Spatiotemporal integration of tactile patterns along and across fingers

Jörg Trojan a,b,*, Maruschka Heil c, Christian Maihöfner d,e, Rupert Hölzl b,c, Dieter Kleinböhl c, Herta Flor b, Justus Benrath f

a Department of Psychology, University of Koblenz-Landau, Fortstraße 7, 76829 Landau, Germany
b Department of Neurology, University of Erlangen-Nuremberg, Schwabachanlage 6, 91054 Erlangen, Germany
c Otto Selz Institute for Applied Psychology, University of Mannheim, 68131 Mannheim, Germany
d Department of Neurology, University of Erlangen-Nuremberg, Schwabachanlage 6, 91054 Erlangen, Germany
e Department of Physiology and Pathophysiology, University of Erlangen-Nuremberg, Universitätsstraße 17, 91054 Erlangen, Germany
f Centre of Pain Therapy, Clinic of Anaesthesia and Intensive Care, University Medical Centre Mannheim, Medical Faculty Mannheim, Heidelberg University, 68167 Mannheim, Germany

ARTICLE INFO
Article history:
Received 29 April 2013
Received in revised form
14 October 2013
Accepted 26 October 2013
Available online 12 November 2013
Keywords:
Somatosensory perception
Localisation
Spatiotemporal integration
Touch
Perceptual map

ABSTRACT
The volar sides of the fingers can be seen as the haptic counterpart to the fovea for visual perception. This study assessed the localisation of individual tactile stimuli and spatiotemporal patterns presented to the volar side of the fingers. Participants performed the localisation task by pointing at the perceived positions with a 3D tracker. Based on the pointing data, perceptual maps were devised in which perceived positions, their relationship to each other and to veridical stimulus positions could be analysed. Participants were able to accurately and consistently report the locations of the stimuli. Localisation of stimuli presented within a spatiotemporal pattern generally differed from localization of individual stimuli presented to the same positions. In most cases, stimuli were perceived as being spatially closer when they were presented within a spatiotemporal pattern compared to when being presented individually. Spatiotemporal integration along the fingers followed the predictions of the sensory saltation paradigm: The shorter the temporal delay between the two stimuli, the closer together they were perceived. For spatiotemporal patterns across fingers, the results were inconclusive: No general relationship between temporal delay and the difference between the perceived positions could be demonstrated, presumably because the effect could only be elicited in some finger combinations. Temporal delay did have, however, an effect on overall lateral shifts in localisation.

© 2013 The Authors. Published by Elsevier Ltd. Open access under CC BY license.

1. Introduction

1.1. The hands: Mostly uncharted territory

Hands are the tools we use to interact with the world and they are the body parts in which the tight coupling between action and perception is most obvious: The volar hand, and in particular the fingertips, can be seen as the somatosensory counterparts to the fovea for visual perception. In contrast to the eyes, however, in the hands the capacity to explore the environment and to act on it are implemented in the same organ.

The field of haptics has studied these integrated functions of the hand for several decades now and has yielded important insights into the psychological and neurophysiological foundations of active touch as well as into its application to aesthetics, ergonomics, and the design of user interfaces (for an introduction see Grunwald, 2008). At a more fundamental level, however, tactile perception has received relatively little interest to date. Intriguingly, there are very few studies on the localisation of tactile stimuli at the volar hands, and most of them neglect the fingertips (e.g. Culver, 1970; Rapp, Hendel, & Medina, 2002; Ylloja, Carlson, Raji, & Pertovaara, 2006; Mancini, Longo, Ianetti, & Haggard, 2011).

1.2. Spatiotemporal integration

Both passive somatosensory perception and active haptic exploration heavily rely on dynamics, e.g. for the perception of
textures and forms and in the perception of movement on the skin. Contrary to other sensory modalities, however, spatiotemporal integration has rarely been studied in somatosensation.

One of the few approaches to systematically tackle the role of spatiotemporal integration in the perception of touch is sensory saltation (Geldard & Sherrick, 1972; Geldard, 1975): If two stimuli are presented at two different positions with a short delay, the perceived position of the first stimulus – the attractee – is mislocalised toward the position of the second stimulus – the attractant – and this mislocalisation increases with decreasing delays between the two stimuli.

Sensory saltation has been studied at several body sites, but apart from the original work (Geldard & Sherrick, 1983), only one study of spatiotemporal integration at the hand has been conducted to date: Warren, Santello, and Helms Tillery (2010) presented tactile spatiotemporal patterns across fingertips and could demonstrate that when the tips of the second and fifth digit were stimulated with a delay of 100 ms, the stimulus presented to the second digit was reported to be perceived at the tip of the third digit in 20–30% of the trials. These findings can be interpreted as indicating that spatiotemporal integration does occur over the range of several fingers.

Warren et al. (2010) only used one temporal delay and did not assess the direct localisations of the perceived stimulus positions, but used a forced-choice paradigm. This procedure does not allow to determine the quantitative relation between displacement and attractee–attractant delay. Thus, it is not possible to distinguish whether the observed mislocalisation actually represents the result of sensory saltation in particular or other aspects of spatiotemporal integration, which have been observed for a variety of conditions in which two stimuli follow each other closely in time (Goldreich, 2007).

1.3. Perceptual maps of the hand

In earlier publications, we have introduced the concept of perceptual maps as a means of deriving parametric representations of what people perceive based on direct localisation of perceived positions via pointing (Trojan et al., 2006, 2009, 2010; Steenbergen, Buitenweg, Trojan, Klaassen, & Veltink, 2012; Steenbergen, Buitenweg, Trojan, & Veltink, 2013). Based on this concept, Mancini et al. (2011) conducted a study in which a map of localisations on the hand was assessed, both for tactile and for nociceptive stimuli.

Mancini et al. (2011) let participants use a mouse cursor on silhouetted photographs of the hand presented on a computer screen to report positions. In that study – deviating from the original concept of perceptual maps – participants did not perform actual pointing movements but rather reported judgements of perceived positions. In addition, the study focused on stimuli presented to the hairy skin at the dorsum of the hand. No stimuli were presented to the glabrous skin at the volar side of the fingers.

