



# **Haptic Perception as a Dynamic Process - How Movements and Perception Evolve**

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## Abstract

In order to experience something through our sense of touch, we usually have to actually ‘touch’, in other words, to actively move the fingers for a certain time. During this period of time, several sequential movements generate new sensory information (Gibson, 1962; Klatzky & Lederman, 1999). Haptic perception can, therefore, be considered as a dynamic process in which the sensory basis for perception and movements is continuously updated. In the past, several studies investigated how sensory information from multiple sources is integrated into a final percept (e.g., Ernst & Banks, 2002). Other studies examined movement control in haptic exploration (e.g., Klatzky & Lederman, 1987; Kaim & Drewing, 2011). However, existing literature on natural haptic exploration did not consider dynamic developments in movements and perception over the entire process. Within my thesis, I aimed to overcome these limitations by studying the sequential nature of the haptic perceptual integration and the online adjustments of movements in natural haptic exploration.

Across the first two studies, I investigated how sequentially gathered sensory information is integrated into a unified percept for two central haptic dimensions, softness and texture. First, in Study I, participants compared two textures after exploring them one after the other with varying numbers of exploration movements. The integration of the sensory information from sequential movements resulted to be more complex than predicted by an optimal integrator model which is known from the integration of simultaneous information (MLE, e.g., Ernst & Bühlhoff, 2004). Second, Study II focused on the contributions of individual sequential movements for softness judgments. The psychophysical results of this study were well in agreement with neurophysiologic literature on decision-making (e.g., Deco, Rolls, & Remo, 2010) and - again - not consistent with a simple MLE model. In order to account for the temporal

dynamics of the sequential exploration process, I developed a Kalman filter model (Kalman, 1962) as an expanded optimal integrator model. Predictions from this model resulted to be consistent with the empirical data. In sum, the model incorporates online comparisons between a memory representation of the first object and the current sensory information about the second object during each movement over the second object (see e.g., Romo & Salinas, 2003). The memory representation of the first object, however, is additionally assumed to decay during the exploration of the second object (see e.g., Murray, Ward & Hockley, 1975).

Studies III and IV investigated whether sequentially gathered sensory information impact the control of key movement parameters for softness and texture perception. Specifically, Study III examined peak indentation forces during the process of softness exploration. The results revealed that sensory information had less impact on the executed movements than predictive information. However, the impact of sensory information was moderated by motivation, which is in line with models on optimal movement control (e.g., Todorov & Jordan, 2002). Study IV, focused on movement directions during the process of texture exploration. Within this study, I developed a novel method that allows directly comparing the use of sensory signals in movement control to its use in perception. The results indicated that sensory signals are incorporated in movement control and that this can improve perception. In sum, movements were reported to be adjusted over the exploration process with the goal to optimize haptic perception while minimizing motor costs.

Taken together, the presented thesis expands the exciting literature by demonstrating that due to the sequential gathering of sensory information perception and movements continuously evolve and mutually influence each other in a process of natural haptic exploration.



## **Zusammenfassung**

Um etwas mit unserem Tastsinn zu erfühlen, müssen wir üblicher Weise ‚tasten‘, also einige Zeit die Finger aktiv bewegen. In dieser Zeitspanne werden mit mehreren sequentiellen Bewegungen sensorische Information erzeugt (Gibson, 1962; Klatzky & Lederman, 1999). Haptische Wahrnehmung kann somit als ein dynamischer Prozess verstanden werden, bei dem die sensorische Basis für Wahrnehmen und Bewegen kontinuierlich aktualisiert wird. Einige Studien haben in der Vergangenheit erforscht, wie sensorische Informationen verschiedener Quellen zu einem finalen Perzept integriert werden (e.g., Ernst & Banks, 2002). Andere Studien untersuchten Bewegungskontrolle innerhalb haptischer Exploration (e.g., Klatzky & Lederman, 1987; Kaim & Drewing, 2011). Jedoch wurden bisher die dynamischen Entwicklungen der Bewegung und Wahrnehmung im Laufe des Explorationsprozesses nicht beachtet. Das Ziel meiner Thesis ist es die Integration sequentieller Informationen und die laufenden Bewegungsanpassungen zu untersuchen und damit die bestehenden Limitationen zu überwinden.

Die Studien I und II erforschten für zwei zentrale haptische Dimensionen, nämlich Weichheit und Textur, wie sequentiell erzeugte sensorische Informationen zu einer einheitlichen Perzeption integriert werden. In Studie I, verglichen Versuchsteilnehmer zwei Texturen nachdem sie diese mit einer variablen Anzahl an Bewegungen hintereinander exploriert hatten. Hierbei schien die Integration der durch die einzelnen sequentiellen Bewegungen erzeugten sensorischen Informationen komplizierter zu sein als ein Modell optimaler Integration für simultane Informationen vorhersagen würde (MLE, e.g., Ernst & Bühlhoff, 2004). Im Fokus von Studie II stand welche Bedeutung die durch einzelne Bewegungen erzeugten sensorischen Informationen für Weichheitsbeurteilung haben. Die Ergebnisse waren im Einklang mit neurophysiologischer Literatur zur Entscheidungsfindung (z.B. Deco, Rolls, & Remo, 2010) aber - wieder - im

Widerspruch zu einem einfachen MLE model. Um zeitliche Dynamiken sequentieller Exploration zu berücksichtigen, habe ein Kalman Filter Model (Kalman, 1962) als ein erweitertes Modell optimaler Integration entwickelt. Die Vorhersagen dieses Models waren konsistent mit den empirischen Daten. Hierbei nimmt das Modell an, dass während jeder Bewegung über das zweite Objekt ein Vergleich zwischen der Gedächtnisrepräsentation des ersten Objekts und der aktuellen Information über das zweite Objekt stattfindet (vgl. z.B. Romo & Salinas, 2003). Jedoch wird angenommen, dass die Gedächtnisspur des ersten Objekts während der Exploration des zweiten Objekts zerfällt (vgl. z.B. Murray, Ward, & Hockley, 1975).

In den Studien III und IV habe ich untersucht ob die Bewegungsparameter haptischer Exploration von Weichheit und Textur durch sequentiell erzeugte sensorische Information beeinflusst werden. Im Speziellen, erforscht Studie III Weichheitswahrnehmung angewandte Maximalkräfte. Sensorische Informationen beeinflussten Bewegungen weniger als prädiktive Informationen. Jedoch schien Motivation den Effekt sensorischer Signale zu moderieren, was zu Modellen optimaler Bewegungskontrolle passt (z.B. Todorov & Jordan, 2002). Studie IV untersuchte die für Texturexploration genutzten Bewegungsrichtungen. Hierbei habe ich eine neuartige Methode entwickelt, welche ermöglicht den Gebrauch sensorischer Information in Bewegungen und Wahrnehmung miteinander zu vergleichen. Die Ergebnisse zeigten, dass sensorische Informationen in die Bewegungssteuerung einfließen und, dass dies die Wahrnehmung verbessern kann. Zusammengefasst scheinen Bewegungen über den Explorationsprozess so angepasst zu werden, dass sie die haptische Wahrnehmung optimieren und motorische Kosten minimieren.

Insgesamt liefert die vorgelegte Thesis einen bedeutenden Beitrag da sie aufzeigt, dass aufgrund des sequentiellen Erzeugens sensorischer Informationen sich im Laufe eines Explorationsprozess Wahrnehmung und Bewegung kontinuierlich verändern und gegenseitig beeinflussen.



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# 1. Introduction

When people use the expression ‘at first glance’, they refer to the first impression of something, before having looked at it carefully. This first impression is rather unreliable and will most probably be adjusted after a proper examination. Similarly, a ‘haptic glance’ refers to first contact between the fingers and the object, which is spatially and temporally restricted and involves no or minimal movement (Klatzky & Lederman, 1995). The ‘haptic glance’ may allow judging some coarse material or local shape properties. However, a big part of relevant object information cannot be processed within this initial contact. Therefore, natural haptic perception includes more than just a ‘first glance’. In natural circumstances, haptic perception extends up to several seconds in time (Klatzky & Lederman, 1999). Within this time, active finger movements are performed in order to generate sensory information (Gibson, 1962). Movements and perception evolve over the course of exploration (e.g., Saig, Gordon, Assa, Arieli, & Ahissar, 2012). The percept is updated by the added sensory information of each additional movement. Also movement control can rely on an increasing amount of sensory information with more extended exploration. In the past, several studies investigated the integration of sensory information for perception (e.g., Ernst & Banks, 2002) and movement control in haptic exploration (e.g., Klatzky & Lederman, 1987). But, these studies did not consider developments over the entire exploration process and, thus, lack to represent the sequential nature of the perceptual integration and the movement adjustments in natural haptic exploration. Therefore, I aim to overcome these limitations by providing a model for the integration of sequential sensory information and investigating dynamic adjustment of movements within the entire exploration process. Further, I will investigate the interdependencies between perception and movements, which result from the dynamic nature of the exploration process. I aim to describe how

perception and movements influence each other mutually and provide suggestions about the basis and goal of such sensorimotor interdependencies.

### 1.1. Sensory Integration of Simultaneous Signals

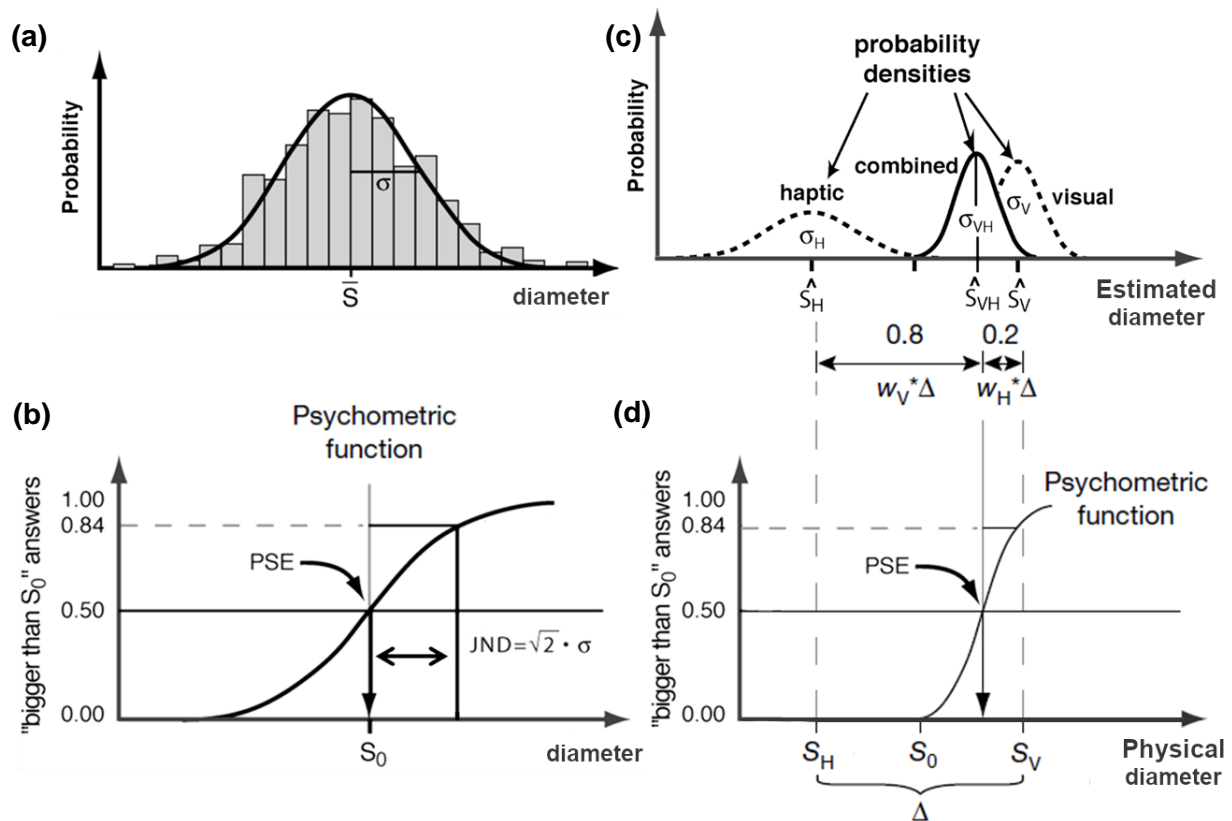
Perception is multimodal by nature. All our senses constantly receive sensory information about the external world. Information coming from different sources is often referred to as different ‘signals’ or ‘cues’. When multiple signals complement each other, that is to say, provide information about different content, they can be combined (Ernst & Bühlhoff, 2004). So for instances, if you grab a mug from its back and see its front side, the visual and haptic signals can be combined to improve the estimated diameter of the mug. However, if you would hold the mug on the front side, visual and haptic signals would be redundant (provide information about the same content) rather than complementary. Redundant signals can be integrated to a unified percept. For the integration of simultaneous redundant information the Maximum Likelihood Estimation (MLE) model is well-established (overview in Ernst & Bühlhoff, 2004). Here, all redundant signals are assumed to be used in integration (Jacobs, 2002). Each signal  $i$  is transferred into a signal-specific estimate  $S_i$  of the property of interest. All available estimates are, then, integrated into a unified perceptual estimate  $\hat{E}$  by weighted averaging:

$$\hat{E} = \sum_i w_i \hat{S}_i \quad \text{where} \quad \sum_i w_i = 1 \quad \text{and} \quad w_i \in [0,1]. \quad (1)$$

