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RESEARCH ARTICLE

Jörg Trojan · Annette M. Stolle · Dieter Kleinböhl
Carsten D. Mørch · Lars Arendt-Nielsen · Rupert Hölzl

The saltation illusion demonstrates integrative processing of spatiotemporal information in thermoceptive and nociceptive networks

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Abstract In sensory saltation, first reported by Geldard and Sherrick (Science 178:178–179, 1972), a stimulus is displaced towards a second one following closely in time and space as a function of the delay between the stimuli. The distance between stimulus locations is restricted by the extension of sensory fields in the primary somatosensory cortex. Saltation is assumed to reflect dynamic changes in these cortical representations. The present study demonstrates for the first time saltation in thermoceptive and nociceptive pathways with CO_2 laser stimulation. Stimuli were presented to the dorsal forearms of 18 healthy subjects at two intensities. Saltation patterns consisted of a reference stimulus S0 near the wrist, the first test stimulus S1 at the reference location after a fixed onset delay of 1,000 ms, and a second test stimulus S2 at a location 105 mm distant from reference after a variable onset delay of 60–516 ms. Perceived positions were indicated by the subjects without skin contact with a 3D tracker. As expected, subjects mislocalized S1 towards S2. Mean S1 displacement was 51 ± 36 mm. Decreasing delays between S1 and S2 resulted in increasing displacements, independent of intensity. However, since no clear-cut discrimination of thermal versus nociceptive activation could be achieved definite conclusions about differences between the two modalities cannot be drawn. In addition, effects of body site on the saltation characteristics were observed. The saltation paradigm constitutes a promising approach to the functional analysis of spatiotemporal dynamics in thermoceptive and nociceptive networks to supplement brain-mapping approaches to cortical sensory fields.

Keywords Psychophysics · Perception · Illusion · Lasers · Human

Introduction

Saltation is an illusion that consists in distortions in the spatial perception of stimuli presented in spatiotemporal patterns on the skin: the perceived displacement of a stimulus is dependent on the time interval to a second stimulus presented at a distant location (Geldard and Sherrick 1972; Geldard 1975; Cholewiak and Collins 2000). The phenomenon is restricted to a certain distance between the presented stimuli, the so-called 'saltatory area', which is related to the cortical magnification factor (Geldard and Sherrick 1983). Saltation was first demonstrated in the tactile modality (Geldard and Sherrick 1972), but it exists also in the visual and auditory systems (Lockhead et al. 1980; Shore et al. 1998) and seems to represent a common property of sensory networks in the CNS. Saltation has been implemented in several variations. The original publication focused on the 'multiple rabbit' paradigm, where multiple tactors were arranged on the arm and the illusion of a series of jumps from wrist to shoulder was elicited (Geldard and Sherrick 1972). However, the main principles of this illusion can be demonstrated best with the so-called 'reduced rabbit' paradigm, which consists of three stimuli presented at two locations (cf. Fig. 1).

The psychophysically well-defined saltation illusion offers potentials as a research tool for the assessment of the somatosensory perceptual space (the 'body map'). Wiemer et al. (2000) introduced a neuronal network model explaining cortical topography from the

J. Trojan (✉) · A. M. Stolle · D. Kleinböhl · R. Hölzl
Laboratory for Clinical Psychophysiology,
Otto Selz Institute for Psychology and Educational Science,
University of Mannheim, Schloss EW 182,
68131 Mannheim, Germany
E-mail: joerg.trojan@osi.uni-mannheim.de
Tel.: +49-621-1812110
Fax: +49-621-1812115

J. Trojan · C. D. Mørch · L. Arendt-Nielsen
Center for Sensory-Motor Interaction (SMI),
Aalborg University, Fredrik Bajers Vej 7, D-3,
9220 Aalborg, Denmark

