BRAIN RESEARCH 1417 (2012) 9–15

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BRAIN RESEARCH

Research Report

Pleasantness of touch in human glabrous and hairy skin: Order effects on affective ratings

Line S. Löken[a,b,*], *Mika Evert*[a,1], *Johan Wessberg*[a,1]

[a]*Institute of Neuroscience and Physiology, University of Gothenburg, Gothenburg, Sweden*
[b]*Nuffield Department of Clinical Neurosciences and FMRIB Centre, University of Oxford, UK*

ARTICLE INFO

Article history:
Accepted 5 August 2011
Available online 11 August 2011

Keywords:
C fiber
Affective
Pleasant
Touch
Human

ABSTRACT

The tactile sense comprises pathways for both discriminative and affective touch. Low threshold unmyelinated mechanoafferents (C tactile, CT) in the human hairy skin have recently been linked to pleasant touch sensation. Here, we investigated how perception of the hedonic aspect of tactile stimulation differs between the hairy skin of the arm, and the glabrous skin of the palm, which is not innervated by CT afferents. Three groups of naïve, healthy subjects (total n = 28) rated pleasantness on a visual analogue scale (VAS) when we stroked with a soft brush with speeds from 0.1 to 30 cm/s on the palm or forearm. We used two different experimental approaches: in experiments 1 and 2, stimuli were delivered successively on the palm and arm (or arm and palm) in temporally separate sequential blocks. In experiment 3, stimuli were delivered alternately on arm and palm. We found that the order of stimulus presentation, palm/arm or arm/palm, has an effect on pleasantness ratings of gentle brush stroking with varying velocity. Notably, the perception of pleasantness for palm stimulation was affected by previous stimulation of the arm, but not vice versa. Thus, assessment of valence of touch may be influenced by affective reactions elicited by activation of the CT afferent pathway.

1. Introduction

Recent advances on the physiology of affective touch suggest that there is a peripheral pathway for pleasant touch in parallel to the pathway for discriminative touch (McGlone et al., 2007; Morrison et al., 2010; Olausson et al., 2008). We recently described a unique psycho-neural correlate where the firing of a group of unmyelinated low threshold mechanoreceptors (C tactile, CT) was linked to the coding of pleasant, hedonic touch and showed that their firing correlates with perception of pleasantness (Löken et al., 2009). CT afferents are a distinct type of unmyelinated, low threshold mechanoreceptive C fibers existing in hairy but not glabrous skin of humans and other mammals (Liu et al., 2007; Vallbo et al., 1993, 1999). Although CT afferents are lacking in glabrous skin this does not preclude perceiving pleasantness, for example, when exploring a soft object with the hand (Francis et al., 1999; Rolls et al., 2003). The glabrous skin of the palm has evolved to perform exploratory and manipulative tasks that by far surpass this function in other primates (Johansson and Flanagan, 2009; Johansson and Vallbo, 1979). Not only is the peripheral innervation distinctly different between glabrous and hairy skin, but

* *Corresponding author at:* FMRIB Centre, John Radcliffe Hospital, Headington, OX3 9DU, UK. Fax: +44 1865 222717.
E-mail addresses: lloken@fmrib.ox.ac.uk (L.S. Löken), mika.evert@lthalland.se (M. Evert), wessberg@physiol.gu.se (J. Wessberg).
[1] Dept. of Physiology, University of Gothenburg Box 432 SE-405 30, Göteborg, Sweden.

0006-8993/$ – see front matter
doi:10.1016/j.brainres.2011.08.011

there may also be a different neural organization in the central nervous system for touch processing for the different skin sites (McGlone et al., 2007).