This is to say, in our example the diameter of the mug would be computed as the weighted average of individual estimates derived from the visual ( $\hat{S}_V$ ) and haptic ( $\hat{S}_H$ ) sense. However, estimates derived from each signal are prone to noise. In other words, multiple judgments of the same property result in slight variation of the signal-specific estimate. Thus,



each estimate can also be described by its specific variance ( $\sigma_i^2$ ). Figure 1.1a schematically illustrates a probability density distribution for multiple judgments of one property, which follows a Gaussian shape.



**Figure 1.1.** (a) Gaussian shaped probability density distribution: The probability of the estimate resulting in a particular diameter is plotted against all possible diameter estimates. The mean ( $\bar{S}$ ) defines the final signal-specific diameter estimate and the standard deviation ( $\sigma$ ) defines the perceptual noise of this signal. (b) Psychometric function: Cumulative Gaussian function, which is fitted to the proportion of trials, in which the participant indicated that the comparison diameter was bigger than the standard diameter ( $S_0$ ) for each diameter of the comparison. PSE is defined as the comparison value for which discrimination performance at chance level (50%). JND is defined as the difference between the PSE and the comparison value, for which the comparison is judged bigger than standard in 84% of the time. (c) Probability density distributions of visual, haptic and visual-haptic estimates. Based on the MLE integration rule the visual-haptic distribution has the smallest variance and its mean ( $\hat{S}_{HV}$ ) is closer to the less variant signal-specific estimate (in this example:  $\hat{S}_V$ , as  $\sigma_H = 4 \cdot \sigma_V$ ). (d) Psychometric function of the visual-haptic estimate: PSE indicates with which weights the visual and the haptic estimate have contributed to the final percept (Figure adapted from Ernst, 2006 and Ernst & Banks, 2002).

Within the MLE approach, weights are considered optimal if they are in inverse proportion to estimate's variance ( $w_i \propto 1/\sigma_i^2$ ). Thus, in optimal integration less variable estimates contribute more to the final percept. Weighted averaging with optimal weights leads to the minimal variance of the final percept ( $\sigma_E^2$ ; Landy, Maloney, Johnston, & Young, 1995).

$$w_j = \frac{1/\sigma_j^2}{\sum_{i=1\dots j, \dots N} 1/\sigma_i^2} \quad \text{with} \quad \sigma_E^2 = \frac{1}{\sum_i 1/\sigma_i^2}. \quad (2)$$

Whether integration follows MLE principles can be tested when participants can make use of multiple signals which are slightly discrepant (e.g., Ernst & Banks, 2002; Gepshtein & Banks, 2003; Alais & Burr, 2004). Due to this discrepancy, it is possible to measure the weight given to each signal. To do so, usually discrimination tasks are implemented. If one implemented such a discrimination task for our example of the mug diameter estimated from vision and haptics, participants would judge whether the diameter of a comparison (S) is bigger than the diameter of the standard ( $S_0$ ) in each trial. Under the assumption that standard and comparison constitute independent percepts with the same level of internal noise ( $\sigma_{S_0}^2 = \sigma_S^2$ ), responses can be fitted by a cumulative Gaussian (Fig. 1.1b), which is commonly referred to as psychometric function. In the psychometric function, the comparison value corresponding to discrimination at chance level (50%) is defined as the Point of Subjective Equality (PSE). PSEs from a multi-signal discrimination task can assess weights of signal-specific estimates, when slight discrepancies between signals were introduced ( $S_V = S_H + \Delta$ ). The Just Noticeable Difference (JND) in the same task measures the estimate's variance ( $\text{JND} = \sqrt{2}\sigma$ ). JNDs can be defined as the difference between the PSE and the comparison value, for which the comparison is judged bigger than standard in 84% of the time. The optimal final estimate should be less variable than each unimodal estimate. Therefore, in our example, the combined estimate should be less

variable than the visual and the haptic estimate. Additionally, if we assume that the visual estimate of the mugs diameter is less variable than the haptic estimate (e.g.,  $\sigma_H = 4 * \sigma_V$ ), the final estimate should be more influenced by the visual estimate according to MLE ( $w_V = 4 * w_H$ ; see Fig.1.1c-d).

Several studies compared MLE predictions on the weighted average (measured by the PSE) and noise reduction (measured by the JND) with empirical data for multimodal perception. For instance, Alais and Burr (2004) investigated the visuo-auditory integration of brief visual “blobs” and sound “clicks”. The authors showed that for not-blurred vision the bimodal localization followed almost only the visual location of the event. This can basically explain the ventriloquist effect, in other words the subjective impression that a voice originates from the puppets mouth and not it’s actual sounds source (the performer’s mouth). The more blurred the presentation of the visual stimulus was, the more the perceived location shifted towards the sound source. Additionally, bimodal localization was less variable then unimodal localization. Similarly, visual-haptic size perception was found to follow MLE principles (Ernst & Banks, 2002). Ernst and Banks (2002) used a 2-interval forced-choice (2-IFC) discrimination task on the height of visual-haptically experienced bars. The visual and the haptic representation of the stimulus were rendered independently so that slight discrepancies between the two signals were introduced in the bimodal standards. The haptic representation was rendered with two PHANToM force-feedback devices, one for the thumb and one for the index finger. The visual representation constituted a random-dot stereogram. The reliability of the visual representation was manipulated by adding noise to a random-dot stereogram (0%-200% noise in depth relative to the height the bar). Both predictions from the MLE modal were consistent with the empirical data. First, when the visual variance increased (with more added noise) the perceived height

(measured by the PSE) was increasingly closer to the haptic height estimate and further from the visual height estimate. Second, the visual-haptic estimates were less variable (lower JNDs) as compared to the unimodal estimates. More specifically, based on the unimodal distribution (measured in separate unimodal conditions) the final estimate (PSE) and the variance (JND) for each bimodal visual-noise conditional was predicted using MLE. The authors found a good correspondence between predicted and observed values in both measures. More recent studies additionally reported neurophysiologic correlates of optimal multisensory integration (e.g. Fetsch, DeAngelis, & Angelaki, 2013; Helbig et al., 2012; Seilheimer, Rosenberg & Angelaki, 2014) and even trimodal optimal integration (Wozny, Beierholm & Shams, 2008).

However, optimal integration was also reported for multiple signals coming from the same modality. For instance, when judging surface slant visually, the integration of texture and stereo information was consistent with MLE predictions (Knill & Saunders, 2003; Hillis, Watt, Landy & Banks, 2004). Also, texture frequency and orientation were shown to be combined optimally for the visual localization of texture-defined edges (Landy & Kojima, 2001). MLE optimality principles were not only tested for visual integration, but also for multiple haptic signals that were simultaneously available. For instance, object shape is haptically experienced by a position signal and a force signal (Robles-De-La-Torre & Hayward, 2001). The position signal is defined by the surface geometry and refers to up- and down shift in the finger position when sliding over an object. The force signal is defined by the direction of reaction force produced when sliding over the object and therefore is depended on the surface slope. Drewing and colleagues (Drewing & Ernst, 2006; Drewing, Wiecki & Ernst, 2008) showed that for perceiving the shape of a virtual bump force and position signals are integrated in agreement with MLE predictions.

In total, optimality principles were tested for multi-signal integration between sense and also within the haptic sense. The reported studies, however, investigated integration of simultaneously available signals. In contrast to this, natural haptic perception extends in time (Klatzky & Lederman, 1999) and, therefore, also sequentially available redundant signals need to be integrated (Henriques & Soechting, 2005).

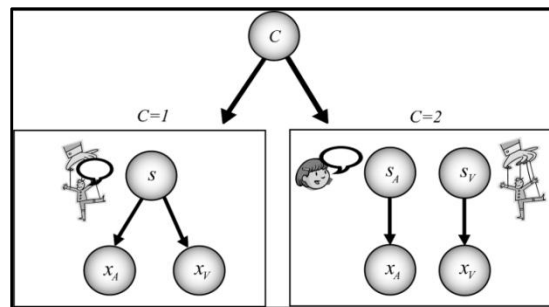
## 1.2. Sensory Integration of Sequential Signals

If multiple signals for integration are gathered sequentially, several possible consequences for the optimal integration model arise. On the one hand, assumptions of the MLE model might be violated and, on the other hand, the classical MLE might not capture temporal dynamics, which arise for sequential signals. One assumption of the MLE model is that the noise of signal-specific estimates is uncorrelated. However, when estimates are based on signals that are generated by multiple movements of the same finger over the same object, they possibly have correlated noise. Oruç, Maloney and Landy (2003) investigated the integration of signals on linear perspective and texture gradient for the visual perception of surface slant without the assumption of uncorrelated noise. The results indicated that correlated noise increased the final estimate variance and slightly changed weights. However, estimates still benefitted from integration. For two correlated estimates the final percept's variance could be well predicted by the following formula with  $\rho$  being the correlation:

$$\sigma_E^2 = \frac{1-\rho^2}{\sum_i 1/\sigma_i^2 - 2\rho/(\sigma_1\sigma_2)} \quad (3)$$

A second assumption of the MLE model is that the observer believes that signals originated from the same source. Besides spatial coincidence, temporal synchrony is one of the

most important cues for the implicit knowledge that multiple signals refer to the same source (Helbig & Ernst, 2007). Therefore, temporal segregation of cues, as it is the case for sequentially generated signals, might potentially influence their integration. For instance, auditory and tactile stimuli were integrated automatically if appearing simultaneously, and this effect disappeared gradually with temporal asynchrony (Bresciani et al., 2005). Similar synchrony effects were reported for two signals within the haptic modality. When virtual bumps were presented to thumb and index finger while sliding over an surface, synchrony increased the probability that both events are attributed to a common source (Manuel, Klatzky, Peshkin & Colgate, 2015) and reduced variance in the localization of the assumed object (Lezkan et al., 2016). Such variations in temporal segregation could be incorporated in an extended model of optimal perception. Similarly, for spatial coincidence variations, Körding et al. (2007) suggested that the model of optimal perception should include priors which specify the probability that certain signals are generated by the same source and therefore has to be expanded to the framework of Bayesian inference. The probability of a common source determines whether signals will be integrated or not. The authors argue that their data on audio-visual localization (like in the ventriloquist effect) is best explained by a mixture model, in which integration takes place or does not take place depending on the probability of a common source given the spatial separation between the signals (see Fig. 1.2).