A. M. Stolle
Department Neuropsychology,
Central Institute for Mental Health,
J5, 68159 Mannheim, Germany

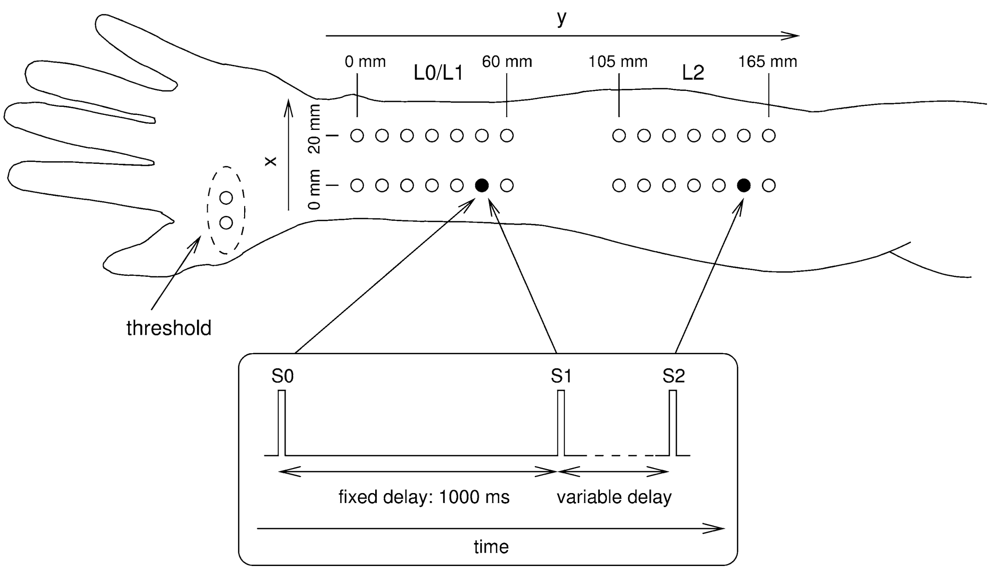

Fig. 1 Stimulation sites on the right forearm and temporal sequence. *Circles* denote the sites stimulated by the laser. Saltation patterns consisted of a group of three stimuli, S0, S1, and S2. S0 and S1 were presented at the L0/L1 locations, which were shifted within the distal group of fourteen sites close to the wrist. S2 stimuli were presented at corresponding proximal locations L2, 105 mm apart. Thresholds were assessed on the right dorsal hand. Stimulation sites on the left arm were arranged accordingly

spatiotemporal characteristics of incoming stimuli, and argued that the saltation phenomenon may be the perceptual correlate of the dynamic behaviour of sensory maps. From this perspective, saltation is the result of dynamic changes in the perceptual space where the distance between two stimuli in the body representation is a function of their temporal pattern, and the saltatory area is connected to receptive fields. Consequently, saltation also offers the possibility to assess changes in the spatial representation and the dynamic characteristics in the somatosensory cortex due to plastic processes. This is corroborated by the finding that the size of the saltatory area is not only dependent on the body site but that it can be modified by repeated stimulation (Stolle 2004), consistent with reports on alterations in cortical receptive field size under repetitive stimulation and chronic pain (Flor et al. 1998; Braun et al. 2000).

In the present study, the 'reduced rabbit' paradigm (Geldard 1975) was implemented for the first time with cutaneous CO_2 laser stimuli. Our goal was to elicit saltation in the thermoceptive and nociceptive domain without any tactile stimulation. CO_2 laser stimuli are suitable to activate nociceptive Aδ- and C-fibers as well as thermoceptive C-fibers without activating mechanoceptors (Bromm and Treede 1984). Furthermore, CO_2 laser beams are invisible, thus providing us with a technique to assess subjective localization data independent from visual cues. We expect that the technique described in this article adds a valuable tool to the investigation of alterations in the cortical representation of thermoceptive and nociceptive information.

Materials and methods

Subjects

Eighteen healthy subjects took part in the study (14 males). Mean age was 25.6 ± 4.9 years (range 19–35). Sixteen subjects were right-handed, one was left-handed, and one subject showed no clear preference for either side, as assessed by the Edinburgh Handedness Inventory (Oldfield 1971). All subjects were informed and gave written consent according to the declaration of Helsinki. The study design was approved by the local ethics committee.

Apparatus for stimulus application and psychophysical scaling

Subjects sat down in a chair and the arm scheduled for stimulation was fixed by a vacuum pillow. Infrared laser pulses of 20 ms duration were applied by a CO_2 laser system (Synrad 57-1, 100 W, Synrad Inc., Mukilteo, WA, USA). The area covered by the laser beam on the skin was approximately 44 mm^2. A visible low-power diode laser beam collinear with the CO_2 laser beam allowed precise localization and adjustment of stimulation sites. The laser beam was applied to the skin via a computer-controlled mirror-scanner (GSI Lumonics, Billerica, MA, USA). Stimulus intensity and location patterns were pre-programmed. The shift from one location to another could be performed in a matter of microseconds.

Laser energy was measured with a laser energy meter (Nova, Ophir Optronics Ltd., Wilmington, MA, USA). Peak surface temperatures on the skin were calculated with a time constant model using thermal properties of water (van Gemert and Welch 1989; Brugmans et al. 1991).