1.4. Aims of this study

In this study we examined the spatial and spatiotemporal characteristics of tactile perception at the volar side of the hands with a set of three experiments. First, we presented individual tactile stimuli to a set of nineteen anatomically well-defined positions and let participants point to where they perceived them. The data were analysed with respect to accuracy and consistency. In a second experiment, we studied spatiotemporal integration of tactile stimuli along fingers with patterns of two stimuli presented to the distal and proximal phalanges of the same finger. We varied the time interval between the two stimuli and the order in which the positions were stimulated. In a third experiment, we studied spatiotemporal integration of tactile stimuli across fingers by stimulating the distal phalanges in all possible combinations and varying time intervals.

2. Materials and methods

2.1. Participants

A total of 19 participants (9 female) were studied; they were on average 23.5 years old; 18 of them were right-handed and one was ambidextrous; 16 were students, 1 was in civilian service, 1 was an employee and 1 was a PhD candidate. All gave written informed consent.

2.2. Tactile stimulation device

Stimuli were presented via a custom-built tactile display, consisting of a half-cylindrical plastic mounting with a grid of 376 holes containing threads, forming the possible stimulation positions (Fig. 1). These positions can be adapted to each participant’s hand in order to yield anatomically comparable stimulus positions, regardless of hand size. The stimulators consist of pneumatically driven actuators with blunt metal rods (EG-2.5-10-PK-2, Festo, Esslingen, Germany). All stimulators have a thread at their top end, which makes it possible to screw them into the intended positions. Plastic tubes connect the stimulators to valves (CPV10, Festo, Esslingen, Germany), which are controlled via digital ports (NI 6501, National Instruments, Austin, Texas). For each participant, the positions were stimulated. In a second experiment, we studied spatiotemporal integration of tactile stimuli across fingers by stimulating the distal phalanges in all possible combinations and varying time intervals.
Instruments, Austin, TX, U.S.A.) connected to a personal computer running Presentation (version 14.2, Neurobehavioral Systems, Albany, CA, U.S.A.). During the experiment, the participant’s hand covered all stimulators so that their movements were not visible. We cannot rule out the possibility that, in some cases, the mechanical stimulation may have led to minimal deformation or even movement of the fingers. However, even if participants detected such visual cues, their potential effect on reports of the perceived positions is assumed to be small. Spatial accuracy on the fingers is very good, even in the absence of vision (Kalisch, Kagert, Schwenkreis, Dinse, & Tegenthoff, 2009; Peters, Hackeman, & Goldreich, 2000), so there is not much room for improvement.

The faint sound made by the stimulators was muffled by the hand lying on top of them. Even under optimal conditions, auditory localisation blur can already amount to several degrees, so substantial influences on the stimulus localisation can be safely ruled out.

2.3. Position tracking system

A 3D tracking system (ISOTRAK II, Polhemus, Colchester, VT, U.S.A.) with a pen-shaped pointing device (‘stylus’) was used to record the spatial coordinates. After the stimulus positions had been adjusted to the participant’s hand (see Fig. 1), cardinal points of the stimulation device as well as the coordinates of the adapted stimulators were recorded.

2.4. Experimental protocol

The study was conducted in the Laboratory for Clinical Psychophysiology of the Otto Selz Institute for Applied Psychology, Mannheim. The participants were informed that the study examined the perception of tactile stimulation on the hand. Three separate experiments were conducted in direct succession. In total, one session took about 90 min.

2.4.1. Experiment 1

Participants had their eyes open and watched their hand. They had to localise individual stimuli at 19 different positions on the volar side of their left hand (see Fig. 1). Their task was to hold the stylus above the dorsum of their hand and to point to the perceived position of a stimulus, without touching their hand. The position was confirmed by pressing a button on the Stylus. Each position was repeated 10 times, yielding a total of 190 stimuli. Stimuli were presented in randomised order and the participants had a short break after 95 trials.

In cases in which participants had not perceived the stimulus, they indicated this by pointing the tracker high above the hand, so that these trials could be identified automatically during preprocessing (see below).

2.4.2. Experiment 2

Participants had their eyes open and watched their hand. Patterns of two stimuli were presented in longitudinal direction to the left hand, one at the proximal phalanx and one at the distal phalanx of the same finger. Participants were instructed to localise both of them using the same method as described above in the order in which they had perceived them. Patterns differed in respect to which finger was used (index finger, middle finger, ring finger, little finger), temporal order (proximal/distal or distal/proximal), and stimulus onset asynchrony (50 ms, 100 ms or 200 ms). Each of these 24 combinations was repeated 10 times in randomised order, leading to a total of 240 trials. The participants’ task was to hold the stylus above the dorsum of their hand and to point to the perceived positions of the stimuli in the order in which they had perceived them, without touching their hand. The position was confirmed by pressing a button on the Stylus. After 120 trials, participants had a short break.

The presented stimulation patterns were equivalent to the “utterly reduced rabbit” pattern according to the terminology by Geldard (1975). A shift of the first stimulus towards the second stimulus is expected, and the amount of this shift increases with shorter delays.

In cases in which participants had not perceived one of the stimuli, they indicated this by pointing the tracker high above the hand, so that these trials could be identified automatically during preprocessing.

2.4.3. Experiment 3

Patterns of two stimuli at different positions were presented in transverse direction to the left hand. Each of the stimuli was presented at one of the distal phalanges, resulting in 6 finger combinations (index/middle, index/ring, index/ little, middle/ring, middle/little, ring/little). Again, stimulus onset asynchrony was varied (50 ms, 100 ms or 200 ms). With 10 repetitions, this led to a total of 180 trials, which were presented in randomised order. The participants’ task was to hold the stylus above the dorsum of their hand and to point to the perceived positions of the stimuli in the order in which they had perceived them, without touching their hand. After 90 trials, participants had a short break.

The presented stimulation patterns were equivalent to the “utterly reduced rabbit” pattern according to the terminology by Geldard (1975).

In cases in which participants had not perceived one of the stimuli, they indicated this by pointing the tracker high above the hand, so that these trials could be identified automatically during preprocessing.

2.5. Preprocessing

All data were aligned to the cardinal points of the stimulation device. Differences in vertical direction were omitted. The remaining two-dimensional data were converted to standard units by normalising them to individual hand size using the same approach as Mancini et al. (2011); cf. Bookstein (1991). See Appendix for details.

In experiments 2 and 3, participants were instructed to report positions in the order in which they had perceived them. Due to the close temporal proximity, it is not uncommon that participants confuse the first and the second stimulus (cf. Trojan et al., 2016). Because the correct order is relevant for the graphic display of the data and partly for the calculation of dependent measures (see next subsection), we switched the reported order where appropriate (experiment 2: 1087 of 4560 trials; experiment 3: 441 of 3420 trials) and excluded implausible data (experiment 2: 6 of 4560 trials; experiment 3: 11 of 3420 trials). See Appendix for details.