The neuroanatomical regions implicated in pleasant and discriminative touch has been studied with functional magnetic resonance imaging. Brain activation in response to a pleasant touch stimulus applied to the palm has been found in the anterior cingulate cortex, orbitofrontal cortex and interestingly a weak signal was also found in the amygdala. Comparisons of pleasant and neutral touch showed greater activation in the orbitofrontal cortex when the stimulus was perceived as pleasant and greater activation in somatosensory cortex when the stimulus was affectively neutral (Rolls et al., 2003). Stimulating CT afferents has been shown to activate the insular cortex (Björnsdotter et al., 2009; Olausson et al., 2002, 2008).

Here, we investigated how perception of the hedonic aspect of tactile stimulation differs between the glabrous skin of the palm, which is not innervated by CT afferents, and the hairy skin of the arm that is innervated by CT afferents. We also wanted to investigate if the order of stimulus presentation, palm/arm or arm/palm, has an effect on pleasantness ratings of gentle brush stroking with varying velocities. To this end, two different experimental approaches were used: in experiments 1 and 2, stimuli were delivered successively on the palm and arm (or arm and palm) in temporally separate sequential blocks. In experiment 3, stimuli were delivered alternately on arm and palm. This design counterbalanced the protocol for succession order between stimulation sites. While the purpose of counterbalancing normally is to diminish bias, we will show that utilizing this design revealed a possible affective confound by pre-activation of the CT afferent pathway in the hairy skin of the arm. In perception research, affective laden information has been shown to strongly influence perceptual appraisal (Pessoa, 2008). The impact of affective primes on assessment of value has been shown in the visual realm, where for example subliminally presented pictures have been shown to influence reactions to food (Berridge and Winkielman, 2003; Gibbons, 2009; Winkielman et al., 2005). Here, we show that the perception of pleasantness for palm stimulation is affected by previous stimulation of the arm, but not *vice versa*, suggesting the existence of similar processes in the tactile modality.

2. Results

In a first analysis we pooled data from experiments 1 and 2 (see Section 4.3). A statistical test for all the VAS scores showed that brush stroking was perceived as more pleasant on the arm compared to palm (*t*-test, $p<0.001$). However, further analyses revealed differences in results for the two experiments.

We have previously shown that the regression of pleasantness as a function of velocity can be described as an inverted U-shaped (negative quadratic) curve (Löken et al., 2009). In experiments 1 and 2, we tested the best model fit (linear or quadratic) for the rating pattern for each skin site, palm or arm. In experiment 1, where stimulation started on the palm, the regression for *arm* ratings was significantly improved by adding a negative quadratic term to velocity (F-test, $p=0.001$, $n=178$, Fig. 1). In the same experiment, the regression for *palm* ratings was not significantly improved by adding a quadratic term ($p=0.232$). Indeed, the linear term was non-significant in the regression model as well, so that the ratings were statistically flat in relation to velocity. In experiment 2, where brushing started on the arm, the regression model for *arm* was again significantly improved by adding a negative quadratic term (F-test, $p=0.005$, $n=179$, Fig. 2). However, in contrast to experiment 1, the regression for *palm* ratings was also significantly improved by adding a quadratic term ($p<0.001$).

We next investigated if the skin site, palm or arm, was a significant variable. In experiment 1, where the protocol started on the palm and then continued on the arm, there was a significant effect of skin site (two-way ANOVA $F_{(1,341)}=11.53$, $p=0.001$, Fig. 1). That is, when the brush protocol was first applied on the palm, pleasantness ratings differed significantly between the palm and arm. In experiment 2, when the brush protocol was first applied on the arm, there was no significant effect of skin site (two-way ANOVA, $F_{(1,344)}=0.24$, $p=0.62$, Fig. 2). This means that pleasantness ratings were statistically different between skin sites only when the palm was stimulated before the arm. Hence, when previously stroked on the arm, stroking on the palm was rated similar to the arm.

For palm stroking, pleasantness ratings were significantly higher for 3 cm/s (independent *t*-test, $p=0.042$, uncorrected) and significantly lower for 0.1 cm/s ($p=0.03$) in experiment 2 (arm first) compared to experiment 1 (palm first) (Fig. 4). For arm stroking, there was no significant difference, at any velocity, between the pleasantness ratings in experiments 1 and 2 (Fig. 5).