Perceived positions of the stimuli on the skin were indicated by the subject by pointing at them with the tip of a 3D tracker system (Polhemus Fastrak II) without skin contact. A one-dimensional scale in proximal-distal direction was anchored to the stimulation area on the forearm. The perpendicular of the three-dimensional coordinates to this scale constituted the position information used in the analysis.

Sensory thresholds procedure

The individual detection thresholds and pain thresholds of single laser pulses (duration 20 ms) were assessed at two sites within the radial nerve area on the dorsum of the right hand (see Fig. 1) with two ascending series in steps of 1.0 mJ/mm^2. This area was chosen to reduce adaptation/sensitization biases during the saltation procedure on the arm. After each stimulus, subjects were asked if they could detect the stimulus, if it was perceived as warm, hot, stinging (pin-prick), or unpleasant. If the stimulus was judged unpleasant, subjects were asked if it was painful. Each ascending series was terminated at the first 'painful' rating. If a painful sensation could not be achieved at 17.0 mJ/mm^2 (corresponding to a temperature change of 26.3°C) the series was nonetheless aborted, because higher intensities were not scheduled for the saltation procedure to avoid skin damage and adaptation/sensitization effects. The lowest detected intensity in the two trials constituted the detection threshold. The highest 'painful' intensity reported during the two trials was chosen as the pain threshold to account for the rapid habituation to laser stimuli. Further spot checks of the stimulus quality were performed during the saltation procedure.

Saltation procedure and design

The experimental design consisted of the factors intensity (two steps) and delay (seven steps) with a four-step repetition factor. A fourth factor, position, was confounded with delay and repetition due to the balancing method described below.

The stimulus sequence was first presented on the right dorsal arm at low intensities of 3.5 mJ/mm^2 above the individual detection threshold. Then it was presented on the left dorsal arm with higher intensities, usually at 1.7 mJ/mm^2 above the individual pain threshold, but never above 17.3 mJ/mm^2 to avoid the risk of skin damage.

Fourteen different pairs of stimulus locations were arranged in a matrix of 20 mm×165 mm located in the radial nerve area in the C7 dermatome (Fig. 1). The stimulation patterns consisted of three stimuli (duration 20 ms), which were arranged according to the 'reduced rabbit' scheme (Fig. 1, inset; cf. Geldard 1975). The first stimulus S0 was presented at the location L0, followed by the second stimulus S1 with a fixed time interval of 1,000 ms at the same location (L1 = L0). The third stimulus S2 followed at location L2, at a fixed distance of 105 mm apart from L0/L1. The delay between the onset of S1 and S2 was 60, 100, 140, 180, 220, 366, or 516 ms. The first stimulus was always presented at the most distal position in the pattern.

Each delay value was repeated four times. To avoid habituation of the skin, stimulus locations were shifted laterally (x-direction: 0 or 20 mm) and in wrist-elbow (y-) direction (from 0 to 60 mm, in 10 mm increments), resulting in the stimulation matrix depicted in Fig. 1. The delay/position combinations and their sequence in the experimental protocol were balanced to minimize effects of expectation by alternating high and low delays and proximal and distal positions in a fixed order. Because not every single delay could be combined with every single position, we decided to use the scheme shown in Table 1 to at least achieve uniform 'mean' y-positions for every delay. This method confounded the interaction of delay and repetition with stimulus position in the y-direction so that delay and position effects had to be tested in separate analysis (see Statistics section).

After each trial, subjects were asked how many stimuli they had detected. Then they were instructed to mark the perceived locations (P0, P1, and P2) of these stimuli with the 3D tracker without actually touching the skin to avoid the establishment of concurrent sensory reference points. As all stimulus locations were aligned to the one-dimensional 3D tracker scale in distal-proximal direction (y), shifts in lateral direction (x) were not taken into account for the data analysis. If more than three pulses were detected, P0 and P2 were defined as the most distal and proximal detections, while P1 was defined as the most proximal of the intermediate values. For the analysis of the saltation effect trials with only one or two detections were discarded, since it was not possible to assign the subjects' responses unambiguously to the three presented stimuli.

Each of the 14 intensity/delay combinations was repeated four times in 18 subjects, resulting in a data matrix with 2×7×4×18 = 1,008 cells.