Trials in which participants failed to perceive any of the presented stimuli were also excluded from the analysis (experiment 1: 135 of a total of 3688; experiment 2: 32 of a total of 4560; experiment 3: 31 of a total of 3420).

2.6. Dependent measures

2.6.1. Experiment 1

The displacement of the perceived from the physical stimulus positions was determined by using the Euclidian distance between these two positions in the 2D plane.

Fig. 2. Accuracy and consistency. (A) Accuracy of the position ratings was measured as the mean distance of perceived positions (black dots) from veridical positions (grey dot); the mean of the perceived position (open grey circle) is irrelevant for this measure. (B) Consistency was measured as the mean distance of perceived positions (black dots) from their respective mean (grey dot); here; the veridical position (open grey circle) is irrelevant.
In experiment 1, two different parameters served as dependent variables: accuracy of the position ratings (in the sense of a constant error) was measured as the mean distance of perceived positions from veridical positions (see Fig. 2A). Consistency (in the sense of a variable error or dispersion) was measured as the mean distance of perceived positions from their respective mean (see Fig. 2B).

2.6.2. Experiments 2 and 3

For experiments 2 and 3, two different indicators of spatiotemporal integration were calculated.

1. The clearest indicator of spatiotemporal integration is the distance between the perceived positions of attractee and attractant, which should decrease with decreasing attractee–attractant interval. This absolute attractee–attractant distance was determined by the Euclidian distances between the perceived positions of attractees and attractants for each individual trial (see Fig. 3A).

2. In order to account for intra- and interindividual differences in finger length (experiment 2) as well as interindividual differences in finger spacing (experiment 3), we calculated another measure, relative attractee–attractant distance: (1) We determined the vector between the veridical stimulus positions of the attractee and the attractant; (2) the perceived attractee and attractant positions were projected onto this vector and the Euclidian distance between these two points was determined for each individual trial; (3) we also projected the perceived positions of individual stimuli presented at the same positions as attractees and attractants, as assessed in experiment 1, and calculated their Euclidian distance; (4) in a last step we divided the prior by the latter distance (see Fig. 3B).

In order to quantify the individual displacements of attractees and attractants, we calculated the distances to their respective reference positions on the vector connecting the two veridical stimulus positions, following the same approach described above for the relative attractee–attractant distance. This results in the relative attractee displacement and the relative attractant displacement. These three distances add up to 1, because all of them are normalised to the same two reference positions.

We also calculated absolute proximal–distal shifts between each reported stimulus and its respective reference position in experiment 2 and absolute medial–lateral shifts between each reported stimulus and its respective reference position in experiment 3.

2.7. Experimental designs and statistical analyses

All experiments were analysed with Linear Mixed Models allowing for individually different intercepts as random effects.

In experiment 1, the fixed factors were finger type (index finger, middle finger, ring finger, little finger), and segment (distal phalanx, intermediate phalanx, proximal phalanx, metacarpal). The thumb was omitted from the statistical analyses due to its fundamental anatomical differences.

In experiment 2, the fixed factors for analysing distances and displacements were finger type (index finger, middle finger, ring finger, little finger), temporal order (proximal/distal or distal/proximal), and stimulus onset asynchrony (50 ms, 100 ms or 200 ms). Absolute proximal–distal shifts over all individual positions were analysed using anatomical position (proximal or distal), role (attractee or attractant) and stimulus onset asynchrony (50 ms, 100 ms or 200 ms) as fixed factors.

In experiment 3, the fixed factors were finger combination (index/middle, index/ring, index/little, middle/ring, middle/little, ring/little) and stimulus onset asynchrony (50 ms, 100 ms, 200 ms). Absolute lateral–medial shifts over all individual positions were analysed using role (attractee or attractant) and stimulus onset asynchrony (50 ms, 100 ms or 200 ms) as fixed factors. Attractees and attractant were not equally distributed over fingers (see finger combinations described above). In order to account for potentially differential effects of the fingers, they were included as a random factor in the latter analysis (random term: ~1 + finger | subject).

In all analyses, values were first aggregated at the individual level in order to yield a stable indicator of the participant’s performance; then these aggregated measures (one per participant and design cell) were entered in the group-level analyses.

All statistics and figures were prepared with R, version 3.0.1 (R Core Team, 2013). Linear Mixed Models were calculated with the nlme package, version 3.1-109 (Pinheiro, Bates, DebRoy, Sarkar, & Core Team, 2013). Post-hoc comparisons were performed via Tukey contrasts using the multcomp package, version 1.2–18 (Bretz, Hothorn, & Westfall, 2010).

3. Results

3.1. Accuracy and consistency of perceived positions of single stimuli (experiment 1)

The accuracy of perceived positions, i.e., their accordane with veridical positions, was high (see Fig. 4). The average absolute displacement over all stimulus positions was 0.17 ± 0.04 standard units, equivalent to a mean displacement of about 10 ± 3 mm. The consistency of perceived positions was 0.09 ± 0.02 standard units, equivalent to a mean displacement of about 5 ± 1 mm.

The tip of the little finger was the position yielding the highest accuracy and consistency (accuracy: 0.11 ± 0.04 standard units, 7 ± 3 mm; consistency: 0.06 ± 0.02 standard units; 3 ± 1 mm), the lowest accuracy was found at the thenar (0.25 ± 0.08 standard units, 16 ± 6 mm) and the lowest consistency was found at the proximal phalanx of the ring finger (0.13 ± 0.06 standard units; 8 ± 4 mm).

Accuracy was strongly determined by segment (F(3, 269) = 324.2, p < .001; Table 1) but only marginally by finger type (F(3, 269) = 2.2, p < .10; Table 1); post-hoc comparisons showed that the effects were mainly driven by particularly low accuracy at the metacarpal bone (Table 2). Consistency was affected by segment as well (F(3, 269) = 308.5, p < .001; Table 3); post-hoc comparisons showed that ratings at the distal and medial phalanx were more
Sensory saltation could be elicited on all four tested fingers, both in proximal-distal and in distal–proximal direction. Fig. 5 shows a perceptual map displaying all positions examined in this experiment; Fig. 6 shows the absolute and relative attractee–attractant distances.