**Figure 1.2.** Causal inference in the ventriloquist effect. Either one cause ( $C=1$ ) or two different causes ( $C=2$ ) are assumed for the visual and auditory signals. Perception is modeled by a mixture of both situations depending on their probabilities (reprinted from Körding et al., 2007).

Because sequential signals are natural to haptic perception one might argue that this kind of temporal separation between signals will not harm the assumption of a common source as long as the finger stays in continuous contact with the object. Nevertheless, introducing Bayesian inference might be fundamental for the integration of sequentially gathered signals because it allows implementing priors. When signals are generated sequentially, what is considered to be a current signal and what a prior changes dynamically. Earlier signals also constitute the priors for later signals. Therefore, including priors is an important improvement for the optimality model. In Bayesian inference the prior  $P(X)$  is combined with the signal-specific estimates (e.g.  $S_1$  &  $S_2$ ). The aim of an optimal integration would be to compute the conditional density function of the object property value ( $X$ ) - the posterior probability - given the sensory estimates. The posterior probability  $P(X|S_1, S_2)$  is proportional to the product of the likelihood function  $P(S_1, S_2|X)$  and prior probability distribution  $P(X)$  (Ernst, 2006; Knill & Pouget, 2004). Further, if the noise of individual estimates is independent, the likelihood function is the product of the likelihood functions associated with each individual estimate. Thus, the following formula results:

$$P(X|S_1, S_2) \propto P(S_1|X) P(S_2|X) P(X) \quad (4)$$

When no prior is given, the Bayesian inference makes the same predictions as the MLE model. In the case of two sequentially generated signals, the first estimate (i.e., posterior after the first signal) can be considered the prior for the calculation of the second estimate (i.e., posterior after both signals). However, when more than two signals are given, Bayesian inference would have to be applied several times in a row. This process of continuously applying Bayesian inference (e.g., for multiple sequential movements) was also described as the Kalman filter

framework (Kalman, 1962). In the Kalman filter framework the posterior estimate ( $\hat{E}^{(i+1)}$ ) after gathering the signal  $i$  is computed in the following way (cf. Shadmehr & Mussa-Ivaldi, 2012):

$$\hat{E}^{(i+1)} = \hat{E}^{(i)} + k^{(i)}(E^{(i)} - \hat{E}^{(i)}) \quad (5)$$

$$\text{where} \quad k^{(i)} = \frac{p^{(i|i-1)}}{p^{(i|i-1)} + \sigma_{E^{(i)}}^2} \quad \text{and} \quad p^{(i|i-1)} = \frac{p^{(i-1|i-2)} * \sigma_{E^{(i-1)}}^2}{p^{(i-1|i-2)} + \sigma_{E^{(i-1)}}^2} \quad (6)$$

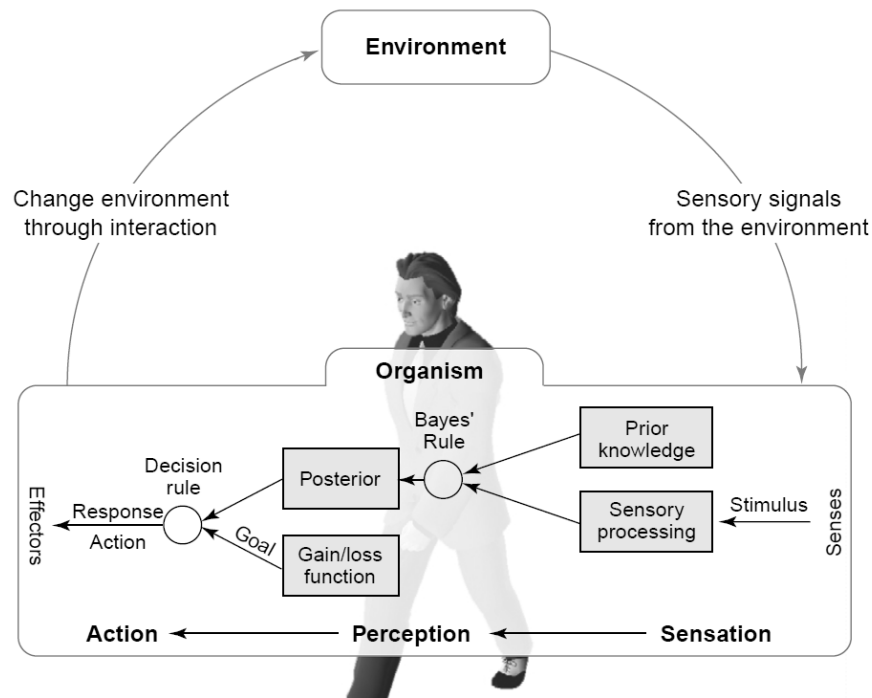
The posterior estimate  $\hat{E}^{(i+1)}$  is derived from the prior  $\hat{E}^{(i)}$  (that is given by the estimate from the previous signal) plus the prediction error of the previous estimate ( $E^{(i)} - \hat{E}^{(i)}$ ) weighted by Kalman gain  $k^{(i)}$ . The Kalman gain describes the ratio between the prior variance ( $p^{(i|i-1)}$ ) and the sensory variance ( $\sigma_{D^{(i)}}^2$ ). This is to the say, in the Kalman filter priors and present information are combined as in Bayesian interference, but it additionally incorporates potential changes in the estimates over time. Also the MLE model is captured within the Kalman filter framework as a simple case with no priors and stable estimates over time (Battaglia, Jacobs, & Aslin, 2003; Ernst & Bühlhoff, 2004). However, the Kalman filter can also describe how a series of sequential estimates are used for estimating a property in a way that the variance of the final estimate is minimized in more general circumstances. For instance, if estimates have to be stored in memory, they get noisier over time (e.g., Murray, Ward & Hockley, 1975; Olkkonen, McCarthy & Allred, 2014). This kind of temporal dynamics can only be included when modeling optimal perception with the Kalman filter framework.

Taken together, previous research successfully modeled how the brain integrates different simultaneously available sources of information by the MLE approach. However, integrating sequentially gathered information presumably leads to more complex processing then we would predict from MLE. More specifically, the MLE model would be especially challenged to



represent temporal dynamics, as for instance changes in estimate variance over time. Together with my colleagues, I investigated the integration of sequentially gathered haptic signals for softness and texture, which are considered to be two central dimensions of haptic perception (Bergman Tiest & Kappers, 2006), in the first two studies. Further, I proposed and tested a Kalman filter model of optimal perception that can account for temporal dynamics of a 2-IFC texture discrimination task.

### 1.3. Exploration Movements



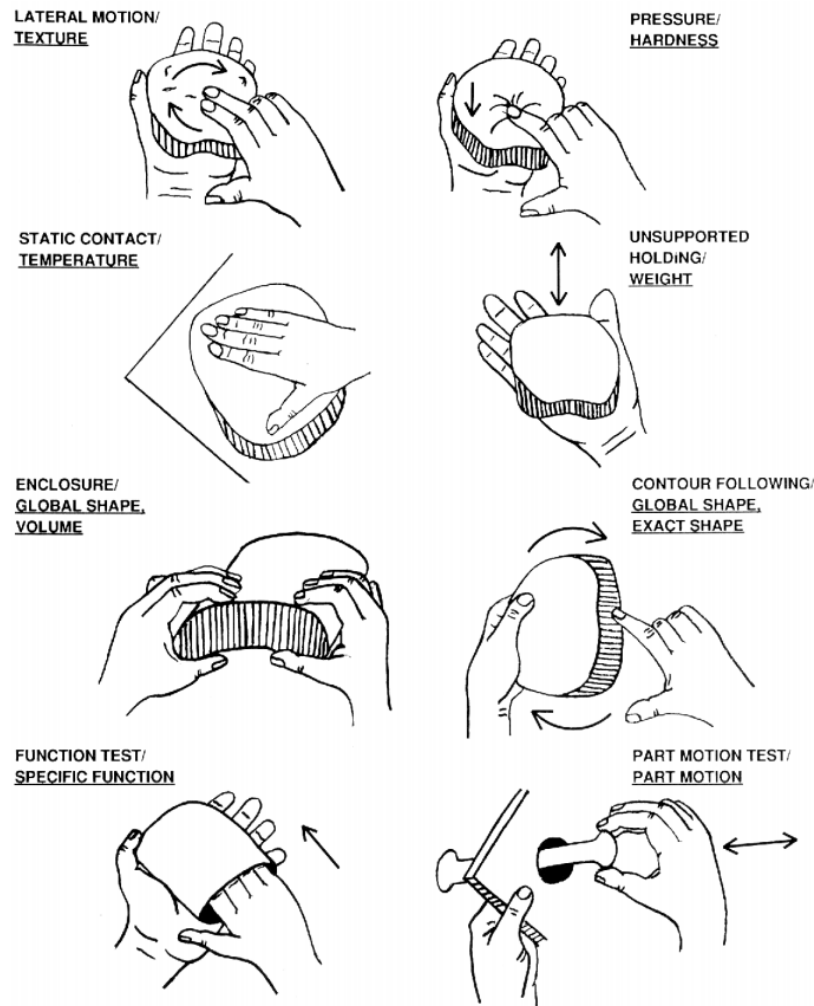
**Figure 1.3.** Sensation-Perception-Action Loop including Bayesian inference (reprinted from Ernst & Bühlhoff, 2004).

So far, I described how sensations (signals) might lead to a specific percept. However, perception is usually not an aim on its own; people perceive in order to interact with the environment (see Fig. 1.3). When the movements for this interaction are selected, not only the

priors and the sensory signals (which are integrated in the posterior) play a role. Also, a motivational (gain/loss) value of the task might be important (Ernst & Bühlhoff, 2004). Additionally, exploratory movements have to be considered in a repetitive cycle, where every movement produces new sensory signals. These signals constitute the basis for the control of the upcoming movement. In the following paragraphs, I will review previous literature on natural exploration movements in haptic perception and I will question whether movements are adjusted or even optimized online, i.e. within one exploration process.

In the concept of the sensation-perception-action loop sensations are the basis for movements and movements serve the generation of new sensations. In 1962 Gibson described in an article on a number of behavioral and introspective observations that “*when one explores anything with his hand, the movements of the fingers are purposive*”. In other words, hand movements are actively chosen in order to generate sensations and, therefore, haptic perception is considered to be an active process. Lederman and Klatzky (e.g., Lederman & Klatzky 1987; Klatzky, Lederman & Reed, 1989) extended Gibson’s ideas by providing a systematic overview of ‘purposive’ finger movements stereotypically performed for specific object properties. In their seminal work (Lederman & Klatzky, 1987), the authors used a ‘match-to-sample’ task, in which blindfolded participants had to learn about one object property of a standard stimulus and then to match the most similar stimulus out of three comparisons based on this property. In every set, the four objects varied among several object properties, for example, softness, texture or shape. The participants chose different movement patterns depending on the object property they were instructed to focus on. Movement patterns were classified into so-called ‘exploratory procedures’ (EPs). Figure 1.4 depicts typical EPs and the associated properties. For instance, in order to match softness/hardness, participants typically applied a force normal to the object

surface. Texture matching, in contrast, was performed after using *lateral motion*. In this EP, participants typically make side-to-side movements (strokes). In the second experiment of that study the authors restricted the participants to execute a specific EP in each trial. After pairing each property task with each EP, Lederman and Klatzky concluded that spontaneously executed EPs tended produce optimal performance.