In the classic tactile experiments (Geldard and Sherrick 1972; Geldard 1975), the displacement of S1 was measured as a proportion of the distance defined by the fixed positions of the first and the last stimulus on the skin (L0 and L2), which were visible to the subjects. With this partitioning technique with P0 and P2 anchored to L0 and L2, only variations of the perceived location of S1 were assessed. In the present study, no visual cues for the physical location of S0 and S2 were available to the subjects, so the perception of their locations as measured by P0 and P2 could also vary. Distances between the perceived positions P0, P1 and P2

Table 1 Correspondence of delays and positions in the stimulation matrix with the amount of trials presented during one intensity condition

Delay (ms)	S0/S1 y-position (mm)						
	0	10	20	30	40	50	60
60	2						2
100			2		2		
140			2		2		
180	2						2
220		2				2	
366				4			
516		2				2	

served as basis of analysis. Relative S1 displacement was defined as the distance between P0 and P1 as a percentage of the distance between endpoints P0 and P2.

Statistics

The multi-factorial repeated-measurements design was analysed by maximum-likelihood-estimated linear mixed models (Littell et al. 1998). This method has significant advantages compared to classic MANOVA repeated-measures analyses, as missing values are allowed to enter the analysis and the model can be fitted to the repetition-dependent autoregressions found in the data. Two separate models were fitted, one including intensity, delay and repetition, the other with intensity, position and repetition as experimental and control factors, thus separating the main factors delay and position confounded by the balancing of stimulus combinations over repetitions (see previous section). The significance level was set to 5% with sequential adjustments for multiple testing (Benjamini and Hochberg 1995). Location tests were performed with Student's t-statistics. Differences in frequency were tested with χ^2 techniques. Results are reported as means ± standard deviations. Data processing and calculations were performed with the SAS System for Windows, Release 8.2, and R for Windows, Version 1.8.1 (R Development Core Team 2003).

Results

Thresholds, perceived intensities, and detected stimuli

Mean thresholds, mean energies for the two intensity conditions, and corresponding calculated temperature changes are listed in Table 2. During the threshold procedure with the maximum intensity set to 17.3 mJ/mm^2, 'unpleasant' sensations could be elicited in 13 out of 18 subjects, additional 'painful' sensations in eight subjects.

The quality of the sensations on the dorsal forearm during the experiment was assessed by spot checks. The perceptual qualities on the arm reflected those assessed on the hand satisfactorily: at the lower intensity, which corresponded to a mean peak temperature rise from baseline skin temperature of 15.3°C, 10 subjects (56%) reported 'unpleasant' sensations, four subjects (22%) reported 'unpleasant' and 'painful' sensations. At the higher intensity with mean peak temperature changes of 25.4°C 'unpleasant' sensations were reported by 16 subjects (89%), accompanied by 'painful' sensations in ten subjects (56%). In two subjects, intensity had to be set to a lower value in the high-intensity condition, because sensations reached the individual tolerance threshold.

In only three of the total of 1,008 trials no stimulus at all was detected, one pulse was detected in 147 trials (15%), two pulses were detected in 516 trials (51%), and three or more pulses in 342 trials (34%). Intensity improved the amount of stimulus detections significantly (McNemar χ^2-test, $P < 0.001$): three or more pulses were detected in 115 of 504 trials (23%) at the lower stimulation intensity, whereas in 227 of 504 trials (45%) at the higher intensity. The amount of trials with three or more detected stimuli grew slightly smaller with repetition in the high-intensity condition (Cochran χ^2-test, $P < 0.05$), but not in the low-intensity condition. The y-position had no significant effect on the amount of trials with three or more detections at either intensity (Cochran χ^2-tests, n.s.).

Table 2 Mean laser intensities and peak temperature changes on the skin

	Energy (mJ/mm^2)	Temperature change (°C)
Detection	5.7 ± 2.4	8.7 ± 3.6
Pin-prick	7.0 ± 2.6	10.6 ± 4.0
Warmth	8.8 ± 4.8	13.4 ± 7.3
Heat	9.6 ± 3.1	14.5 ± 4.8
Unpleasantness	12.9 ± 3.9	19.6 ± 5.9
Pain	13.9 ± 2.1	21.1 ± 3.1
Low-intensity condition	10.1 ± 2.2	15.3 ± 3.4
High-intensity condition	16.8 ± 1.4	25.4 ± 2.1

Note: Temperature changes calculated according to the procedure described in the Methods section

Five subjects had general difficulties in detecting the stimuli: in this subgroup, three or more pulses were detected only in two low-intensity trials (1%) and in six high-intensity trials (4%), thus biasing the overall percentage of trials with three detected stimuli. However, there was no difference in the number of trials with two detected stimuli compared to the other subjects.

Due to technical artifacts from the 3D tracker arising from rapid hand movements by the subjects 47 trials of the 342 trials with three or more detected stimuli had to be discarded, leaving 295 trials for the analysis of the saltation effect.