We pooled the results from experiments 1 and 2 and divided the VAS data into the first and last parts of the

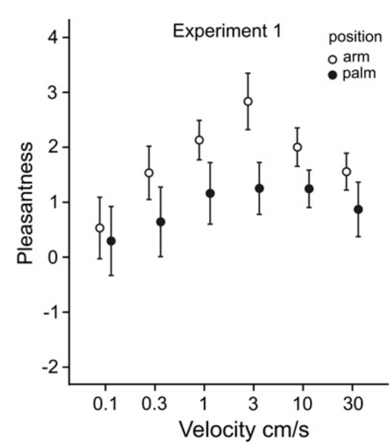

Fig. 1 – Experiment 1, visual analogue scale (VAS) scores of pleasantness in relation to brush stroking velocity. Ten subjects tested with moving brush stimulation first on the left palm and subsequently on the left arm. Regression for arm ratings was significantly improved by adding a quadratic term to velocity (*p* = 0.001). The regression for palm ratings was not significantly improved by adding a quadratic term (*p* = 0.232). All stimuli used a calibrated normal force of 0.4 N. Bars show means and standard error of the means (s.e.m.).

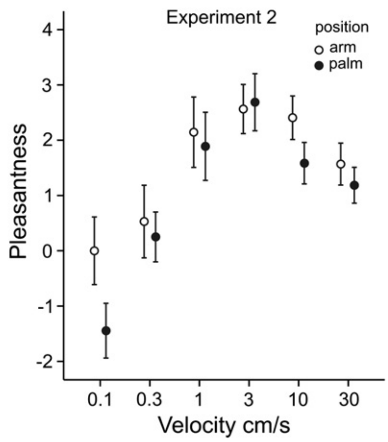

Fig. 2 – Experiment 2, VAS scores of pleasantness in relation to brush stroking. Ten subjects tested with moving brush stimulation first on the left arm and subsequently on the left palm. The regression model for arm was significantly improved by adding a quadratic term ($p=0.005$). In contrast to experiment 1, the regression model for the palm was significantly improved by adding a quadratic term ($p=0.001$). All stimuli used a calibrated normal force of 0.4 N. Bars show means and standard error of the means (s.e.m.).

experiments. Using pleasantness as a dependent variable, grouping the first and last parts of the experiment as a fixed factor and the velocity as covariate, we found no significant effect of group (first or last, ANOVA, ($F_{(1,711)}=2.12$, $p=0.15$), i.e. there was no significant shift in pleasantness ratings over time in experiments 1 and 2.

In experiment 3, the arm and palm were alternately stimulated in close temporal succession in the same session. To achieve this, brush stimuli were delivered by a trained experimenter under direction from a computer program, see Section 4. In experiment 3, pleasantness ratings were again better described by adding a negative quadratic term to velocity for both palm and arm ratings, similar to experiment 2 (F-test palm, $p=0.015$, $n=120$; F-test arm, $p=0.026$, $n=120$, Fig. 3). There was no significant effect of skin site, i.e. palm brushing was rated equally pleasant as arm brushing (two-way ANOVA, $p=0.304$). There were no significant differences between males and females for the overall pooled ratings of experiments 1 and 2 or divided by location (t-test, $ps>0.06$).

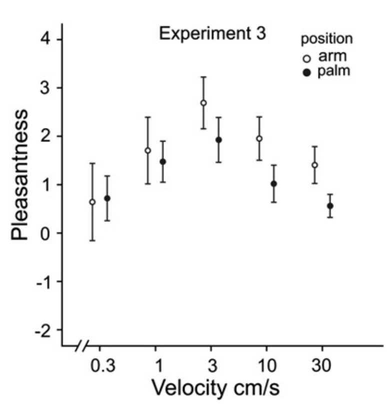

Fig. 3 – Experiment 3, VAS scores of pleasantness in relation to brush stroking velocity. Arm and palm were alternately stimulated in close temporal succession in the same session in eight subjects. Pleasantness ratings were significantly better explained by adding a quadratic term to velocity for both palm ($p=0.015$) and arm ($p=0.026$). Bars show means and standard error of the means (s.e.m.).