**Figure 1.4.** Exploratory procedures with their linked properties (reprinted from Lederman, 1991).

Further, Klatzky and Lederman (1999) suggested that individual EPs optimize the signal for the sensory receptors and higher-order neural computations. In the example of temperature perception, the EP called *static contact* is usually performed. This EP allows heat flow between

skin and surface. In contrast to static touch, dynamic interactions with the object inhibit thermal sensations (Green, 2009). Another example is surface roughness, which is perceived by the spatial pattern of slowly adapting (SA1) afferent activation at the macroscale and vibration based Pacinian (PC) afferent activation at the microscale (Hollins & Bensmaïa, 2007). Roughness, as a texture property, is usually explored with the EP *lateral motion*. The resulting tangential movement between skin and surface, enhances the responses of SA1 (Johnson & Lamb, 1981) and PC afferents (Weber et al., 2013) and, therefore, potentially optimizes the signals for the task. However, we still lack a complete understanding of the optimization mechanisms.

More recent studies focused on a fine-grained analysis of exploration behavior. Therefore, individual parameters, like force or velocity, of movements within specific EPs were investigated. While some researchers described perceptual biases (e.g., measured by PSEs) depending on the movement parameters (e.g., Armstrong & Marks, 1999; Debats, van de Langenberg, Kingma, Smeets, & Beek, 2010), others focussed on the perceptual performance (e.g., measured by JNDs). For instance, the amount of movement force was reported to improve the perception of details virtually rendered shapes (O'Malley & Goldfarb, 2002). Also for softness judgments, higher normal force during the EP *pressure* was shown to be associated with better discrimination (Srinivasan & LaMotte, 1995; Kaim & Drewing, 2011). Within the EP *lateral motion*, the orientation of finger movements relative to a textures surface can have an impact on perceptual performance (Lamb, 1983).

In sum, previous research showed that variations in individual movement parameters influence haptic perception. Nevertheless, an additionally important question is whether people use these parameters optimally when they explore spontaneously. Some studies reported variations in movement parameters, which seem to be beneficial for the task. For instance, Nefs,

Kappers and Koenderink (2002) reported that participants spontaneously increased the contact force of their lateral movements for higher line frequency of gratings, which might have improved their perceptual performance. Riley, Wagman, Santana, Carello and Turvey (2002) focused on object properties that can be perceived with the EP of wielding. The authors showed that exploratory dynamics within wielding varied depending on the object property of interest. Also Smith, Gosselin and Houde (2002) investigated several movement parameters within one EP and reported that tangential finger speed, normal contact and tangential shear force were selected, in ways which seemed optimal given a specific surface friction. Similarly, Tanaka, Bergman Tiest, Kappers and Sano (2014) described spontaneous effective variations in normal force, scanning velocity, and break times depending on the tasks and roughness of the stimuli. Some other studies investigated the optimality of spontaneous movement parameters more rigorously. Drewing (2012) tested haptic shape discrimination for different movement directions. By experimentally manipulating the noise for certain movement directions, it was possible to change the relation between exploratory direction and discrimination performance. After experience with the new task, participants chose directions that improved perception and, therefore, optimized the movement parameter direction. A similar optimization was reported for the normal force of indentations used for softness discrimination. Kaim and Drewing (2011) measured the first spontaneous indentation peak force for hard and soft stimuli, when their softness category was either predictable or not. For predictably hard stimuli, participants used higher indentation force than for predictably soft stimuli. This was shown to be an optimal behavior when participant were instructed to use more or less force than they would do spontaneously. While using less force for hard stimuli impaired discrimination, more force did not improve discrimination.

Taken together, exploration movements were described to be purposive and even optimally chosen. Depending on the object property people qualitatively change movement pattern, i.e. EPs. Depending on the property value people also quantitatively change the exact movement parameter. However, exploration is an entire process and movements evolve within one exploration. Therefore, it is not enough to represent one exploration with one movement parameter value only, as it was commonly done in the literature. In my thesis I aimed to overcome this limitation and investigate so-called online adjustments of exploration movements.

#### **1.4. Online Adjustments of Exploration Movements**

Given a sensation-perception-action loop, movement control is based on available sensory signals and the resulting percept. Over the course of one exploration additional movements add sensory signals. The availability of more sensory signal should increase the precision (i.e., lower the variance) of the percept (e.g., Quick, 1974; Gescheider, Berryhill, Verrillo, & Bolanowski, 1999; Louw, Kappers, & Koenderink, 2005; Giachritsis, Wing & Lovell, 2009). Additionally, perception might be changed over the exploration. For instance, Lakatos and Marks (1999) described that for short exploration times, local features dominated the overall percept, whereas global features became more important with longer exploration times. Therefore, the basis for motor control changes constantly.

In one of the first studies on how exploration behavior evolves, Lederman and Klatzky (1990) described haptic object identification as a two-stage process. In the first stage, general exploration procedures, like grasping and lifting, were performed. This gave the possibility to obtain information about a variety of properties while the signals were imprecise. Thereafter, in a second step, the specific optimal exploratory procedure was applied. In other words, sensory

information obtained in the first step was used to adjust exploration movements in the second step.

More recent studies reported online adjustments of individual movement parameters. For instance, Weiss and Flanders (2011) showed that gradually gathered sensory signals are used for continuously updating motor commands. Participants followed with their finger the contour of virtual spheres. Within a trial of 2-3 seconds duration participants were able to adjust the velocity and force of finger movements to the unpredictable surface curvature. Additionally, when unexpected changes in surface curvature were introduced a compensatory force adjustment followed in only 50 ms. The authors suggested that a spinal control mechanism compares actual sensory signals with the expected sensory signals on the basis of the efferent copy of the motor command. While there are not many studies, which examined how humans adjust exploratory movements based on sensory signals, as Weiss and Flanders (2011) did, this was widely investigated in rodents (e.g., Mitchinson, Martin, Grant & Prescott, 2007; Deutsch, Pietr, Knutsen, Ahissar & Schneidman, 2012; Saraf-Sinik, Assa & Ahissar, 2015). Inspired by the rodent whisking behavior Saig, Gordon, Assa, Arieli, and Ahissar (2012), used an artificial whisking task for humans. Hereby, artificial whiskers were attached to the right and left index finger of the participant. While sitting between two poles, participants performed self-directed whisking movements and reported which of the poles was more posterior in the horizontal plane. The results showed that sensory signals were used to adjust movement parameters over the exploration process until they converged to a steady state.

In sum, sensory signals gathered during the exploration were previously reported to evoke adjustments of motor variables. However, for most of the natural exploration behaviours of non-virtual objects online adjustments have so far not been investigated. In order to overcome

these limitations within my thesis, I conducted Study III and IV. The studies investigated whether people adjust movement parameters online when judging softness and texture.

Previous research suggested to directly compare movements and perception in order to investigate in how far sensory signals contribute to motor control. In vision research, ‘oculometric’ functions were used for comparisons of eye movements with visual perception (e.g., Kowler & McKee, 1987). Comparing the noise in both systems allowed vision scientist to propose models on whether shared signals are contributing and whether the processing is parallel or rather serial (e.g., Stone & Krauzlis, 2003; Gegenfurtner, Xing, Scott & Hawken, 2003). Similar analyses for online adjustments of movements and their perceptual basis would help to understand the mechanisms behind the sensation-perception-action loop in active touch.

Additionally, based on previous research we know that motor commands will not only depend on current sensory signals but also other factors. The sensation-perception-action loop describes two kinds of processes influencing chosen movements. These are also known from movement control literature, as feedforward processes via prediction/ prior knowledge and feedback processes via sensory signals (e.g., Wolpert, 1997). Therefore, besides sensory signals, prediction was reported to play a role in movement control (e.g., Wing & Lederman, 1998; Johansson & Westling, 1988; Kaim & Drewing, 2011). Prediction was shown to have higher impact on movement control for regular events, like smooth changes in contrast to abrupt ones (Tramper & Flanders, 2013). The relative contribution of different sources of signals, like prediction and sensory signals, for movement control was reported to vary over the exploration process depending on their variances (Saunders & Knill, 2004). Therefore, sensory signals should have more effect on movement control the less noisy they are, which is achieved with increasing accumulated sensory evidence (e.g., Quick, 1974; Gescheider, Berryhill, Verrillo, &



Bolanowski, 1999; Louw, Kappers, & Koenderink, 2005; Giachritsis, Wing & Lovell, 2009). This is to say, later in the exploration process movements should be more influenced by sensory signals. Under the assumption that the overall goal is to get the least noisy final percept, later movement parameters should also be closer to optimal values.

In active touch, additional sensory signals are generated with additional movements generate. However, additional movements are also associated with additional movement costs, in terms of effort (Todorov & Jordan, 2002; Todorov, 2004). This trade-off between movement benefits (more sensory signals) and movement costs (effort) seem to be moderated by reward/motivation (in Fig. 1.3 this is incorporated as the gain/loss function). Studies on eye movements showed that the expectation of reward influences movement costs (e.g., Takikawa, Kawagoe, Itoh, Nakahara, & Hikosaka, 2002; Xu-Wilson, Zee, & Shadmehr, 2009). Similar moderation processes seem to be reasonable for the active haptic exploration movements. However, these were not investigated so far.

Taken together, some first studies focused on online adjustments of exploration movement in haptic perception (Weiss & Flanders, 2011; Saig et al. 2012). Other studies described that prediction influences movement parameters besides sensory signals. When prior knowledge constitutes the prediction it influences first exploration movements (Kaim & Drewing, 2011). But when predictions are continuously updated, they can impact movement control over the entire exploration course (Tamper & Flanders, 2013). However, for most EPs, we lack an understanding of how movement parameters develop in the exploration process. In Study III and IV, I investigated the adjustments in key movement parameters for softness and texture perception, which occur on the basis of previously gathered sensory signals. In contrast to hand movements, exploratory eye movements were more intensively examined (e.g., Najemik &

Geisler, 2005). In the Studies III and IV, I incorporated concepts which are known from visual research into the investigation of exploration movement in the process of natural haptic perception. By doing so, I introduced the concept of motivation in the control of natural haptic exploration movement (Study III) and developed a novel method to compare finger movement and perceptual noise (Study IV).

## **1.5. Aims and Experimental Approaches**

The aim of this thesis '*Haptic Perception as a Dynamic Process - How Movements and Perception Evolve*' was to investigate perceptual and motor dynamics of a natural haptic exploration process. In Study I and II, I investigated how sequential sensory signals are integrated in texture and softness perception. In Study III and IV, I focused on how specific movement parameters, that is, indentation force for softness perception and movement direction for texture perception, evolve over the exploration process.

The aim of the first study was to compare the integration of sequentially gathered sensory signals to predictions for optimal integration of simultaneous signals (MLE; e.g., Ernst & Banks, 2002) and propose a better suited model (Kalman filter; Kalman, 1962). First I investigated how the extension of exploratory movements (i.e., the number of strokes) affects discrimination thresholds for virtual textures with small repetitive structures (rendered with the PHANToM force-feedback device). I derived MLE prediction on discrimination thresholds (see Ernst & Banks, 2002; Quick, 1974) and tested them against the empirical data. Therefore, participants performed a 2-IFC discrimination task on the spatial frequency or the amplitude of textures with small repetitive spatial structures defining the textures, which they explored with one to eight strokes. In both tasks, discrimination thresholds decreased with an increasing number of strokes,

however, the decrease was over 3 times smaller than predicted by MLE. Further, I compared the weighting of individual strokes to MLE predictions. In order to measure with which weight individual strokes contribute to the overall percept, a slight discrepancy between the information presented in one specific stroke and the information presented in the remaining strokes over the standard stimulus was introduced. Empirical weights deviated from MLE predictions. In this study, I proposed that the processing of sequential signals is likely to be more complex than the optimal integration for simultaneous signals (MLE). Based on previous literature, I developed and tested a Kalman filter model, which captured the memory decay in the representation of the first stimulus (e.g., Murray, Ward & Hockley, 1975; Olkkonen, McCarthy & Allred, 2014) and an online comparison process within each stroke over the second stimulus (e.g., Romo, Hernández, Zainos, Lemus, & Brody, 2002; Romo & Salinas, 2003). In contrast to the MLE model, the quantitative Kalman filter model predictions were consistent with empirical weights.