Saltation characteristics

As predicted, the stimulus S1 was perceived at a position different from that of S0 in the direction towards S2 in almost every single trial with three or more detected pulses. The absolute mean deviation of P1 from P0 was 51 ± 36 mm. The mean relative S1 displacement was 51 ± 27% and it increased linearly with decreasing delay (Fig. 2). A linear mixed model analysis for the factors intensity, delay, and repetition showed that only the delay between S1 and S2 yielded a significant effect on the relative displacement of S1 (Table 3).

The second linear mixed model analysis including the factors intensity, position, and repetition showed also a significant effect of stimulus position on the lower arm, that is, the relative displacement of S1 increased linearly with more proximal stimulus sites (Table 3, Fig. 3). This means that the relative S1 displacement not only

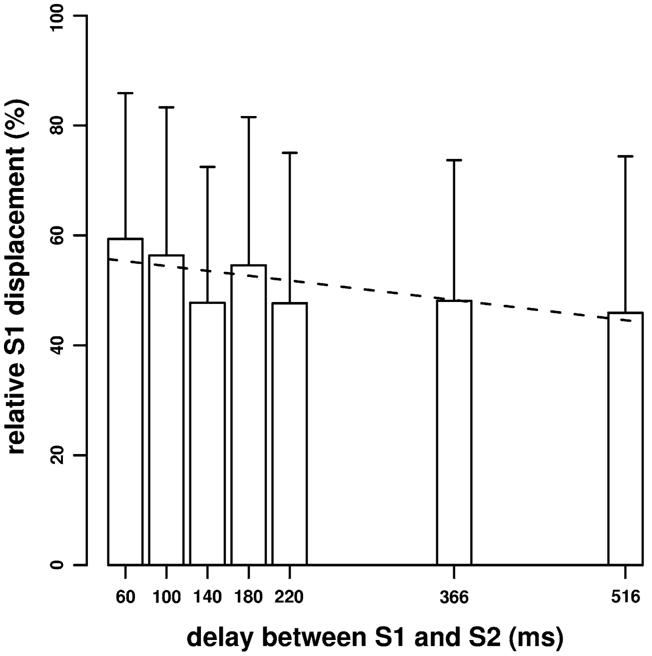

Fig. 2 Relative displacement of 'saltatory' stimulus S1 as a function of delay of the consecutive stimulus S2. Ordinate: mean relative S1 displacement in percent of perceived length of the whole stimulus pattern (distance P0–P2); abscissa: delay between the onsets of S1 and S2; *error bars*: standard deviations; *dashed line*: linear regression of displacement on delay (intercept: 56.69, slope: –0.02). The high standard deviations result from substantial interindividual differences, as well as from the effect of different positions on the forearm (cf. Fig. 3)

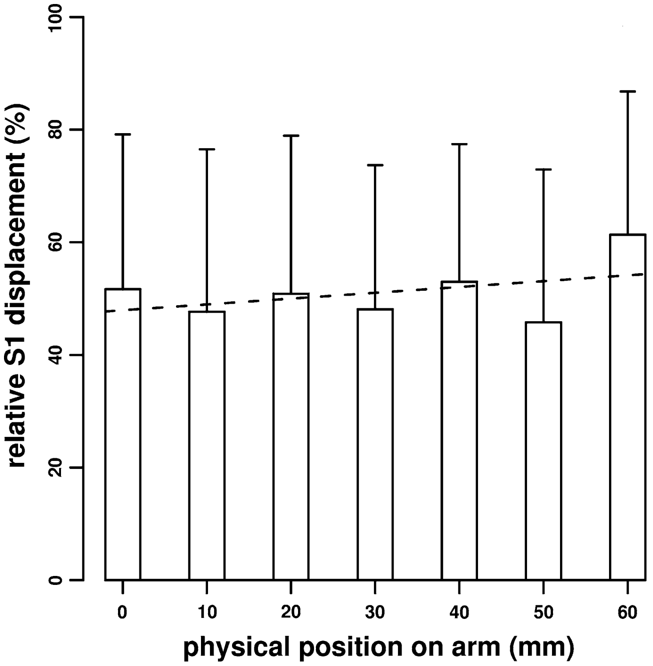

Fig. 3 Relative displacement of 'saltatory' stimulus as a function of location on the lower arm. Ordinate: mean relative S1 displacement in percent of perceived length of the whole stimulus pattern (distance P0–P2); abscissa: position of L0/L1 on the forearm (cf. Fig. 1); *error bars*: standard deviations; *dashed line*: fitted linear regression curve (intercept: 48.06, slope: 0.10). The relative displacement increased significantly towards higher (more proximal) positions (cf. Table 3)

changed with the delay between S1 and S2, as reported in the older literature, but depended also on the absolute position on the arm.