3. Discussion

The perception of pleasantness in glabrous skin of the palm, which lacks CT afferents, was found to be influenced by the order in which a protocol of tactile stimuli was presented. For the hairy, CT innervated, skin of the forearm, this effect was not found. In detail, participants who were first stimulated on the palm followed by the arm perceived brush stroking as less pleasant on the palm compared to the arm. Further, arm ratings showed an inverted U-shaped pattern with a peak at 1–10 cm/s, whereas palm ratings were statistically flat in relation to velocity. In contrast and importantly, participants who were first stimulated on the arm and subsequently on the palm rated palm stimuli in a manner that was statistically indistinguishable from the arm. The same was true when brushing was applied to the arm and palm in an alternating fashion.

The evidence for distinct neural pathways for affective aspects of touch has accumulated through research on both peripheral and central levels. On the peripheral level, a recently discovered type of unmyelinated C fiber, the CT (C tactile) afferent, has been shown to be sensitive to innocuous tactile stimulation (Vallbo et al., 1993, 1999; Wessberg et al., 2003). Notably, in a quantitative comparison of the discharge of cutaneous primary afferent fibers in humans to slow brushing and to psychophysical ratings, we have shown a unique psycho-neural correlate between CT activation and perception of pleasantness in healthy humans (Löken et al., 2009).

On the central level, CT afferents have excitatory projections to the insular cortex, and probably inhibitory projections towards the discriminative tactile cortical systems (classical somatosensory areas SI and SII; Olausson et al., 2002, 2008). The insular cortex is an important homeostatic region of the brain and is thus alleged to play an important role in representing information relevant to well-being (Björnsdotter et al., 2009; Craig, 2003; Olausson et al., 2002, 2008). The affective pathway formed by CT afferents is less accessible to conscious self-report as evidenced by research on two patients (GL and IW) with neuronopathy syndrome (Sterman et al., 1980), who lacks large myelinated afferents but whose C fibers are intact (Olausson et al., 2002, 2008). Both patients lack conscious touch sensation below the level of the nose, but can in a forced choice condition detect light stroking of a brush, and GL reports a vague pleasant sensation in response to this stimulus (Olausson et al., 2002).

The type of gentle slowly moving stimulation of hairy skin that activates CT receptors characterizes social interactions and is typically described as communicating affection and trust (Hertenstein et al., 2006). The glabrous surface of the hand, with areas such as the digit tips being more densely innervated and more cortically represented than other body sites have evolved as a crucial human tool for exploratory tactile behavior and