The aim of the second study was to investigate the sequential integration of signals generated by multiple indentations on silicone rubber stimuli. Specifically, weights of individual indentations within softness exploration were measured. Therefore, haptically perceived softness within individual indentations was manipulated by a novel method. In this method, subtle forces were transmitted to the exploring finger during bare finger contact with natural silicon rubber stimuli. This allowed creating a slight discrepancy between the stimulation in an individual indentation and the stimulation in the remaining indentations and assessing its relative contribution to the overall percept. Participants performed a 2-IFC task with two to five indentations and reported which stimulus felt softer. The weights of individual indentations within the exploration of the first and the second stimulus were compared to MLE predictions. While MLE predicted equal contributions for all indentations (Ernst & Banks, 2002), this was

only true for the indentations on the first stimulus. However, for the second stimulus, estimates from later compared to earlier indentations contributed less. Based on these results, this study suggests that the discrimination of natural softness stimuli fits well the neurophysiologic model of perceptual decision-making by Deco, Rolls and Remo (2010). In sum, Study II was in good agreement with the data and the model presented in Study I and expanded its application to a further EP and more naturalistic stimuli.

Study III investigated movement control during unrestricted exploration of natural silicone rubber stimuli for softness perception. For softness perception, people repeatedly *press* their finger against an objects' surface, i.e., indent the object (Lederman & Klatzky, 1987). Additionally to choosing this optimal EP, peak force of pressing movements is further adjusted to the expected softness in order to improve perception (Kaim & Drewing, 2011). The aim of this study was to disentangle the contribution of predictive and sensory signals in the control of indentation peak forces and to test whether motivation can play a moderating role. In the first experiment, participants explored a stimulus pair from a specific softness category and judged which stimulus was softer while the predictability of the softness category was manipulated. The softness category was predictable when all stimulus pairs of the same category were presented in a blocked fashion (predictive signals high). When trials with stimulus pairs from different categories were randomly intermixed, predictions about the category of the upcoming pair were impossible (predictive signals low). In contrast to predictive signals, sensory signals are gathered during exploration. This is to say, for one exploration process, sensory signals are low in the first indentation and high in the last indentation. We contrasted the cases with low vs. high availability of each signal source in order to estimate the effects of sensory and predictive signals. Participants systematically adjusted indentation forces based on sensory or predictive

signals, in a way that was described to optimize perception (see Kaim & Drewing, 2011). Interestingly, the effect of predictive signals was more pronounced than the effect of sensory signals. In a second experiment, we manipulated participants' motivation by introducing rewards for good performance. The effect of sensory signals was increased when participants were more motivated. Further, higher motivation resulted in more effort to generate of additional sensory signals. In sum, natural movement control within the process of softness exploration was based on predictive and sensory signals with varying contributions depending on the participants' motivation.

The aim of the fourth study was to investigate how movements and perception influence each other mutually in the natural exploration process. In this study we used 3-D printed oriented textures and investigated the movement parameter direction. Periodically repeating grooves defined texture orientation. For these textures, the direction of finger movement relative to texture orientation is theoretically a crucial movement parameter, because it determines the availability of temporal cues to spatial period. Movements orthogonal to texture orientation maximize the temporal frequency of stimulation, i.e. temporal cues. In contrast, movements in line with texture orientation provide no temporal cues. First, I tested whether texture perception gets more precise when movement direction is more orthogonal to the texture, and, therefore, this can be considered an optimal movement direction. In a 2-IFC spatial period discrimination task the movement direction was systematically varied. I restricted movement directions using the PHANTOM force-feedback device by defining specific exploration tunnels and manipulated the movement direction relative to the texture orthogonal. Discrimination thresholds were smaller for directions closer towards the texture orthogonal as compared to in parallel to the texture. Based on this evidence of an optimal movement direction I, further, tested whether in

free exploration movements are optimized based on sensory signals. Only in the last stroke over clearly oriented standards (in contrast to not clearly oriented comparisons) movements were directed orthogonally to the texture. Therefore, sensory signals on texture orientation were gathered over the course of exploration and used to optimize movements. In a further experiment, I tested whether the sensory signals on which movement adjustments are based also constitute the basis for the perception of texture orientation. Therefore, I developed a novel method that allows directly comparing the use of sensory signals in movement control and perception. More specifically, I determined perceptual thresholds for orientation discrimination and computed ‘movometric’ thresholds from the stroke-by-stroke adjustment of movement direction. A common factor, namely spatial period, influenced perception and movements. This indicates that the same sensory signals contributed to perception and movements. Overall, this study described high interdependencies between movements and perception in the process of natural exploration. In line with the results of Study III, this study suggests that the goal of movement control is to optimize haptic perception. Additionally, in this study, I strengthen the evidence that this is achieved by choosing specific parameters of exploratory movement on the basis of previously gathered sensory signals.

## 2. Processing of Haptic Texture Information Over Sequential Exploration Movements

*A similar version of this manuscript has been published as:*

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Where textures are defined by repetitive small spatial structures, exploration covering a greater extent will lead to signal repetition. We investigated how sensory estimates derived from these signals are integrated. In Experiment 1, participants stroked with the index finger one to eight times across two virtual gratings. Half of the participants discriminated according to ridge amplitude, the other half according to ridge spatial period. In both tasks just noticeable differences (JNDs) decreased with an increasing number of strokes. Those gains from additional exploration were over 3 times smaller than predicted for optimal observers who have access to equally reliable, and therefore equally weighted estimates for the entire exploration. We assume that the sequential nature of the exploration leads to memory decay of sensory estimates. Thus, participants compare an overall estimate of the first stimulus, which is affected by memory decay, to stroke-specific estimates during the exploration of the second stimulus. This was tested in Experiments 2 and 3. The spatial period of one stroke across either the first or second of two sequentially presented gratings was slightly discrepant from periods in all other strokes. This allowed calculating weights of stroke-specific estimates in the overall percept. As predicted, weights were approximately equal for all strokes in the first stimulus, while weights decreased during the exploration of the second stimulus. A quantitative Kalman filter model of our

assumptions was consistent with the data. Hence, our results support an optimal integration model for sequential information given that memory decay affects comparison processes.

## 2.1. Introduction

Textures are preferably judged by touch. Heller (1982, 1989) reported a greater contribution from touch as compared to vision to texture perception. Given that textures are defined by repetitive small spatial structures on an object's surface, exploration covering a greater extent result in repetitive, redundant, intake of the same stimulus signals. Texture perception can therefore benefit from integrating sensory information over time. Current models of information integration mostly refer to simultaneously presented redundant signals (e.g. Ernst & Banks, 2002; Drewing et al., 2008); e.g., holding a pen in the hand simultaneously results in both tactile and kinesthetic information about its diameter. In the present study, we investigate information integration for sequentially gathered signals in texture perception. In three experiments we challenge predictions from models on simultaneous information and develop and test a more general Kalman filter model which allows accounting for specific observations in the integration of sequential information (e.g. Knill & Pouget 2004) by memory-decay affected comparison processes.

To describe the integration of simultaneous redundant information the Maximum Likelihood Estimation (MLE) model is well-established (overview in Ernst & Bühlhoff, 2004). Jacobs (2002) suggested that integration uses all signals available for a property. First, signal-specific estimates  $s_i$  for the property are derived from each signal  $i$ . Second, all estimates are combined into a coherent percept  $P$  by weighted averaging:

$$P = \sum_i w_i s_i \quad \text{where } \sum_i w_i = 1 \text{ and } w_i \in [0,1]. \quad (1)$$



Estimates derived from each signal are prone to noise  $\sigma_i^2$ . Averaging different estimates can decrease the perceptual variance ( $\sigma_s^2$ ) of the combined percept (Landy, Maloney, Johnston, & Young, 1995). According to the maximum likelihood estimation (MLE) model, the variance ( $\sigma_s^2$ ) of a percept is lowest and the weights ( $w_i$ ) are optimal if the weights are proportional to the inverse variances of the signal-specific estimates ( $1/\sigma_i^2$ ):

$$w_j = \frac{1/\sigma_j^2}{\sum_{i=1 \dots j \dots N} 1/\sigma_i^2} \quad \text{with} \quad \sigma_s^2 = \frac{1}{\sum_i 1/\sigma_i^2}. \quad (2)$$

Weighted averaging (Eq. 1) well describes the percept of a property, when stimuli with signals slightly conflicting in their information on this property are created (e.g., Ernst and Banks, 2002). Experimental data also quantitatively confirm the predicted reduction of perceptual variance (measured via discrimination thresholds) in multi-estimate as compared to single-estimate situations (Eq. 2), and even the predicted optimal weights, e.g. for the case of visuo-haptic and visuo-auditory integration of size and location (Alais & Burr, 2004; Ernst & Banks, 2002). Recent studies found neurophysiological correlates of optimal multisensory integration (e.g. Fetsch, DeAngelis, & Angelaki, 2013; Helbig et al., 2012).

Within haptic perception, observers use multiple redundant signals that are simultaneously available and integrate them in agreement with MLE predictions (Drewing & Ernst, 2006; Drewing, Wiecki & Ernst, 2008). However, in haptic perception, the integration of information over time is at least as important as integration over different sensory sources (Henriques & Soechting, 2005). Typical haptic exploratory procedures extend over time and space, and can be decomposed into several exploration segments. For specific object dimensions, such as surface orientation or texture, exploratory behavior comes along with a systematic repetition of the same stimulus information. In texture exploration individual exploration segments refer to scans of the finger over the same spatial region. Thereby, extending the

exploration by repeating exploration segments increases the amount of redundant information. In order to formulate a model for such sequential and not simultaneous information, a Kalman filter (Kalman, 1962) may be better suited than the MLE model. The Kalman filter takes a more general approach to optimal information integration: It is able to describe how a series of sequential estimates are used for estimating a property in a way that the variance of the final estimate is minimized. The Kalman filter uses Bayesian interference, combining prior with present information, and can account for changes in the estimates over time. Thus, a Kalman filter approach can, e.g. model if memorized information from sequentially gathered signals gets noisier over time. First empirical studies observed correlates of fundamental Kalman filter characteristics, prediction and updating, in the brain activity of mice (Funamizu, Kuhn, & Doya, 2016). The MLE model and its predictions are captured within the Kalman filter framework as a (simple) special case with non-informative prior information and estimates that are stable over time (Battaglia, Jacobs, & Aslin, 2003; Ernst & Bühlhoff, 2004).