Representation of the stimulated area

Since there was no visual cue for the locations of S0 and S2, subjects' perception of these locations was free to vary. The distance between the perceived endpoints P0 and P2 of the stimulation pattern decreased linearly from more distal to more proximal stimulation sites on the forearm (Fig. 4). In trials with S0 and S1 applied close to the wrist (e.g. L0/L1 at $y=0$ mm, cf. Fig. 1), the mean distance between P0 and P2 was 111 ± 46 mm and thus not significantly different from the physical distance of 105 mm between L0/L1 and L2 (Student's *t*-test, n.s.). In contrast, at more proximal positions the distance between the perceived positions was significantly smaller than the physical distance (e.g. 84 ± 35 mm with L0/L1 at $y=60$ mm; Student's *t*-test, $P<0.001$). In the linear mixed model analysis with the factors intensity, position, and repetition as predictors, the distance between P0 and P2 depended significantly on position, but not on the delay between S1 and S2 (Table 2). There was a significant interaction effect on P0–P2 distance between delay and repetition which, however, only reflects an artifact from the fixed sequence of stimulus combinations of the balancing method (cf. Methods section).

Table 3 Effects of stimulus intensity, delay and position on the relative displacement of the target stimulus S1 and distances between perceived positions

Factors	Relative S1 displacement		Distance between P0 and P2	
Intensity	$F_{1,11}=0.8$	n.s.	$F_{1,11}=3.5$	n.s.
Delay	$F_{6,71}=4.0$	$P<0.05$	$F_{6,71}=0.4$	n.s.
Position	$F_{6,70}=3.7$	$P<0.05$	$F_{6,70}=4.9$	$P<0.01$
Repetition	$F_{3,38}=0.3$	n.s.	$F_{3,38}=1.2$	n.s.

Note: Results of two separate linear mixed models including (a) intensity, delay, and repetition and (b) intensity, position, and repetition as experimental factors; *F* values with corrected probabilities; cf. Statistics section. No significant interactions except the balancing effect discussed in the Methods and Results sections

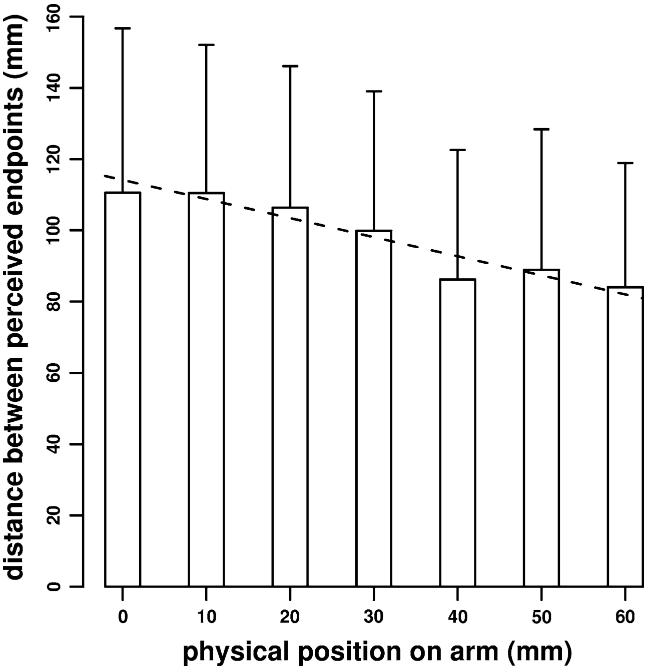

Fig. 4 Distance between perceived stimulus positions as a function of location on the lower arm. Ordinate: mean distance between the perceived positions of S0 and S2 (P0 and P2) with standard deviations; abscissa: position of L0/L1 on the lower arm (cf. Fig. 1); *error bars*: standard deviations; *dashed line*: fitted linear regression curve curve (intercept: 113.41, slope: –0.51). The distance between the two endpoints of the stimulus pattern decreased significantly towards higher (more proximal) positions (cf. Table 3)

Discussion

Saltation elicited by thermal stimulation

This study demonstrated for the first time the existence of the saltation phenomenon in the processing of heat and pain stimuli without involvement of touch sensations. The displacement of the target stimulus S1 increased linearly with decreasing delays of the following stimulus S2 applied 105 mm apart, which is in line with the classic tactile studies (Geldard and Sherrick 1972; Geldard 1975; Cholewiak and Collins 2000) as well as with more recent results (Stolle 2004). The observed systematic deviations are substantial, taking into account that the localization accuracy of heat stimuli is almost as good as in mechanoceptive sensation (Moore and Schady 1995; Schlereth et al. 2001).

