] \).

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 and the peak force rate. All of these physical variables were of course correlated with the stimulus direction and presumably also with the afferent discharges on which the subjects decided between clockwise and counterclockwise. 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. Because of 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 study 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 characterized the above variables as a function of the stimulus direction, \( x \), as follows: we 1) low-pass filtered both the reference, \( x_r \), and the test stimulus curve, \( x_t \), and calculated their difference \( \Delta x(x, t) = x_r(x, t) - x_t(x, t) \) and 2) estimated the means, \( \mu_{\Delta x}(x) \), and SD, \( \sigma_{\Delta x}(x) \), across repetitions, of the peak value, \( \Delta x_{\text{peak}} \), assumed by the variable \( \Delta x(x, t) \) 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 protaction only or retraction only. Peak values could assume either positive or negative values. We conducted two parallel analyses which differed by the cut-off frequency used for the low-pass filter, i.e., 5 and 50 Hz. Our purpose was to analyze how the decision process was complementarily affected by slowly (SA) and fast adapting (FA) afferents. In fact, low-pass filtering at 5 Hz drastically reduces frequency components to which FA afferents are sensitive, thus complementarily affected by slowly (SA) and fast adapting (FA) 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 \( \mu_{\Delta x}(x) \) and SD \( \sigma_{\Delta x}(x) \) for each applied stimulus direction. We computed the probability that the stimulus direction was clockwise with respect to the reference as follows:

\[
P_{\text{CK}}(x) = \int_{-\infty}^{+\infty} \frac{1}{\sigma_{\Delta x}(x)} \sqrt{2\pi} e^{-\frac{(x - \mu_{\Delta x}(x))^2}{2\sigma_{\Delta x}(x)^2}} \, ds
\]

Probability values at different stimulus directions \( x \) were 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 the measured variables 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 \( \sigma_{\Delta x}(x) \) 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 because 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 \( \Delta x(x) \) to be known but \( \sigma_{\Delta x} \) to be unknown and looked for the values of this latter parameter that 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). Before the optimization, \( \Delta x(x) \) was offset so that \( x = 0 \) 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 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 nonlinear 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, \( P_{\text{CK}}(x) \) and the probability that the stimulus direction was clockwise with respect to the reference, \( P_{\text{CK}}(x)(\phi) \). Therefore the optimum \( \sigma_{\Delta x} \) represented the noise value that 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.

Because the transfer functions that described the neural signals as a function of the measured variables were unknown, we tested both linear and nonlinear (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 cut-off frequencies × 2 session types × 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 2 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° (4.9–12°; 95% CI) and the PSE was estimated to be \( -1.1^\circ \) (3.2 to 11.1°), 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° (range, 4.3–12°), whereas the value for the sessions with dynamic phases only, i.e., the No Plateau sessions, was 10° (range, 7–14°). 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, \( t_{10} = 24 \); \( P = 0.72 \)): \( -0.8^\circ \) (4.6 to 2.2°) during the Plateau session and \( -0.6^\circ \) (7.8 to 5.2°) during the No Plateau session. Notably, the directions of the PSEs were not consistent within participants across sessions. The PSEs and discrimination thresholds were not correlated during either type of session (\( r^2 \leq 0.006 \), \( P \geq 0.8 \)).

Trials with clockwise or counterclockwise 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 counterclockwise stimulations. A 2 × 2 repeated-measures ANOVA with the factors session type (Plateau and No plateau) and preceding test stimulus direction (clockwise and counterclockwise) showed a significant but small main effect of session type (a difference of 0.5°; \( F_{1,9} = 13.5 \), \( P = 0.005 \)) 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 toward clockwise directions when the previous stimulus was counterclockwise 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% CIs of the estimated PSE values did not cross 0° (Fig. 3A). The experimental protocol itself did not promote such biases. The previous analysis showed an aftereffect of previous stimulations on PSE (cf., Fig. 2), 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 nonlinear (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., $\sigma$ independent of the stimulus direction).

We explored six apparently pertinent variables—the maxi-
mum deviation in position and force and the maximum velocity
and force rates during the protraction and retraction phases—in
a $2 \times 2 \times 6$ repeated-measure ANOVA [2 cut-off frequencies
(5 and 50 Hz) $\times$ 2 session types (Plateau and No Plateau) $\times$ 6
variables]. The quality of the fits depended on the cut-off fre-
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
cut-off frequency and session type, i.e., the best fits were
obtained with force, peak force rate during the retraction phase,
and the position ($P < 2 \times 10^{-5}$; Fig. 4B). Moreover, with the
$0–50$ Hz 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 show representative data, we show data from a single
subject for the No Plateau condition (Fig. 4, C and 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 subject’s behavior, $P_{\text{crit}}(\varphi)$ plotted
against the mean of the variable at each stimulus direction $\varphi$,
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 left panel shows
$P_{\text{crit}}(\varphi)$ 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. Three of 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 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, and 1/9 to use skin stretching information, whereas
the remaining 2/9 were unable to specify their strategy. Two
subjects reported to be biased to respond counterclockwise
when they felt uncertain: subject 2 only for the Plateau sessions
and subject 9 for both sessions.

Analysis of response latencies failed to show 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; Wilcoxon matched pairs test, $t_{1.2} = 16; P = 0.07$).
Moreover, the estimated discrimination thresholds were not
correlated with mean response latencies for either type of
sessions ($r^2 \leq 0.02, P \geq 0.72$).

**DISCUSSION**

We showed that subjects can discriminate the direction of
3D force stimuli applied to the volar surface of the fingertip
with a discrimination threshold of $\sim 10^\circ$ for dynamic stimuli
and slightly better ($\sim 7^\circ$) 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 Bir-
znieks 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). SAI afferent and in particular the
so-called SAIinal 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 stim-
ulus 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 this study (Saal et
al. 2009): very little additional information about force direc-
tion 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) and Tan et al. (2006) recently reported an
averaged force-direction discrimination threshold of $>25^\circ$
and that the threshold was dependent on whether 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 this 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 representa-
tion 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 affer-
ents but also other sensory systems.

It is obvious that direction per se is not encoded by tactile
afferents. Because of 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 pro-
traction 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 slow 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 5 Hz.

We know that tactile stimuli are represented by human afferents in a nonlinear fashion (Knibestöl 1973, 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 nonlinear 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. However, 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 nonlinear afferent representations, as previous neurophysiological studies seem to confirm (Knibestöl and Vallbo 1980).

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DISCLOSURES

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

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