The present study aimed to challenge predictions from the MLE model and to develop a better-suited Kalman filter model for the sequential integration of texture information. The exploratory procedure for textures includes several lateral strokes in different directions (Lederman & Klatzky, 1987). We define an exploration segment as a single uni-directional stroke across the texture. Then, a segment-specific estimate for a property is derived from the information gathered during a single stroke. We assume that each exploration segment  $i$  yields an estimate with equal variance ( $\sigma_i^2 = \sigma_0^2$ , with  $\sigma_0^2$  being a constant value). The assumptions underlying the MLE model, then, predict that all estimates are weighted equally in the percept (Eq. 2, left) and the final variance of the percept ( $\sigma_s^2$ ) can be computed by  $\sigma_s^2 = \sigma_0^2/N$  (Eq. 2, right) with  $N$  being the number of redundant estimates. Given that the discrimination threshold

$(t_s^2)$  assesses the percept's variance ( $\sigma_s^2$ ) with  $t_s^2 = 2\sigma_s^2$  (Jovanovic & Drewing, 2014; Lezkan et al., 2016) it follows for discrimination thresholds:

$$t_s = \sqrt{2\sigma_0^2/N} \quad \text{and} \quad \log(t_s) = -\frac{1}{2}\log(N) + \text{const.} \quad (3)$$

That is, discrimination thresholds should depend on the number of exploration segments in a well defined fashion and a linear fit on log-log scales should have a slope of -1/2. Previous research on sequential integration of extended haptic stimulation seems not to support these predictions. Quick (1974) had already suggested in his model that visual thresholds linearly decrease with increasing stimulation on a log-log scale, but with diverse slopes. For haptic detection thresholds, the observed slope in Quick's model was close to -1 (Gescheider, Berryhill, Verrillo, & Bolanowski, 1999; Gescheider, Bolanowski, Pope, & Verrillo, 2002; Gescheider, Güçlü, Sexton, Karalunas, & Fontana, 2005; Louw, Kappers, & Koenderink, 2005), and thus clearly below the slope of -1/2 predicted from the assumptions underlying the MLE model. However, performance in detection tasks might not be relevant, because detection does not require perceiving the magnitude of a stimulus property (Louw et al., 2005). In a discrimination task on felt surface orientation, thresholds decreased with increasing length of exploration, and the decrements were smaller the longer the explored surface was (Giachritsis, Wing & Lovell, 2009). This is qualitatively in line with the threshold predictions but was not quantitatively analyzed, and thus is not conclusive. Importantly, results from Metzger, Lezkan and Drewing (2017) are at odds with the prediction of equal weights in the integration of sequential haptic information. The authors investigated softness discrimination, where people typically indent a soft stimulus repeatedly, and determined the weights of indentation-specific softness estimates for the first and the second stimulus in a trial. While a rather equal weighting was visible for the

indentations of the first stimulus, during the exploration of the second stimulus weights decreased for later indentations.

Thus, Metzger et al.'s (2017) results casts the assumptions of the MLE model into doubt and call for a more complex model of the processes of sequential integration during discrimination tasks. These results seem to be in agreement with a model of the comparison process between first and second stimulus that can be derived from single cell measurements on monkeys: In a vibrotactile discrimination task, Romo and colleagues (Romo, Hernández, Zainos, Lemus, & Brody, 2002; Romo & Salinas, 2003) found that neuronal responses in area SII are different for the first and the second stimulus in a trial. While the response to the first stimulus was only associated with the first stimulus' characteristics, the response to the second stimulus also included information about the first remembered stimulus. This is to say, neural responses during the second stimulus reflected the comparison between the two stimuli, which was the task of the monkey. Hernandez et al. (2010) measured the monkey's cortical activity during vibrotactile discrimination. The activity of frontal lobe circuits was associated with the result of the sensory decision which of the two stimuli had higher frequency as well as with the past information about the stimuli. Most importantly, cortical areas that receive inputs from area SI were reported to combine present sensory information from SI with sensory representations stored in working memory. Overall the results suggest that comparison processes take place during the presentation of the second stimulus, after the first stimulus has been captured and memorized as a reference.

This can explain the data from Metzger et al. (2017) on decreasing weight of sequential estimates during the exploration of the second stimulus in softness discrimination, as follows: During the exploration of the second stimulus a comparison between present sensory signals and

the remembered estimate is continuously going on. Within this comparison process the variance of the estimate of the remembered first stimulus increases due to memory decay. Hence, information gathered sooner after the first stimulus may have lead to a more precise judgment on the difference between the two stimuli than later information and was therefore weighted higher. Such a process will not be captured by the rather simple assumptions underlying the MLE model, but requires a Kalman filter model that can additionally account for changes in the estimates' variance.

In the first experiment of the present study, we investigated for texture discrimination how the (spatio-temporal) extension of exploratory movements, i.e. the number of strokes across the texture, affects discrimination thresholds. The assumptions underlying the MLE model predict that the reduction of thresholds follows a power function of the number of strokes with exponent  $-1/2$ , whereas the outlined model on the comparison process with memory decay predicts less reduction (i.e. a larger exponent). In the second experiment we tested whether stroke-specific estimate weights are unequal, and follow the pattern predicted from the outlined model on the comparison process. Finally, in Experiment 3 we tested quantitative predictions for the estimate weights that stem from a Kalman filter model of optimal integration given memory decay affected the comparison process.

## **2.2. Experiment 1**

We created haptic texture stimuli by using a PHANToM force-feedback device. The device is attached to a finger via a thimble. It simulates objects by monitoring 3D-finger position and by applying an appropriate reaction force. We used virtual gratings that consisted of sinusoidal ridges on an otherwise planar surface. Different grating stimuli differed in ridge height

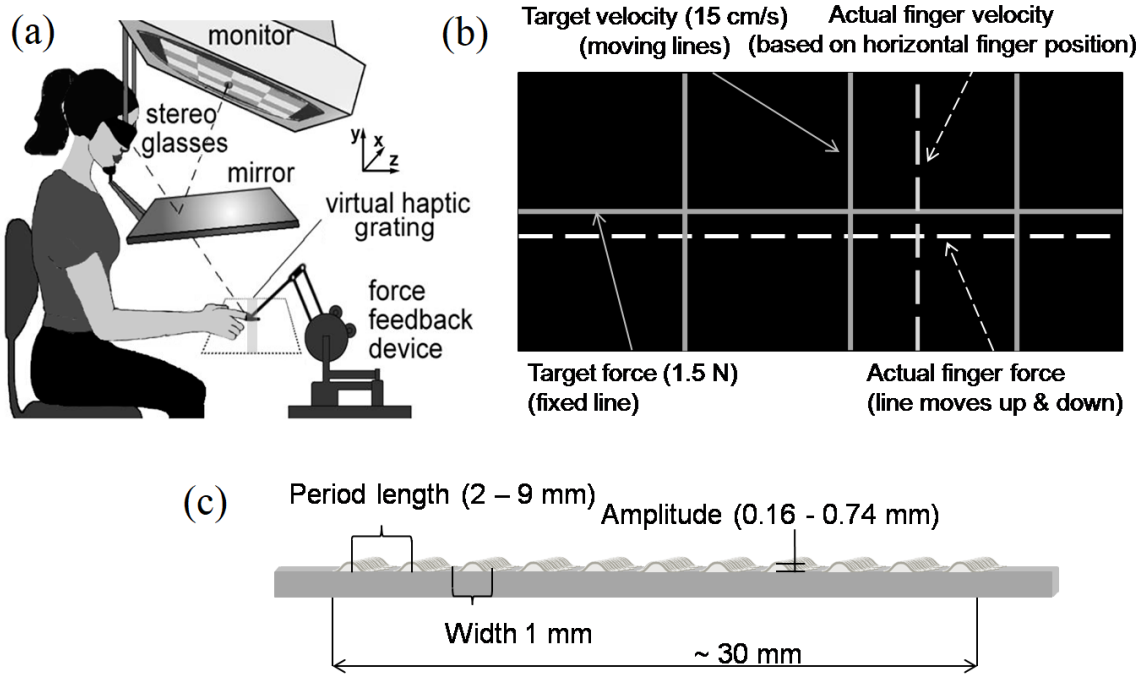
or the distance between adjacent ridges (=period). On each trial, participants explored one of the two possible standard gratings and one comparison grating. Afterwards, half of the participants decided which grating had felt higher (amplitude judgment), the other half decided about grating period (period judgment). Participants were instructed to explore with back and forth movements having a defined finger velocity and force, in order to avoid confounds. As a consequence, participants had to simultaneously focus on the discrimination task and on their exploratory movement. In order to reduce the attention needed for movement control, the movement was guided by intuitive visual feedback and participants initially practiced the instructed force and velocity.

The experiment started with this “practice phase”. Afterwards, in the “exploration phase”, we varied the number of strokes (1 ... 8) that participants used to explore each stimulus. We measured just-noticeable differences (JNDs; assessing discrimination thresholds) for either task by using the adaptive staircase procedure called BestPEST (Lieberman & Pentland, 1982). We expected that JNDs would decrease with the number of strokes conducted following a power function. Furthermore, we tested the exponent of the power function against  $-1/2$ , which is the value predicted by the assumptions underlying the MLE model.

### **2.2.1. Participants**

A total of 16 healthy participants, students from Giessen University, were tested (mean age: 22 years, range: 19-26 years; 9 females, 7 males). All participants had normal or corrected-to normal visual acuity, were right-handed and none of them reported cutaneous or motor impairments. Participants were naïve to the purpose of the study. They participated for course credit. Methods and procedures of both experiments were approved by the local ethics committee

LEK FB06 at Giessen University and they were in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. Participants gave written informed consent.



**Figure 2.1.** Sketch of the visuo-haptic setup (a), the visualization presented during exploration (b) and a stimulus (c). (a) Participants were sitting in front of the workbench, wearing earplugs and headphones. A head and chin rest limited head movements. (b) Visual feedback on the two movement parameters velocity and force. Feedback lines were only displayed while the finger was outside the grating area. Please notice: what is depicted as solid lines were actually blue lines and what is depicted in dashed lines were red lines. (c) Stimuli were virtual gratings, which varied in the period length for half of the participants and in the amplitude for the other half.

### 2.2.2. Apparatus and Stimuli

The apparatus can be seen in Figure 2.1a. Participants sat in front of a custom-made visuo-haptic workbench, which comprised a PHANToM 1.5A haptic force feedback device and a 22"-computer screen (120 Hz, 1024 x 1280 pixel). The right index finger was connected to the PHANToM via a thimble-like holder, which allows for free finger movements having all six degrees of freedom in a 38x27x20 cm<sup>3</sup> workspace. Simultaneously, the participants looked

through stereoglasses (CrystalEyesTM) and via a mirror onto the screen (40-cm viewing distance). The mirror prevents participants from seeing their hand and enables spatial alignment of the 3D-visual with the haptic display. The participants' heads were stabilized by a chinrest. The devices were connected to a PC. A custom-made software controlled the experiment, collected responses and recorded finger positions and reaction forces (from PHANToM, every 2 ms). Noise presented via headphones and ear plugs masked sounds generated by the PHANToM.

Both stimuli were presented after each other in front of the participants. The stimuli were virtual gratings covering an area of about 30 mm width ( $x$ -axis) X 15 mm depth ( $z$ -axis). Gratings consisted of ridges (width 1 mm; extending over the entire depth) on an otherwise planar surface. Ridge height was a sine-function (within 0 to  $\pi$ ) of  $x$ -position. Programmed peak amplitudes of the ridges varied between 0.16 and 0.74 mm; the peak-to-peak period between ridges varied between 2 and 9 mm. In each single stimulus, ridge amplitudes and periods were constant. Strokes started left or right from the grating. Haptic grating stimuli were created using the PHANToM force feedback device. The device simulates objects by applying reaction forces  $\vec{F}_p$  as a function of the 3D-finger position  $P$ . Force magnitude linearly increases with the indentation depth of the finger into a virtual object ( $i_p$ ) and force direction is normal to the object's surface ( $\vec{n}_p$ : normal vector,  $D$ : spring constant):

$$\vec{F}_p = \vec{n}_p * |\vec{F}_p| \quad \text{and} \quad |\vec{F}_p| = D * i_p \quad (4)$$

The spring constant  $D$  was replaced by the variable  $K$  in order to keep object indentation constant under differing finger forces. The variable  $K$  was defined such that for the target indentation  $I$  (set to 1 mm) the magnitudes of finger force and reaction force were (approx.) equal. Vertical finger force was estimated from the device's reaction forces in  $y$ -direction  $F_y(j)$  ( $y$ -axis = height) in the previous device cycles  $j = 1 \dots n$  (~previous 300 ms):



$$K = \frac{1}{n} \sum_{j=1 \dots n} F_y(j) / I \quad (5)$$

### 2.2.3. Design and Procedure

Participants successively explored two gratings. Between participants we varied the Judged Dimension (Amplitude, Period). Half of the participants judged which of the two gratings had felt higher (Amplitude); the other half judged which grating had higher spatial period (Period). We further varied the *Number of strokes* (1, 2, 3, 4, 5, 6, 7, 8) that participants used to explore each of the two stimuli (within-participant variable). A single stroke was defined by a single unidirectional exploratory movement across the grating. We measured 75%-discrimination thresholds (JNDs) for two standard stimuli. The standard stimuli in the Amplitude group had amplitudes of 0.4 or 0.5 mm and periods of 5 mm. In the Period group the standard stimuli had periods of 5 or 6 mm and amplitudes of 0.4 mm.