Apart from the general correspondence, our results differ in detail from the classic saltation studies. In our experiment, even at the shortest delay of 60 ms high S1 displacements of up to 100% ('coinicidence') were rare. Further, even at long delays of 516 ms, displacements were generally substantial, and a complete lack of displacement ('exodus', e.g. S0 and S1 are perceived at the same site) was observed only in a negligible amount of trials. These results conflict with the original experiments by Geldard and co-workers (Geldard 1975), where at short delays coincidence was regularly reported and at delays above 300 ms no displacement of S1 occurred. To explain these discrepancies, the methodological differences between our study and the classic reports have to be considered. In Geldard's original setup (a) the delays were manipulated by the subjects to achieve a given displacement (method of adjustment), and (b) the 'endpoints' P0 and P2 were visually anchored. If however the same psychophysical scaling method as in the present study is used, comparable results are also yielded in tactile saltation (Stolle 2004).

The distance between the perceived locations of the endpoints (P0, P2), that is, the perceived length of the spatiotemporal stimulus pattern decreased from distal to proximal sites on the forearm (Fig. 4). At the most proximal pair of stimulation sites it was only 80% of the physical distance. This phenomenon is known from tactile saltation as well, where it is even more prominent (Stolle 2004). It is unlikely that visual perspective biases might have led to this effect, as there were no visual anchor points for the stimuli. The effect can rather be related to the decreasing resolution of the cortical representation towards the elbow. Such differences in the cortical magnification factor (Sur et al. 1980) would also explain the increase of the relative displacement of the 'saltatory' stimulus (S1) at more proximal sites (cf. Table 3, Fig. 3; position effect on relative S1 displacement): due to the decrease of the cortical magnification factor in distal-proximal direction the same amount of displacement in the cortical representation refers to a larger proportion of the skin surface for areas near the elbow and to a smaller proportion for areas near the wrist. Correspondingly, this results in larger S1 displacements in perceptual space for more proximal areas. However, this question remains open to discussion, because to our knowledge no systematic studies on the variability of RF sizes on the body surface have been carried out for thermoception and nociception to date.

Variations in intensity did not lead to substantial differences in saltation characteristics (cf. Table 3). The intensity dimension was originally introduced to differentiate between thermal and nociceptive activation. It is however disputable if this discrimination could indeed be achieved, as will be discussed in the following section.

Sensory networks involved in thermal saltation

CO_2 laser stimuli activate nociceptive Aδ and C multimodal (mechano-heat) fibers (AMH-II, CMH), but no mechanoceptors (Bromm and Treede 1984). C-fiber warm receptors in humans respond to thermal stimuli up to 46°C with a peak discharge frequencies between 40 and 45°C (Hensel 1981). Nociceptive AMH-II and CMH fibers respond to temperatures starting at 43°C. AMH-II fiber activation is known for a well-detectable sharp pin-prick sensation (Konietzny et al. 1981), also called 'first pain', whereas CMH fibers are responsible for the dull, burning ‘second pain’ component (Ochoa and Torebjörk 1989). Low intensity stimulation of nociceptive fibers leads to non-painful ‘pre-pain’ sensations; temporal and/or spatial summation of several activations is needed to result in a subjective experience of pain (Pertovaara et al. 1988).

The laser pulses used in our study induced mean peak temperature changes of 15°C in the low-intensity condition and 25°C in the high-intensity condition (cf. Table 2). Assuming a baseline skin temperature of 30°C, a typical low-intensity pulse resulted in peak skin temperatures around 45°C and thus probably both thermoceptor and nociceptor activations, whereas high-intensity pulses reached peak temperatures of more than 55°C where thermoceptor activation can be discounted.

Consequently, the failure to find significant differences in saltation characteristics between the two intensity conditions can possibly be explained by the fact that a clear-cut discriminination between thermal and nociceptive activation could not be achieved. Thus, we can draw no final conclusions on saltation characteristics of exclusive thermoceptor activation. It is however safe to say that a concurrent activation of both systems, as present in the low-intensity condition does not lead to results different from exclusive nociceptor activation.