As expected, we found a main effect of attractee–attractant interval on absolute attractee–attractant distance \( (F(2, 414) = 368.6, p < .001; \text{Table 5}) \). The smaller the interval, the closer together attractee and attractant were perceived (Fig. 6A). Post-hoc tests showed that the effect was mainly driven by a difference between the 50 ms vs. 100 ms intervals (Table 6). Absolute attractee–attractant distance was generally smaller in proximal-distal than in distal–proximal direction (\( F(1, 414) = 7.8, p < .01; \text{Table 5} \)). We also found a main effect for finger type (\( F(3, 414) = 48.7, p < .001; \text{Table 5} \)), which was based on the generally reduced distances for stimulus patterns presented to the little finger (Table 7).

For the relative attractee–attractant distance, the effects were smaller, but showed the same pattern: The main effects of attractee–attractant interval and finger type were significant, direction differences were only present at the trend level (attractee–attractant interval: \( F(2, 414) = 5.9, p < .01; \) finger type: \( F(3, 414) = 4.5, p < .01; \text{Table 5} \)), which was based on the generally reduced distances for stimulus patterns presented to the little finger (Table 7).

### 3.2. Spatiotemporal integration along fingers (experiment 2)

#### 3.2.1. Effects on the distances between perceived attractee and attractant positions

In line with earlier results, we expected the effect of spatiotemporal integration to be higher in the distal–proximal than in the proximal-distal direction. In addition, the overall amount of displacement at the well-represented index finger was expected to be lower than at the more poorly represented other fingers.

### Table 1

| Experiment 1. Linear Mixed Model accuracy. |
|-------------------------------------------|
| \hspace{2cm} | \hspace{1cm} \hspace{1cm} | \hspace{1cm} \hspace{1cm} |
| \textbf{df} | \textbf{F} | \textbf{Sig} |
| \text{Intercept} | 1, 269 | 324.2 | *** |
| \text{Segment} | 3, 269 | 19.1 | *** |
| \text{Finger} | 3, 269 | 2.2 |  |
| \text{Segment} × \text{finger} | 9, 269 | 1.1 |  |

\*p < .05; \**p < .01.  
***p < .001.  
1 p < .10.

### Table 2

| Experiment 1. Tukey contrasts of the effects of segment on accuracy. |
|-------------------------------------------------------------------|
| \hspace{2cm} | \hspace{1cm} \hspace{1cm} | \hspace{1cm} \hspace{1cm} |
| \textbf{z} | \textbf{Sig} |
| Distal phalanx vs. medial phalanx | 1.1 |  |
| Distal phalanx vs. proximal phalanx | 0.8 |  |
| Distal phalanx vs. metacarpus | 3.8 | *** |
| Medial phalanx vs. proximal phalanx | -0.2 |  |
| Medial phalanx vs. metacarpus | 2.8 | * |
| Proximal phalanx vs. metacarpus | 3.0 | * |

\*p < .01; \*p < .10.  
1 p < .05.  
***p < .001.

### Table 3

| Experiment 1. Linear Mixed Model consistency. |
|------------------------------------------------|
| \hspace{2cm} | \hspace{1cm} \hspace{1cm} | \hspace{1cm} \hspace{1cm} |
| \textbf{df} | \textbf{F} | \textbf{Sig} |
| \text{Intercept} | 1, 269 | 308.5 | *** |
| \text{Segment} | 3, 269 | 32.5 | *** |
| \text{Finger} | 3, 269 | 0.3 |  |
| \text{Segment} × \text{finger} | 9, 269 | 1.6 |  |

\*p < .05; \**p < .01; \*p < .10.  
***p < .001.

### Table 4

| Experiment 1. Tukey contrasts of the effects of segment on consistency. |
|---------------------------------------------------------------------|
| \hspace{2cm} | \hspace{1cm} \hspace{1cm} | \hspace{1cm} \hspace{1cm} |
| \textbf{z} | \textbf{Sig} |
| Distal phalanx vs. medial phalanx | 1.4 |  |
| Distal phalanx vs. proximal phalanx | 3.9 | *** |
| Distal phalanx vs. metacarpus | 5.3 | *** |
| Medial phalanx vs. proximal phalanx | 2.5 |  |
| Medial phalanx vs. metacarpus | 3.9 | *** |
| Proximal phalanx vs. metacarpus | 1.4 |  |

\*p < .05; \**p < .01.  
***p < .001.  
1 p < .10.

consistent than at the distal phalanx and the metacarpal bone (Table 4).

### 3.2. Spatiotemporal integration along fingers (experiment 2)

#### 3.2.1. Effects on the distances between perceived attractee and attractant positions

In line with earlier results, we expected the effect of spatiotemporal integration to be higher in the distal–proximal than in the proximal-distal direction. In addition, the overall amount of displacement at the well-represented index finger was expected to be lower than at the more poorly represented other fingers.
Fig. 5. Perceptual maps of spatiotemporal stimulus patterns presented to the fingers in experiment 2. The upper row shows results from the distal–proximal condition, the lower row shows data from the proximal–distal condition. From left to right, conditions with attractee–attractant intervals of 50 ms, 100 ms and 200 ms are shown. Opaque colours indicate the perceived positions of the attractee (red) and attractant (blue); translucent colours indicate the reference positions from experiment 1, i.e. the average perceived positions of individual stimuli presented at the same locations as attractee and attractant; grey indicates veridical stimulus positions. Dots indicate the mean positions (first aggregated at the participant level over 10 repetitions, then aggregated at the group level over all 19 participants); bars indicate standard deviations of the data aggregated at the participant level in x and y direction.

Fig. 6. Spatiotemporal integration in experiment 2. (A) Absolute attractee–attractant distance. (B) Relative attractee–attractant distance. Colours indicate different attractee–attractant intervals. Dark grey: 50 ms; middle grey: 100 ms; light grey: 200 ms. Results of distal–proximal patterns are shown at the left; results of proximal–distal patterns are shown at the right.
surprising, because the distance of the veridical stimulus positions differed. However, we also found an effect of finger pattern on the relative attractee–attractant distance ($F(5, 306)=12.6, p < .001$; Table 13). In particular, patterns including non-adjacent fingers generally yielded smaller distances, that is, more spatiotemporal integration, than patterns including adjacent fingers.