JNDs were determined using the BestPEST adaptive staircase procedure combined with the two-interval forced-choice task. In the BestPEST method (Lieberman & Pentland, 1982) before each stimulus presentation, the likelihood distribution of possible thresholds is calculated by using the sigmoid-shaped psychometric function with a slope of one, on the basis of all previous responses of the participant. The value with the maximum likelihood of being the threshold value is then chosen as the comparison stimulus. This method is an optimum strategy for fast threshold determination. In effect, the procedure raises the difference between the values of comparison and standard after a wrong response and lowers it after a correct response. We terminated the procedure after 26 trials per staircase, estimating the 75%-threshold (JND) by the final maximum-likelihood estimate. For each *Number of strokes* and each standard stimulus two up- and two down- staircases measured the upper and lower JNDs, respectively. In the

Amplitude condition, initial amplitudes of the comparison stimuli were given by the standard's amplitude plus or minus 0.35 mm; the comparisons' period was always 5 mm. In the Period condition, initial periods of the comparisons were the standard's period plus/minus 3 mm; the comparisons' amplitude was always 0.4 mm. Trials from all staircases were randomly interleaved in the measurement phase. Overall, the measurement phase consisted of 2 [standards] \* 2 [staircases] \* 26 [staircase length] \* 2 [repetitions] \* 8 [*Number of strokes*] = 1664 trials. The entire experiment consisted of 5 sessions lasting about 2 hours each. Prior to the experiment, participants were trained for about 30 min to execute exploratory movements with constant instructed finger velocity (15 cm/s) and force (1.5 N). The training consisted of two parts. In the first part participants trained on a virtual plane without ridges. In the second part of the training movements were performed on virtual gratings. Each part ended after participants had performed 20 trials in a sequence with maximally 3 movement errors. We defined movement errors as a deviation of actual velocity or force values by more than 60 % from the target velocity and force.

Each trial started with a visual representation of the upcoming stimulus and start point (left or right of the grating, balanced). Participants initiated the trial with a button press at the start point location. Then, participants stroked across a first grating back and forth. The computer program stopped the stimulus presentation, when the required number of strokes had been conducted. Afterwards a second grating was explored using the same number of strokes as for the first grating. Finally, participants had to decide by a button press (done with the PHANToM) which grating had felt higher in amplitude / had higher spatial period. During the strokes, a vertical line that moved forth or back along the exploratory axis indicated the prescribed finger velocity (15 cm/s) and stroke direction. A stationary horizontal line indicated prescribed force (1.5 N). Participants monitored their current velocity and force by further feedback lines, which

were displayed while the finger was outside the grating area. A vertical line displayed the current 1D-finger position on the x-axis; a horizontal line moved up and down with exerted force. Trials were repeated later in the session when a movement error was detected.

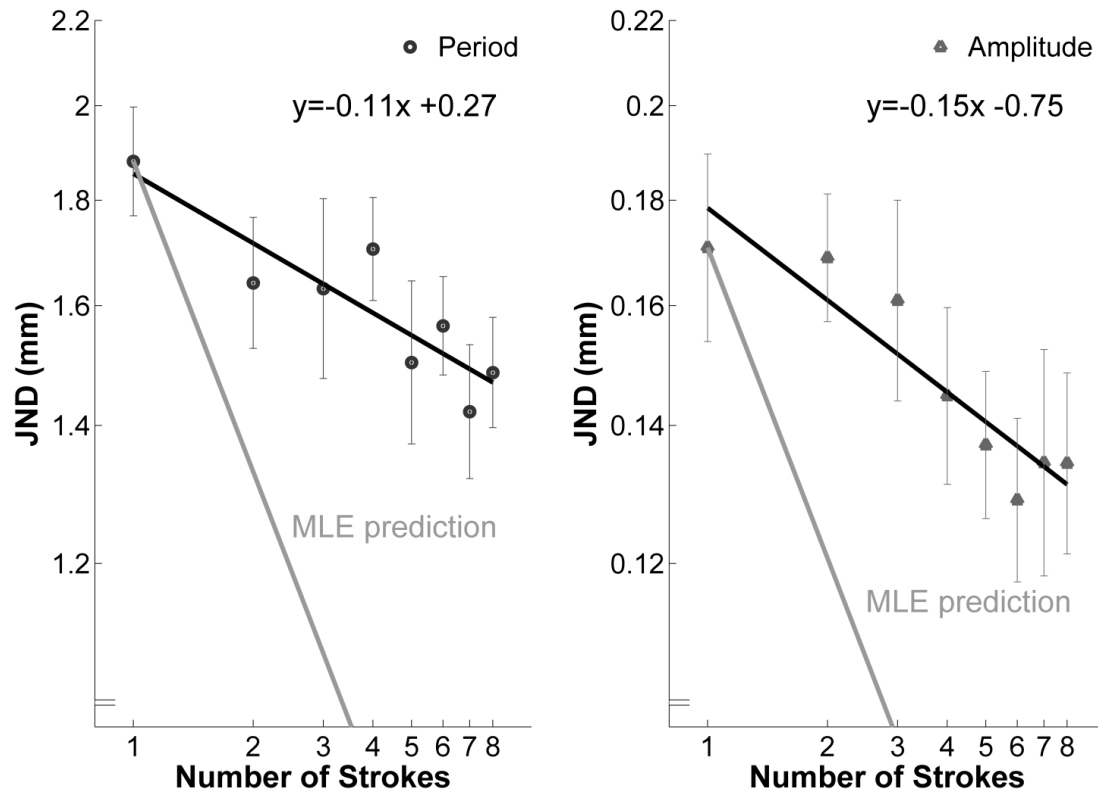
#### **2.2.4. Data Analysis**

We calculated individual JNDs per *Number of strokes* condition by averaging across the two upper and the two lower JNDs for each standard stimulus (8 JND values). These values were log-transformed (base 10) before analyses. According to the predictions it is the log JNDs that should linearly decrease with the log *Number of strokes*. In addition, the log-transformation allows comparing gain ratios in the amplitude and the period conditions: It transforms the ratios between JNDs for different Numbers of Strokes into differences, which can be directly analyzed by an ANOVA.

#### **2.2.5. Results**

Individual log JND values entered an ANOVA with the within-participant variable *Number of strokes* (1...8) and the between-participant variable Judged Dimension (Amplitude, Period). For the variable *Number of strokes*, we calculated linear contrasts, which provide a targeted test of our hypotheses. The linear contrast of *Number of strokes* was significant,  $F(1,14) = 15.326$ ,  $p < .001$  (one-tailed), confirming the predicted decrease of JNDs with an increasing *Number of Strokes*. The interaction *Number of strokes* (linear contrast) X *Judged Dimension* failed to reach significance,  $F(1,14) = .350$ ,  $p = .563$ , which may suggest that both amplitude and period JNDs depend in similar manner on the *Number of strokes*. To be more precise, the lack of effects on log values suggests that the ratios between the JNDs of different *Number of strokes*

conditions are similar. Finally, the main effect of *Judged Dimension* was significant,  $F(1,14) = 584.050$ ,  $p < .001$ , which is, however, essentially non-interesting, because it only reflects the fact that (log) amplitude and period JNDs differ in scale. Figure 2.2 shows a log-log plot of the JNDs.



**Figure 2.2.** Exp.1: Log-Log plot. Average JNDs for frequency discrimination (left; expressed as period) and amplitude discrimination (right) and standard errors as a function of *Number of strokes* and *Judged Dimension*. The gray line represents the MLE model prediction of an optimal integration.

We fit a power function separately to the amplitude JNDs and to the period JNDs. To achieve this aim, we linearly regressed log transformed JNDs on log transformed stroke numbers. As a consequence, the slope of the fitted line corresponds to the exponent of a power function fitted to the non logarithmized data. In both cases the fitted line described the data well. For the Amplitude group the regression line explained  $r^2 = 88\%$  of the variance. For the Period

group the explained variance was  $r^2 = 80\%$ . According to the MLE predictions the slope is expected to be -0.5. In contrast, the slopes of the fitted lines reached values of -0.148 for the Amplitude group and -0.112 for the Period group. By fitting regression lines to the individual log-log data we were able to calculate a  $t$ -test against the predicted slope of -0.5. In the Amplitude group ( $M=-.148$ ,  $SD=.151$ ) as well as in the Frequency group ( $M=-.112$ ,  $SD=.066$ ) the slopes differed significantly from the MLE prediction,  $t(7)=6.580$ ,  $p<.001$  and  $t(7)=16.673$ ,  $p < .001$ .

### 2.2.6. Discussion Experiment 1

In Experiment 1, we found that participants discriminate grating stimuli the more precisely the longer they explore them. Such redundancy gains were smaller than predicted by the assumptions underlying the MLE model. According to these assumptions each single estimate is weighted according to its inverse variance. In case of repeated strokes across the same stimulus, estimates from each single stroke should have equal variance and, hence, each estimate should obtain equal weight. The present results disprove the MLE predictions, and thus extend the previous evidence (Metzger et al.'s, 2017), suggesting that the assumptions underlying the MLE model do not apply to sequential integration.

As outlined in the introduction, an alternative model, which may explain the present and previous observations on sequential integration, links to memory decay during the comparison process of the discrimination task: There is evidence that discrimination performance is based on a continuously ongoing comparison process between a remembered estimate from the first stimulus and present sensory signals from the second stimulus (Romo et al., 2002; Romo & Salinas, 2003; Hernandez et al., 2010). During the comparison process, i.e. during exploration of

the second stimulus, the memory trace of the first stimulus might diminish from stroke to stroke, and thus the variance of the remembered estimate increases. Memory decay and increasing variance will, as observed, lead to lower redundancy gains than predicted from the MLE assumption of equal variance, and higher overall estimate variance. An optimality model including these factors in sequential presentation, would further predict that strokes within the second stimulus are not weighted equally, but decrease for later strokes. We designed further experiments to test whether information from different strokes during the exploration is unequally weighted in the grating percept.

### 2.3. Experiment 2

In Experiment 2 participants discriminated a standard and a comparison stimulus according to grating period using a two-interval forced choice task combined with the method of constant stimuli. They stroked 3 times across each stimulus. While participants explored the standard stimulus, we presented slightly discrepant period information in one of the strokes. That is, the grating period of each stroke in the standard stimulus could take one of two values. The stroke with the deviant period in the standard stimulus is the discrepant stroke. We defined several standard stimuli by varying the *Position* [1, 2, 3] of the discrepant stroke within the presentation of the standard. Additionally, the standard was either presented as the first or as the second stimulus of the trial, which is represented in the variable *Stimulus order* [first vs. second]. Each standard stimulus was combined with 14 comparisons. The comparisons differed in their periods, but for the strokes across each single comparison stimulus the period was kept constant. For each of the standards we determined the point of subjective equivalence (PSE) with the comparison. Based on this we calculated the weight of the discrepant information in the standard

stimulus for each combination of *Position* and *Stimulus order*. We predicted an interaction between those two variables. Weights were expected to decrease with higher *Position* in the second but not in the first stimulus.

### **2.3.1. Participants**

The final sample included eleven students (8 females, 3 males). Four additional participants had been excluded because they had problems with the task, either with the movement (>30% trials with movement error) or with the discrimination ( $JND \geq 6$  mm in experimental conditions, exceeding the effective range of measurement of the present design). Participants in the final sample were naïve to the purpose of the study, right handed, had an age range of 19-26 years, no sensory or motor impairments and participated for course credit.