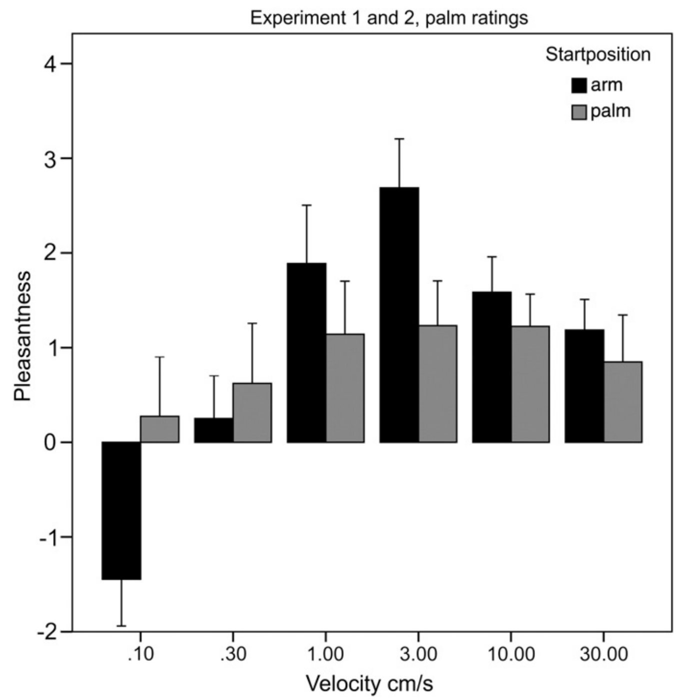

Fig. 4 – Pleasantness ratings for the palm in experiments 1 and 2. Bars represent ratings depending on start position in the experiment (black = arm was stroked before the palm, grey = palm was stroked first). Ratings for palm were significantly higher at 3 cm/s ($p = 0.042$, uncorrected) and significantly lower at 0.1 cm/s ($p = 0.03$) when start position was the arm compared to when starting on the palm. Bars show means and standard error of the means (s.e.m.).

object manipulation (Johansson and Flanagan, 2009; Johansson and Vallbo, 1979). While brush stroking of the palm was here, and has previously been shown to be, perceived as less pleasant in the palm compared to the hairy skin (Essick et al., 1999; Guest et al., 2009), brush stroking of the palm is however still rated as being pleasant. Pleasant touch stimuli of the palm give rise to

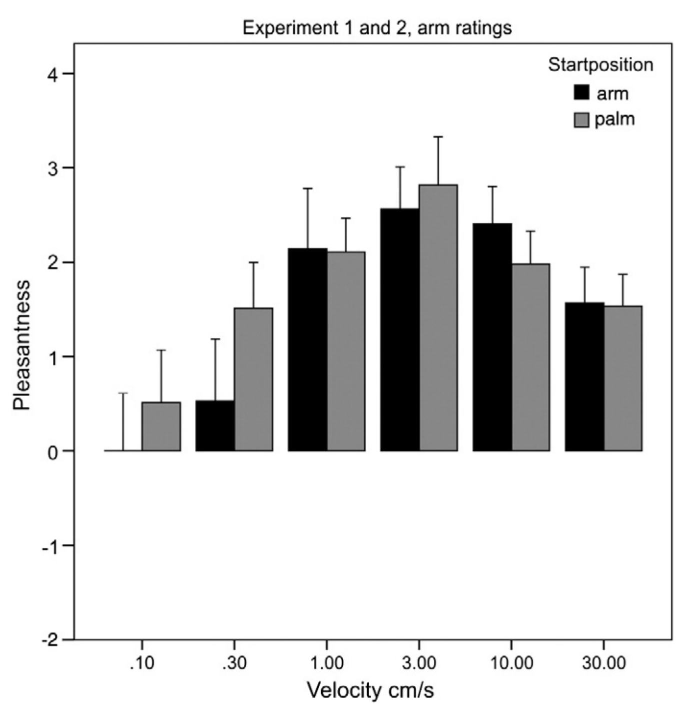

Fig. 5 – Pleasantness ratings for the arm in experiments 1 and 2. Bars represent ratings depending on start position in the experiment (black = arm was stroked first, grey = palm was stroked before the arm). There were no significant differences at any velocity dependent on start position. Bars show means and standard error of the means (s.e.m.).

functional magnetic resonance imaging responses in orbitofrontal cortex, anterior cingulate cortex and amygdala (Francis et al., 1999; Rolls et al., 2003), key areas for emotional appraisal and hedonic impact (Gorwood, 2008; Kringelbach, 2005). There are dense connections between the orbitofrontal, anterior cingulate, insular cortices and amygdala, suggesting that the activation of insular cortices (e.g. by CT stimulation) can influence processing in this network (Augustine, 1996; Kringelbach, 2005).