### 3.3.2. Direction-specific attractee and attractant displacements

The relative attractee displacement was significantly affected by finger pattern differences only ($F(5, 306)=12.0, p < .001$; Table 14).
This effect was driven by the ring finger–little finger pattern, in which the attractee was not mislocalised toward the attractant, but away from it (see Fig. 7, lower right corner). Attractor–attractor interval did not have a significant effect on the relative attractee displacement ($F(5, 306) = 2.3, p = .10$; Table 14). However, visual inspection showed that, in line with the above results, the index–ring finger and the middle-finger–little finger patterns showed a relationship between decreasing attractee–attractor interval and increasing relative attractee displacement. The relative attractant displacement also was only affected by finger pattern differences ($F(5, 306) = 16.0, p < .001$; Table 15). In the majority of cases, the attractant was perceived beyond its reference position, and this effect was especially prominent in the index–middle finger and middle finger–ring finger patterns (see Fig. 7).

### 3.3.3. Absolute shifts in lateral–medial direction

Shifts in lateral direction were stronger in stimuli serving as attractees than in those serving as attractants ($F(1, 660) = 27.9, p < .001$; Table 16). Strikingly, visual inspection shows that, contrary to this overall result, stimuli presented at the ring finger are predominantly mislocalised medially when they serve as attractees while they are predominantly localised laterally when serving as attractants (see Fig. 7). There was also a significant effect of attractee–attractor interval ($F(1, 660) = 6.3, p < .01$; Table 16). The differences between the three intervals were small and not significant, but on the descriptive level the shifts did reflect the order of the time intervals.

### 4. Discussion

#### 4.1. Accuracy and consistency of single stimuli

The quality of the localisation can be expressed by two indicators: accuracy, i.e., how well the participants’ responses fitted to the veridical positions, and consistency, i.e., how well participants were able to replicate their localisation of a given position. Accuracy was very high: On average, participants missed the veridical stimulus positions by only about 10 mm. This is noteworthy, because pointing movements may suffer from a variety of confounding influences, e.g. the way the pointing device is held or errors due to visual perspective. Consistency was even higher: on average, the localisations varied only by a distance of 5 mm from the individual mean. This measure is equally important for judging the participants’ pointing performance as accuracy, because it is less prone to cognitive biases and errors due to visual perspective.

In this study the localisation of tactile stimuli on the volar side of the fingers was examined via direct pointing. The general approach by Mancini et al. (2011) was similar, but in that study localisation was performed on a depiction of a hand presented on a computer screen and stimuli were applied to the dorsal side of the fingers. There is no indication that the localisation pattern of dorsal stimuli differs systematically from that of volar stimuli as presented in our study (Mancini et al., 2011, Fig. 2 vs. Fig. 4 in this paper). However, the methodological differences do not allow a direct comparison of the results beyond this superficial similarity.

#### 4.2. Spatiotemporal integration along fingers

Our findings clearly indicate sensory saltation along the fingers, i.e., with increasing temporal proximity the two stimulated positions were perceived closer together in space. In addition, this effect was slightly stronger in the proximal–distal than in the distal–proximal direction.

In the study by Geldard and Sherrick (1983) the "saltatory area" for an attractee presented to the tip of the index finger did not extend beyond the distal phalanx. This area, however, was based on the subjective judgement of three trained observers on whether saltation was present or not. The inconsistency between these previous findings and our demonstration of sensory saltation along the entire finger is hard to reconcile, but may be related to methodological differences. Geldard and Sherrick (1983) presented an attractee to the tip of the index finger and attractants to several positions surrounding the attractee position. The three trained observers who took part in the study had to judge whether saltation was present or not. Based on these ratings a "saltatory area" was determined, which did not extend beyond the fingertip. It is known that the perceived position of a stimulus is strongly determined by attention (cf. Kilgard & Merzenich, 1995). Thus, focusing on the attractee position may have inhibited its mislocalisation and/or may have concealed the fact that the attractant was mislocalised as well. In addition, it is unclear how well the subjective judgment on whether a stimulus was mislocalised relates to the mislocalisation itself. It is possible that participants are not aware of a displacement even though it can be detected via a localisation task.

There were two unexpected results: First, we found slightly higher spatiotemporal integration in proximal–distal than in distal–proximal direction. One might have expected effects in the opposite direction than observed, because the general proximal shift of perceived positions should have actually eased the proximal displacement of distal attractees and diminished the distal displacement of proximal attractees. Second, based on earlier studies (Trojan et al., 2010), we had expected localisations to be mainly anchored in the attractant region. In addition, given the neurophysiological and psychophysical properties of the fingertips, we assumed that these might serve as anchors as well. Our results, however, met neither of these expectations: The reported locations were generally anchored at the proximal finger phalanges, independent of whether stimulus patterns were presented in proximal–distal or distal–proximal direction. Our data do not allow unambiguous conclusions on these two puzzling findings and whether they are connected to each other. Future studies will have to take a more detailed look at factors influencing the overall localisation patterns.
4.3. Spatiotemporal integration across fingers

Our findings on spatiotemporal integration across fingers were mixed. On the one hand, a relationship between attractee–attractant interval and the distance between the perceived positions of attractees and attractants, the hallmark of sensory salutation, could not be demonstrated in terms of a significant main effect. On the other hand, however, some aspects of our results

Table 15
Experiment 3: Linear Mixed Model relative attractant displacement.

|                          | df | F    | Sig |
|--------------------------|----|------|-----|
| Intercept                | 1  | 306  | 1.7 |    |
| Attractee–attractant interval | 2  | 306  | 0.8 |    |
| Pattern                  | 5  | 306  | 16.0| ***|
| Attractee–attractant interval × pattern | 10 | 306  | 0.2 |    |

*p < .05; **p < .01; †p < .10.

***p < .001.

Table 16
Experiment 3: Linear Mixed Model shifts in lateral–medial direction.

|                          | df | F    | Sig |
|--------------------------|----|------|-----|
| Intercept                | 1  | 660  | 0.2 |    |
| Attractee–attractant interval | 2  | 660  | 6.3 | ** |
| role                     | 1  | 660  | 27.9| ***|
| Attractee–attractant interval × role | 2  | 660  | 1.3 |    |

*p < .05; †p < .10.