Cortical areas commonly activated by laser stimuli include the insula, the anterior cingulate cortex, suprasylvian areas, and the postcentral gyrus (cf. Garcia-Larrea et al. 2003). The latter is of particular interest for the explanation of the saltation effect. As discussed before, tactile saltation is thought to result from activation patterns in the primary somatosensory cortex (Geldard 1975; Wiemer et al. 2000). The representation of nociceptive and thermal stimuli in the postcentral gyrus is somatotopically organized, and activation was found close to the corresponding tactile activations (Chatt and Kenshalo 1977; Tarkka and Treede 1993; Andersson et al. 1997), however outside the somatosensory representation in areas 3b and 1, presumably rather in area 3a (Ohara et al. 2004). These findings suggest that a ‘body map’ for warmth and/or pain exists next to the tactile representation, basically sharing its somatotopical characteristics.

Limitations

The full set of three stimuli applied in one saltation trial was detected in 342 trials only, representing 34% of the total sample. However, two pulses at two distinct locations were detected in another 51% of all trials. The consistent reports of at least two separate perceived locations in 85% of the trials show that subjects detected pulses from both stimulation sites in a majority of cases. Nonetheless, one of the three pulses frequently remained undetected.

It is known that the S1 stimulus is usually perceived as less intense than S0 and S2 (Geldard 1975), thus we suppose that in most of the cases it was S1 that was missed by the subjects. Fatigue in AMH-II and CMH fibers possibly contributes to this effect (cf. Treede et al. 1995; Olausson 1998). It is however questionable if fatigue alone can explain the large amount of missed S1 stimuli, considering that repetitive laser stimulation at 1 Hz rather leads to an increase in perceived intensity (Trojan et al. 2002), probably due to spinal ‘windup’ (Mendell 1966).

A more detailed study of backward and forward masking effects in spatiotemporal stimulation paradigms is needed to clarify this issue and reduce dropout rates. In this connection, individual differences in detecting complex stimulus patterns should also be taken into account, since a subgroup of our subjects barely detected a third pulse at all but did not substantially differ from the rest of the sample otherwise.

Assessment of cortical representations with spatiotemporal stimulus patterns

Contrary to the static model of SI topography by Penfield and Rasmussen (1950), cortical representations (‘body maps’) are dynamic, i.e. dependent on spatiotemporal characteristics of incoming stimuli. This ability to adapt the sizes of cortical receptive fields to changing sensory input is well-known to come into effect as a result of regular training (Rockstroh et al. 1998), repetitive stimulation (Godde et al. 1996; Shimojo et al. 2000), or amputations and nerve damage (Flor et al. 1998; Ramachandran and Hirstein 1998).

However, the causes for plastic changes do not have to be this massive. Focusing the subjects’ attention to specific positions may be sufficient for cortical reorganization (Braun et al. 2000). The saltation effect itself is an example for dynamic (mal–) adaptation on a much smaller time scale. But even a few repetitions of such stimulation patterns seem to be sufficient to trigger lasting biases in perception (Stolle 2004). Perhaps plasticity in spatial representations can be described in stages of activation-dependency, modulation, and modification, similar to those introduced by Woolf and Salter (2000) for the plasticity in pain intensity.

At present, somatosensory representations—and their dynamics—are almost solely evaluated by neuroimaging approaches in humans. Adequate methods to identify the perceptual equivalents of spatial changes in the sensory cortices and their temporal dynamics are needed as functional correlates. This is of particular importance for investigating the development of chronic pain after injury and may apply as well to functional pain and other disorders with altered body perception possibly related to distorted ‘body maps’ or disturbed somatic and visceral integration as in the irritable bowel syndrome (Mayer and Raybould 1990; Hölzl et al. 1998a, b).

We suggest that the saltation technique can serve as a tool for the psychophysical assessment of ‘body maps’. Given that the size of the saltatory area is indeed related to the size of cortical receptive fields (Geldard 1985; Wiemer et al. 2000), the spatial representation in the cortex can be mapped by assessing saltatory field sizes. Differences between different modalities—e.g. tactile versus. Nociceptive—may be assessed and interindividual differences of saltatory areas and other saltation characteristics may be used to indicate and/or predict maladaptive cortical reorganization. Recent findings on altered tactile illusions in chronic pain patients (Gonzales et al. 2001) justify further investigation of these questions.

Conclusion

In the present study, saltation was demonstrated for the first time with CO_2 laser stimulation. The results support the view that saltation is a general phenomenon in the sensory system. Saltation stimuli and other spatiotemporal stimulation techniques have the potential to make a substantial and innovative contribution to the functional analysis of the nociceptive system. Applications include basic psychophysical experiments and neuroimaging applications as well as the assessment of stimulus-response characteristics in clinical groups.

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