The present results show that stimulation of the hairy skin influences the appraisal of pleasantness from the glabrous skin. The difference between palm ratings for the subjects who had previously been stimulated at the arm and those who had not, was significant at 3 cm/s, which is an optimal velocity for CT stimulation. This suggests a mechanism where CT stimulation influences the hedonic assessment of gentle slowly moving stimuli in the palm skin as to make it more pleasant than before CT stimulation. The change in perception was observed to stimulate of the glabrous skin that lack CT afferents.

It may be argued that previous CT afferent stimulation and activation of hedonic central circuits may powerfully influence how participants subsequently rate similar stimuli, even on the palm, and hence that participants who were not naïve were strongly influenced by memory from the previous test. However, the characteristic inverted U-shaped pattern was seen for palm ratings also in experiment 3, where arm and palm stimuli were temporally intermixed. Hence, the mechanism through which previous or ongoing CT afferent stimulation influences perception in the palm is likely not through explicit memory of a previously learned task, but more likely involve emotional memory circuits. Neither can the distinct change in the pattern of the relationship to brush velocity from flat to inverted U-shape be explained by a simple shift in overall hedonic tone due to activation of the CT afferent pathway. A similar phenomenon as described here has been shown for another sensory modality, vision, where subliminally presented pictures have been shown to influence affective reactions to food (Berridge, 2003; Gibbons, 2009; Winkielman et al., 2005). These studies described a priming mechanism whereby unconscious affective cues can change behavior. We here find that stimulating an affective tactile pathway can influence participants' rating behavior that suggests that a priming mechanism can be elicited in the tactile domain as shown for other sensory modalities. The structures that have been linked to the mechanisms underlying affective priming are limbic structures in the brain, such as the insular cortices and amygdala (Pessoa, 2008; Whalen et al., 1998).

That perception of pleasantness in the palm can be affected by previous or ongoing arm stimulation, but not *vice versa*, signifies that the central processing differs between these two skin sites. This asymmetrical effect suggests that stimulation on glabrous skin stimulation has less affective consequences than on hairy skin. This could be advantageous from an evolutionary point of view, in order not to confound tactile perception and identification processes that humans rely on so heavily when using their hands.

Relating a particular afferent class to average hedonic ratings in order to study general principles of peripheral encoding of percepts is best estimated from a population of participants (Bensmaia, 2008). However, there are likely a wide range of factors influencing how pleasantness is perceived by an individual at any given time. Peripheral pathways have only recently been considered in the somatosensory hedonic domain, which has led to new insights and questions regarding affective touch processing. The present finding that the order in which different body areas are stimulated influence the results, bears important implications for the future design of studies in affective neuroscience.

4. Experimental procedures

4.1. *Subjects*

Twenty-eight healthy volunteers participated in the study (14 male), age range 21–28 years.

The subjects were paid 200 SEK/hour (about 20 EUR/hour). The study was approved by the local ethics committee at the University of Gothenburg and adhered to the Declaration of Helsinki.

4.2. *Skin stimulation and equipment*

In the first two experiments, a custom-built robotic skin stimulation device, Rotary Tactile Stimulator (RTS; developed by Chris Dancer, Dancer Design, and Unilever Research and Development, Port Sunlight, UK) was used to deliver controlled brush strokes on the left palm or forearm. In experiment 3, the brush was hand-held (see below). Stimulation was made with an artist's flat, soft watercolor brush made of fine, smooth, goat's hair (Vang size 18, type 43718, Oskar Vangerow, Ottobrunn, Germany). The bristles were 22 mm long, and the width of the brush was 20 mm. The RTS produced high-precision brush stroking with a calibrated normal force of 0.4 N (Löken et al., 2009). Brush stroking was applied on the palm in lateral to medial direction and over the arm in proximal to distal direction, The brush was moved over a distance of ~6.5 cm in a rotary fashion by a DC motor (Maxon Motor AG, Sachseln, Switzerland) fitted with a reduction drive and position encoder. A 6-axis force/torque transducer (ATI Industrial Automation, Apex, NC) was mounted between the shaft of the DC motor assembly and the hub, which held a probe and brush. The DC motor and transducer assembly was mounted on a linear drive that could lower the rotary DC motor assembly towards the stimulation site, and thus control the delivered force. The linear drive was controlled by a step motor (Parker Hannifin Corp., Rohnert Park, CA). Both the DC and step motors were under computer control.