**p < .01.

***p < .001.

Fig. 7. Perceptual maps of spatiotemporal stimulus patterns presented to the fingers in experiment 3. Only fingertips are shown. The left columns shows results from the index–middle finger, index–ring finger and index–little finger conditions, the right column shows data from the middle finger–ring finger, middle finger–little finger and ring finger–little finger conditions. For each of these conditions, from top to bottom, conditions with attractee–attractant intervals of 50 ms, 100 ms and 200 ms are shown. Opaque colours indicate the perceived positions of the attractee (red) and attractant (blue); translucent colours indicate the reference positions from experiment 1, i.e. the average perceived positions of individual stimuli presented at the same locations as attractee and attractant; grey indicates veridical stimulus positions. Dots indicate the mean positions (first aggregated at the participant level over 10 repetitions, then aggregated at the group level over all 19 participants); bars indicate standard deviations of the data aggregated at the participant level in x and y direction.
suggested that spatiotemporal integration may be present, but partially occluded by other effects.

First, in only two of the six finger combinations the relationship between attractee–attractant interval and relative attractee–attractant distance was present at all: index–ring finger and middle finger–little finger (see Fig. 8). Remarkably, these two patterns are the ones spanning three fingertips whereas all others span two or four fingertips. It is tempting to interpret this result as indicating a special proneness of three-finger-spanning patterns to sensory saltation. Perhaps two fingertips simply do not offer enough space for mislocalisations showing effects of attractee–attractant interval and the distance across four fingertips is too large. However, these are posthoc explanations and will have to be tested in separate studies.

Second, attractants are generally less mislocalised compared to single stimuli than attractees are. Shifts in lateral direction, that is, toward the attractant, were stronger in stimuli serving as attractees than in those serving as attractants. This is in line with the original concept of sensory saltation (Geldard, 1975) as well as with our own previous findings (Trojan et al., 2010), although not with the results in experiment 2.

Third, the attractee and attractant displacements are not uniform across patterns. Most strikingly and contrary to the previous overall effect, stimuli presented at the ring finger are predominately mislocalised medially when they serve as attractees while they are predominantly localised laterally when serving as attractants. This finding may be related to the fact that the only case in which the ring finger served as an attractee position was in a pattern spanning two fingers (ring finger/little finger), see above. In any case, it indicates that different spatiotemporal patterns yield different localisations of the physically identical stimulus.

Fourth, we found a main effect of the attractee–attractant interval on general shifts in medial–lateral direction. The differences are very small, but on the descriptive level they do reflect the order of the time intervals and are more prominent in the attractee than in the attractant. This unexpected finding indicates that spatiotemporal integration was stronger in respect to external than to anatomical coordinates and hints at the still unsolved question at which representation level(s) spatiotemporal integration of tactile stimuli actually takes place. While Geldard and Sherrick (1983) had originally suggested that sensory saltation is restricted to the two-dimensional representation of the body surface, recent studies indicate that it also works across arms (Eimer, Forster, & Vibell, 2005) and even on a stick between fingers of opposite hands (Miyazaki, Hirashima, & Nozaki, 2010). However, at present it remains unclear to which extent these findings can be generalised because they may in part reflect particular demands of the chosen reporting method (see Section 4.5, cf. Trojan et al., 2010).

Two other studies addressed spatiotemporal integration across fingers: Warren et al. (2010) presented an attractee to the index finger and an attractant to the little finger using a very similar pattern as in one of the conditions of experiment 3. Participants were asked whether this stimulus pattern yielded a perception at the middle finger, and this was the case in about 30% of the trials in a sample of nine participants. This fits remarkably well to our own findings: The area indicated by the standard deviation of the perceived attractee positions overlaps to about a third with the
area indicated by the standard deviation of the veridical positions of the tip of the middle finger (see Fig. 7, lower left corner, opaque red cross vs. second grey cross from the left). In a sample chosen for high tactile acuity, however, this finding could not be replicated and no perception at all was reported at the middle finger (Warren & Helms Tillery, 2011).

In conclusion, while there definitely is an influence of spatiotemporal integration on the localisation of stimulus patterns spanning across fingers, the bulk of the effect appears to be unspecific and not related to sensory salutation in particular.

4.4. ATTRACTEES AND ATTRACTANTS—THE ROLE OF TEMPORAL AND SPATIAL CONFIGURATION

Earlier studies on sensory salutation put a strong focus on the displacement of the attractee towards the attractant and did not consider mislocalisation of the attractant itself (e.g. Geldard & Sherrick, 1972; Geldard, 1975; Geldard & Sherrick, 1983; Eimer et al., 2005; Flach & Haggard, 2006; Warren et al., 2010). Kilgard and Merzenich (1995), however, argued that sensory salutation could be explained by ‘symmetric convergence’ and that the question at which positions the pattern is anchored depends on attention alone. In other words, direction-specific effects (the attractee being ‘drawn towards’ the attractant), might not be as important as originally thought.

In a previous study we found that the perceived attractant position also depends on the attractee–attraction interval, although to a lesser degree than the perceived attractee position (Trojan et al., 2010). Thus, whereas Kilgard and Merzenich (1995) were certainly right in questioning the simplified view of attractees and attractants, their experimental setup might have been biased towards the other extreme and may have concealed direction-specific effects.

At first sight, the results of experiment 2 seem to favour Kilgard and Merzenich’s (1995) view: Fig. 5 shows that stimuli presented to the fingertips were generally localised more proximally than in experiment 1, regardless of whether they served as attractees or attractants. Perceived positions of stimuli presented to the proximal phalanx, however, barely showed such a displacement. This indicates that (for reasons unknown, but see below) localisation was anchored at the metacarpus and whether the distal stimulus was presented shortly before or shortly after the proximal stimulus (i.e. whether it served as attractee or attractant) did not matter much.

Several other findings, however, speak against this interpretation: (1) There were in fact direction-specific differences in experiment 2: The amount of spatiotemporal integration as measured with the absolute and relative attractee–attraction differences was slightly but significantly larger in the proximal–distal than in the distal–proximal direction. This anisotropy would not be expected based on Kilgard and Merzenich’s (1995) explanation. (2) It seems odd that localisation was anchored at the proximal phalanx and not at the fingertips. After all, it is the latter, which is the regular focus of our attention, has a much higher somatosensory resolution, and yielded more congruent localisation in experiment 1. Thus, theoretically, it should be easier to ‘draw’ stimuli from the proximal towards the distal phalanx than vice versa. (3) In experiment 3, localisation depended on whether a stimulus served as attractee or attractant and on how far they were apart. This finding is also not easy to reconcile with Kilgard and Merzenich’s (1995) view, because it is unclear why the focus of attention should have differed so considerably between the patterns.

Taken together, the results of this study question the respective roles of attractees and attractants even further than our previous findings. They do, however, not convincingly reject direction-specific effects. Rather, they indicate that spatiotemporal integration at the hand depends on additional factors, which need to be addressed in more detail in future studies.

4.5. COMPARISON OF THE POINTING METHOD AND OTHER APPROACHES

We have suggested before that pointing is the most natural way to report perceived positions on the body surface (e.g. Trojan et al., 2006, 2010). Pointing is not exclusively based on explicit representations, but also makes use of implicit action-related representations derived from proprioceptive information. This combination makes pointing a more powerful indicator of what we actually perceive in everyday situations and less prone to cognitive biases.

The approach used by Geldard and Sherrick (1983) focussed on the question whether a displacement could be induced at all, i.e., whether a stimulus was judged as being perceived at a position different from that of the stimulus. The attention of the three trained observers taking part in that study was clearly focused on the reference position. Based on Kilgard and Merzenich’s (1995) findings, it seems plausible that this situation may have actively impeded the perception of a displacement and, as a consequence, may have led to an underestimation of the salatory area.

Warren et al. (2010) used an approach based on Eimer et al. (2005): They presented an attractee to the index finger and an attractant to the little finger using a very similar pattern as in the index—little finger condition of experiment 3. Participants were asked whether this stimulus pattern yielded a perception at the middle finger. Although in this particular case the results are consistent with our pointing results (see above, Section 4.3), the sensitivity and specificity of this method may be limited. First and foremost, participants do not localise stimuli but perform yes/no judgments in respect to a given location, making this approach prone to cognitive biases. Second, mislocalisations not extending beyond the finger cannot be detected at all, potentially leading to an underestimation of the effect of spatiotemporal integration. This may be the main reason why in a sample chosen for high tactile acuity no effect of spatiotemporal integration could be demonstrated with this approach (Warren & Helms Tillery, 2011).

Mancini et al. (2011) refer to the concept of perceptual maps, but their maps were based on ratings performed on a computer screen. This approach is very different from directly pointing to the hand: First and foremost, judgments were performed on a computer screen. This approach is very different from directly pointing to the hand: First and foremost, judgments were performed on a computer screen. This approach is very different from directly pointing to the hand: First and foremost, judgments were performed on a computer screen. This approach is very different from directly pointing to the hand: First and foremost, judgments were performed on a computer screen. This approach is very different from directly pointing to the hand: First and foremost, judgments were performed on a computer screen. This approach is very different from directly pointing to the hand: First and foremost, judgments were performed on a computer screen. This approach is very different from directly pointing to the hand: First and foremost, judgments were performed on a computer screen. This approach is very different from directly pointing to the hand: First and foremost, judgments were performed on a computer screen. This approach is very different from directly pointing to the hand: First and foremost, judgments were performed on a computer screen. This approach is very different from directly pointing to the hand: First and foremost, judgments were performed on a computer screen.

4.6. CONCLUSIONS AND OUTLOOK

This study assessed localisation accuracy and consistency of tactile stimuli presented to the volar side of the fingers. The localisation task was implemented via direct pointing movements towards the perceived positions.

The focus of the study was on the spatiotemporal integration of two-stimulus pattern along and across fingers. In all conditions, localisation of stimuli presented within a spatiotemporal pattern differed from localisation of individual stimuli presented to the same positions. In most cases, stimuli were perceived as being spatially closer when they were presented within a pattern compared to when being presented individually. Spatiotemporal integration along the fingers followed the predictions of the
sensory salutation paradigm: The shorter the temporal delay between the two stimuli, the closer together they were perceived. For spatiotemporal patterns across fingers, the results were inconclusive: a general relationship between temporal delay and difference between the perceived positions could not be demonstrated. Some aspects of our results suggested however, that spatiotemporal integration may be present in some conditions, but partially occluded by other effects.

The most obvious conclusion is that there are fundamental differences concerning spatiotemporal integration along and across fingers. Integration in lateral–medial direction is much less pronounced than in proximal–distal direction. In other words: Patterns in lateral–medial direction are more likely to be perceived as distinct stimuli whereas patterns in distal–proximal direction are more likely to be integrated. This shows that the constraint of the fingers being anatomically separated has an influence on how we haptically perceive objects.

Our findings also rekindle questions on when, where, and how spatiotemporal integration takes place. On the one hand, the differences between along- and across-finger processing show that the 2D somatotopic organisation of the body surface has a predominant influence. On the other hand, and in line with several recent studies, tactile spatiotemporal integration is not only determined by somatotopic proximity, but the distances in 3D peripersonal space also play a role. Future studies will face the challenge of dissociating these different levels of perceptual integration.

Acknowledgments

The authors would like to thank Otto Martin for the construction of the hand stimulation device. This research was supported by “Phantom phenomena: A window to the mind and the brain” (PHANTOMMIND) project, which receives research funding from the European Community’s Seventh Framework Programme (FP7, 2007–2013)/ERC Grant Agreement No. 230249. The authors appreciate the helpful comments and suggestions of two anonymous reviewers.

Appendix

Alignment and normalization of 3D tracker data

1. Six reference point locations – four taken at the base two taken at the top of the semicylindrical stimulation array – were realigned to match a predefined model of the device using Matlab 7.10 (MathWorks Inc., Natick, MA, U.S.A.) with the “absor” script (http://www.mathworks.com/matlabcentral/fileexchange/26186-absolute-orientation-horns-script). The resulting realignment parameters were applied to the localization data. This results in a dataset with identical orientation of all individual data.

2. Localisation ratings were performed not directly on the stimulation array surface, but at a short distance above the hand lying on it. In order to analyse the data in a two-dimensional (proximal-distal/ulnar-radial) space, differences in vertical directions were omitted.

3. Finally, following the procedure suggested by Mancini et al. (2011), the data were normalised to hand size by conversion to Bookstein coordinates (Bookstein, 1991) using the knuckle of the little finger as point (0,0) and the knuckle of the index finger as point (1,0). The resulting standard units account for differences in hand width and orientation. The approach cannot, however, fully account for unusually short or unusually long hand lengths in comparison to the hand width. As a consequence, measures of accuracy at the group level are prone to be underestimated at distal positions, where the heterogeneity is strongest.

Correction of stimulus order in experiments 2 and 3

In experiments 2 and 3, participants were instructed to report positions in the order in which they had perceived them. Due to the close temporal proximity, it is not uncommon that participants confuse the order of attractee and attractant (cf. Trojan et al., 2010), e.g. the first reported position is more proximal than the second, although the attractee was presented more distally than the attractant. In cases in which this confusion could be determined unequivocally, this was corrected (experiment 2: 1087 of 4560 trials, 24%; experiment 3: 441 of 3420 trials, 13%).