4.3. *Procedure*

All subjects were given the same, standardized instructions. They were seated comfortably, provided with earplugs, and the stimulation site was covered by a curtain. The subjects were informed that all stimuli were innocuous, but were not informed beforehand of the purpose of the experiment. In experiments 1 and 2, the stimuli were delivered in a randomized order by the RTS, so subjects could have neither predicted the delivery of a given stimulus velocity, nor influenced by implicit cues from the experimenter. The subjects' left arm was fixated with a vacuum pillow and during palm stimulation, the thumb of the subject was held down by a piece of surgical tape so that the brush would not touch the thumb. Following each brush stroke the subjects were instructed to rate their perception of brush evoked pleasantness using a computerized visual analog scale (VAS) shown on a laptop monitor, with the endpoints unpleasant to pleasant (−10 to 10). They rated by repositioning a line from the center of the scale (0) to a chosen position using a computer mouse in their right hand. After rating, the line returned to the center. Subjects were required to rate the pleasantness of the stimulation within a 15 s response interval.

In experiment 1, 10 subjects (5 male) were first brushed with six different velocities (0.1, 0.3, 1, 3, 10 and 30 cm/s) in lateral to medial direction in the palm. The inter-stimulus interval was set to 30 s to allow for fatigue recovery of CT afferents (Vallbo et al., 1999), and each velocity was repeated six times in a pseudo-randomized order. A similar protocol was used in a previous study, and part of experiment 1 has been described in the supplementary information of a previous publication (Löken et al., 2009). The palm stimulation was followed by a 10 minute pause, when the RTS was readjusted for arm stimulation, and subsequently the same stimulation protocol was performed with brushing in proximal to distal direction on the arm.

In experiment 2, another 10 subjects (5 male) were first brushed on the arm using the protocol described above. This was again followed by a 10 minute pause after which the protocol was repeated in the palm. Experiments 1 and 2 lasted for approximately 60 min each.

In experiment 3, a third group of 8 subjects (4 male) was evaluated using brush stimuli alternating between palm and arm in close temporal succession. The RTS could not be quickly shifted between the two stimulation sites, so for technical reasons, brush strokes were delivered manually by an experimenter (ME) over a 10 cm distance at 5 different velocities: 0.3, 1, 3, 10, and 30 cm/s. The experimenter was trained in the delivery of the stimuli, and during the experiment was guided by a display on a computer monitor, not visible to the participant, with a moving bar over 10 cm representing the appropriate velocity in each trial. Each velocity was repeated three times per skin site (palm/arm) in a pseudo-randomized order. The experiment lasted for approximately 40 min.

4.4. *Data analysis*

Regression analysis of psychophysical data was done by first transforming velocity, the independent variable, to $\log^{10}$ values. To test for significance of a quadratic regression term, the curve fit of a linear regression (reduced regression model) was tested against the fit of a quadratic regression (full regression model), with an F-test for significant reduction of the error sum of squares in the full compared to the reduced model (Chatterjee et al., 2000). Analysis was done in SPSS 15.0 (SPSS Inc., Chicago, IL).

Acknowledgments

This work was supported by the Wenner-Gren Foundation, the Swedish Research Council, Sahlgrenska University Hospital, the Mary von Sydow Foundation and Unilever R&D. We are grateful to Professors Håkan Olausson and Irene Tracey for kindly reading the manuscript and providing valuable advice, to Francis McGlone for providing the RTS, and to Karin Göthner and Jenny Lindholm for technical assistance.

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