There were 6 cases in experiment 2 (0.1%) and 11 cases in experiment 3 (0.3%) in which both reported attractee and attractant locations were in front of the average positions of the individual stimulus presented at the veridical position of the attractee stimulus in experiment 1 (e.g. both were reported more distally although they were in fact presented more proximally). These positions were deemed implausible and therefore excluded.

References

Bookstein, F. L. (1991). Morphometric tools for landmark data: Geometry and biology. Cambridge: Cambridge University Press.
Bretz, F., Hothorn, T., & Westfall, P. (2010). Multiple comparisons using R. Boca Raton FL: CRC Press.
Culver, C. M. (1970). Errors in tactile localization. The American Psychological Society, 83(3), 420–427, http://dx.doi.org/10.1037/0096-1523.32.3.717.
Eimer, M., Forster, B., & Vibell, J. (2005). Cutaneous salutation within and across arms: A new measure of the salutation illusion in somatosensation. Perception & Psychophysics, 67(3), 458–468, http://dx.doi.org/10.3758/BF03193324.
Flach, R., & Haggard, P. (2006). The cutaneous rabbit revisited. Journal of Experimental Psychology: Human Perception and Performance, 32, 717–732, http://dx.doi.org/10.1037/0096-1523.32.3.717.
Geldard, F. A. (1975). Sensory salutation: Metastability in the perceptual world. New York: Lawrence Erlbaum Associates.
Geldard, F. A., & Sherrick, C. E. (1972). The cutaneous “rabbit”: A perceptual illusion. Science, 178, 178–179.
Geldard, F. A., & Sherrick, C. E. (1983). The cutaneous salatory area and its presumed neural basis. Perception and Psychophysics, 33, 290–304.
Goldreich, D. (2007). A Bayesian perceptual model replicates the cutaneous rabbit and other tactile spatiotemporal illusions. PLoS One, 2(3), e333, http://dx.doi.org/10.1371/journal.pone.0000333.
Grunwald, M. (2008). Human haptic perception basics and applications. Basel, Boston: Birkhäuser.
Kalisch, T., Ragert, P., Schwenkreis, P., Dinse, H. R., & Tegenthoff, M. (2009). Impaired tactile acuity in old age is accompanied by enlarged hand representations in somatosensory cortex. Cerebral Cortex, 19(7), 1530–1538, http://dx.doi.org/10.1093/cercor/bhn190.
Kilgard, M. P., & Merzenich, M. M. (1995). Anticipated stimuli across skin. Nature, 373(6516), 663.
Mancini, F., Longo, M. R., Iannetti, G. D., & Haggard, P. (2011). A supramodal representation of the body surface. Neurpsychologia, 49(5), 1184–1201, http://dx.doi.org/10.1016/j.neuropsychologia.2010.12.040.
Miyazaki, M., Hirashima, M., & Nozaki, D. (2010). The “cutaneous rabbit” hopping out of the body: The Journal of Neuroscience, 30(5), 1856–1860.
Peters, R. M., Hackeman, E., & Goldreich, D. (2009). Diminutive digits discern delicate details: Fingertip size and the sex difference in tactile spatial acuity. The Journal of Neuroscience, 29(50), 15756–15761, http://dx.doi.org/10.1523/JNEUROSCI.3684-09.2009.
Pinheiro, J., Bates, D., DeBroy, S., Sarkar, D., & R Core Team. (2013). nlme: Linear and nonlinear mixed effects models.
R Core Team (2013). R: A language and environment for statistical computing. Austria: Vienna.
Rapp, B., Hendl, S. K., & Medina, J. (2002). Remodeling of somatosensory hand representations following cerebral lesions in humans. Neuroreport, 13(2), 207–211.
Steenbergen, P., Buitenweg, J. R., Trojan, J., Klaassen, B., & Veltink, P. H. (2012). Subject-level differences in reported locations of cutaneous tactile and nociceptor stimuli. Frontiers in Human Neuroscience, 6, 325, http://dx.doi.org/10.3389/fnhum.2012.00325.
Steenbergen, P., Buitenweg, J. R., Trojan, J., & Veltink, P. H. (2013). Reproducibility of somatosensory spatial perceptual maps. Experimental Brain Research, 224(3), 417–427, http://dx.doi.org/10.1007/s00221-012-3321-3.

Trojan, J., Kleinböhl, D., Stolle, A. M., Andersen, O. K., Hörl, R., & Arendt-Nielsen, L. (2006). Psychophysical “perceptual maps” of heat and pain sensations by direct localization of CO2 laser stimuli on the skin. Brain Research, 1120(1), 106–113, http://dx.doi.org/10.1016/j.brainres.2006.08.065.

Trojan, J., Kleinböhl, D., Stolle, A. M., Andersen, O. K., Hörl, R., & Arendt-Nielsen, L. (2009). Independent psychophysical measurement of experimental modulations in the somatotopy of cutaneous heat-pain stimuli. Somatosensory and Motor Research, 26(1), 11–17, http://dx.doi.org/10.1080/0899020902813493.

Trojan, J., Stolle, A. M., Mešić Carl, A., Kleinböhl, D., Tan, H. Z., & Hörl, R. (2010). Spatiotemporal integration in somatosensory perception: Effects of sensory saltation on pointing at perceived positions on the body surface. Frontiers in Psychology, 1, 206, http://dx.doi.org/10.3389/fpsyg.2010.00206.

Warren, J. P., & Helms Tillery, S. I. (2011). Tactile perception: Do distinct subpopulations explain differences in mislocalization rates of stimuli across fingertips? Neuroscience Letters, 505(1), 1–5, http://dx.doi.org/10.1016/j.neulet.2011.04.057.

Warren, J. P., Santello, M., & Helms Tillery, S. I. (2010). Electrotactile stimuli delivered across fingertips inducing the Cutaneous Rabbit Effect. Experimental Brain Research, 206(4), 419–426, http://dx.doi.org/10.1007/s00221-010-2422-0.

Ylioja, S., Carlson, S., Raji, T. T., & Pertovaara, A. (2006). Localization of touch versus heat pain in the human hand: A dissociative effect of temporal parameters on discriminative capacity and decision strategy. Pain, 121(1-2), 6–13.