### **2.3.2. Apparatus and Stimuli**

The apparatus and the virtual gratings were the same as in Experiment 1. The ridges of all grating stimuli had peak amplitudes of 0.5 mm. Typically, a standard stimulus was explored by 3 strokes. For strokes over standard stimuli we used periods of 6 and 4.5 mm. In the experimental conditions the period presented in two of three strokes is called the dominant period. In the remaining stroke the participant was presented a discrepant period. Thus, if the dominant period was e.g. 4.5 mm, we presented in one stroke the discrepant period of 6 mm. The discrepant period of 6 mm could be presented in either the first, middle or last stroke, while in the other 2 strokes the dominant information of 4.5 mm would be presented. Additionally, in control conditions with 1 or 3 strokes we used standard stimuli, in which no discrepant

information was presented. Further, we presented 14 comparison stimuli that varied in period (2 - 8.5 mm in steps of 0.5mm), and in which also no discrepant information was presented.

### 2.3.3. Design and Procedure

Similar to Experiment 1, in each trial, participants explored a standard and a comparison grating in random order. A trial was constructed as in Experiment 1. Participants always judged which grating had higher spatial frequency. In the experimental conditions, each stimulus was explored with 3 strokes. For the majority of the standards, one stroke (discrepant period stroke) differed in its spatial period from the two others (dominant period strokes). We varied the *Position* of the discrepant stroke within the standard stimulus (1, 2 or 3 strokes) and the *Stimulus order* (standard as 1<sup>st</sup> or 2<sup>nd</sup> stimulus) as within-participant variables. Additionally, we included control conditions, in which we presented standard stimuli with dominant period information from each stroke, either 4.5 mm or 6 mm. Participants explored these stimuli with three or one stroke. In contrast to Experiment 1, the point of subjective equivalence (PSE) and just noticeable differences (JND) of the standard periods were assessed using the method of constant stimuli: for each stimulus order each standard was compared 8 times to each of the 14 comparisons. Overall, the experiment comprised  $10 \text{ [standards]} * 14 \text{ [comparisons]} * 2 \text{ [stimulus order]} * 8 \text{ [repetitions]} = 2240$  trials. The entire experiment consisted of 4 sessions lasting about 2 - 2.5 hours each. In one session each standard-comparison pairing was repeated four times. The first sessions started with a phase for training instructed finger force and velocity as in Exp. 1.



### 2.3.4. Data Analysis

We determined individual psychometric functions for each standard stimulus and each *Stimulus order* (standard is first vs. second stimulus). The percentage of trials in which the participant perceived the standard to be higher in spatial frequency than the comparison was calculated as a function of the comparison stimulus. We fitted cumulative Gaussian functions to the psychometric functions, using the *psignifit* toolbox that implements maximum-likelihood estimation procedures (Wichmann & Hill, 2001) and estimated PSEs by the Gaussian parameter  $\mu$  and JNDs by  $\sigma$  (84% discrimination thresholds). We calculated individual weights of the discrepant stroke ( $w_d$ ) from the PSEs in the experimental conditions ( $P_e$ ), and from the two average PSEs in the control conditions ( $P_d$ : PSEs for standard with the same period as the discrepant stroke,  $P_o$ : PSEs relating to period of dominant strokes):

$$w_d = (P_e - P_o) / (P_d - P_o) \quad (6)$$

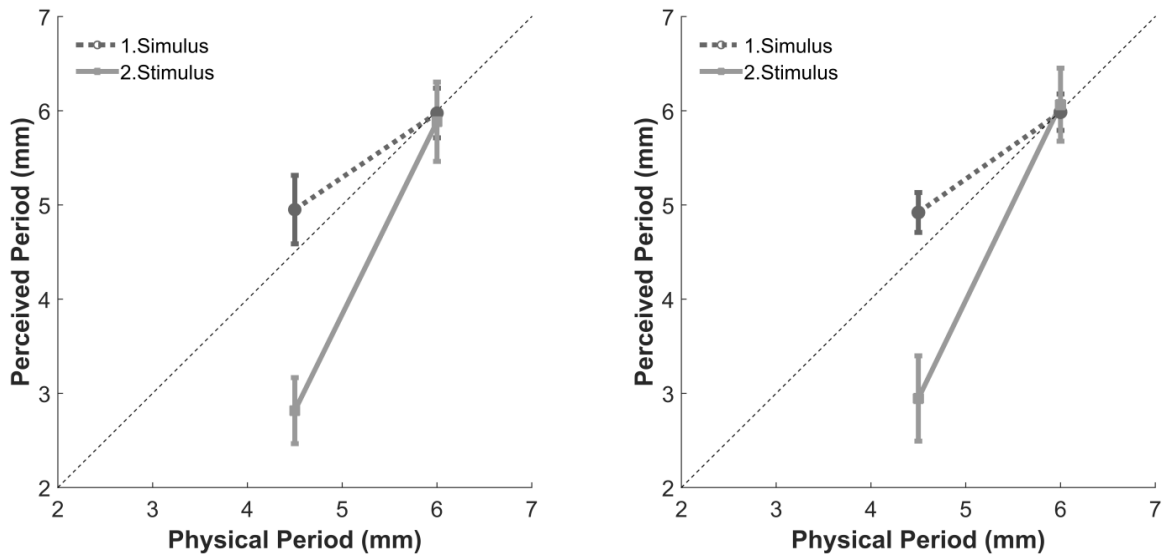
We averaged over the two weights for the two standard stimuli in each condition. Additionally, all weights were restricted to have values within 2 standard deviations from the condition average (5 outliers in 66 cases). The individual average weights of the discrepant stroke were analyzed by ANOVAs.

### 2.3.5. Results

#### 2.3.5.1. PSEs

In the control condition, participants explored either with one or three strokes two sequential gratings without any discrepant information within the standard. The PSEs represent the perceived period of the stimuli and are plotted in Figure 2.3. We analyzed the PSEs by an ANOVA with the three factors *Period in the standard stimulus* (4.5 mm vs. 6 mm), *Number of*

*strokes* (1 vs. 3) and *Stimulus order* (1<sup>st</sup> vs. 2<sup>nd</sup>). The PSEs in the control conditions differed significantly regarding the spatial Period of the standard stimulus,  $F(1,10) = 166.57$ ,  $p < .001$ , which ensures our manipulation. There was no significant effect of the *Number of strokes*,  $F(1,10)=0.22$ ,  $p=.651$ , the *Stimulus order*,  $F(1,10)=3.90$ ,  $p=.077$ , *Number of strokes* x *Stimulus order*,  $F(1,10)=1.02$ ,  $p=.336$ , or the *Number of strokes* x *Period* x *Stimulus order*,  $F(1,10)=0.001$ ,  $p=.981$ . However, the interaction between *Stimulus order* and *Period* was significant,  $F(1,10) = 18.29$ ,  $p=.002$ . As it can be seen from Figure 2.3, the difference between the percepts of the 4.5 mm stimulus and the 6 mm stimulus was higher in the second in contrast to the first stimulus. It is important to note that these effects will not affect our predictions about the weights, as average PSEs measured in the control condition are accounted for in the computation of weights.



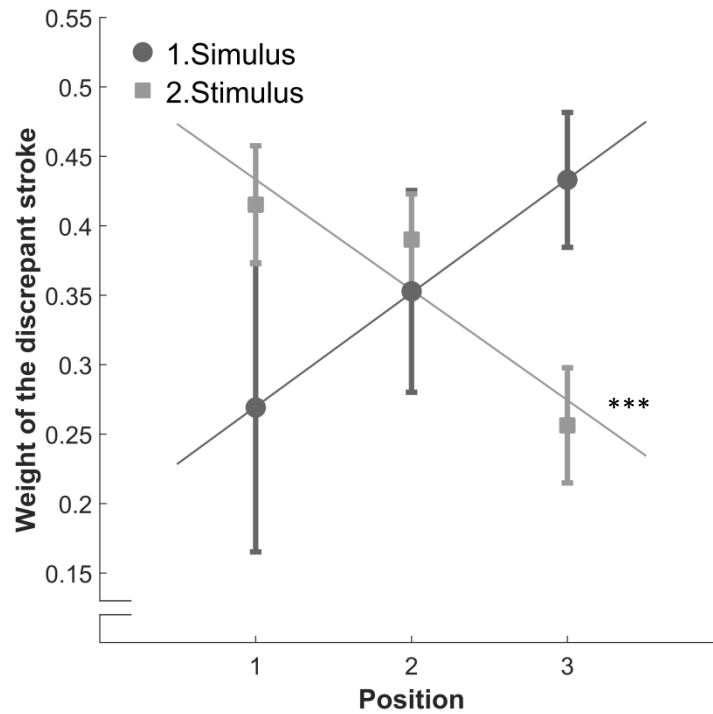
**Figure 2.3.** Exp.2, control condition: Average PSEs and standard errors (11 participants) as a function of the spatial period of the standard and of the Stimulus order. Left is the control condition with 1 stroke, right the control condition with 3 strokes.

In order to check whether the discrepant information influenced perception, we compared the PSEs from experimental conditions, i.e. from standards including discrepant information, to

the PSEs from the control conditions. This analysis was done separately for the first and the second stimulus and each dominant period. As should be the case, discrepant stimuli with the dominant period of 4.5 mm were perceived to have higher period than the corresponding control stimuli ( $t(11)=2.242$ ,  $p=.024$  and  $t(11)=4.986$ ,  $p<.001$ , one-tailed, for first and second stimulus, respectively), and discrepant stimuli with the dominant period of 6 mm were perceived as having lower period ( $t(11)=-3.050$ ,  $p=.006$  and  $t(11)=-3.332$ ,  $p=.004$ ).

### 2.3.5.2. Weights of Discrepant Information

The position of a stroke in a stimulus differently affected this stroke's weight depending on whether the first or the second stimulus was considered (see Fig. 2.4). Individual weights were entered into an ANOVA with the within-participant variables *Stimulus order* (1st vs. 2nd in trial) and *Position* within stimulus (1st vs. 2nd vs. 3rd stroke). The *Position* of the discrepant stroke within the stimulus did not show a significant main effect on the weight,  $F(2,20)=.166$ ,  $p=.849$ . The main effect of *Stimulus order* was also not significant,  $F(1,10)=0.019$ ,  $p=.894$ . More importantly and as expected, the interaction of *Stimulus order* and *Position* was significant,  $F(2,20)=4.666$ ,  $p=.022$ . We tested further whether, as also predicted, weights in the first stimulus do not depend on the *Position* within the stimulus, while weights in the second stimulus decrease the further their position is from the first stimulus. We calculated linear contrast analyses separately for the first and the second stimulus. In the first stroke these analyses did not reveal a significant linear effect of position,  $F(1,10)=4.065$ ,  $p=.071$ . Also as predicted, in the second stroke weights systematically decreased with increasing stroke position,  $F(1,10)=6.233$ ,  $p=.016$  (one-tailed).



**Figure 2.4.** Exp. 2, Average estimated weights and standard errors of the discrepant stroke as a function of *Position* within the stimulus and *Stimulus* order within the trial.

### 2.3.5.3. JNDs

In Experiment 1 the participants showed better discrimination thresholds for increasing numbers of strokes. In the present Experiment, we can test with the two control conditions if this effect can be replicated. We expect better discrimination thresholds in the 3-stroke condition than in the 1-stroke condition. A paired one-tailed  $t$ -test of the log-transformed (base 10) JNDs showed a significant difference between the two control conditions,  $t(10)=3.347$ ,  $p=.004$  (JNDs 1-stroke condition:  $M=4.32$ ,  $SEM=0.70$ ; JNDs 3-stroke condition:  $M=3.24$ ,  $SEM=0.43$ ).

### 2.3.6. Discussion Experiment 2

We introduced slight discrepancies in spatial period information in a one of several strokes across a grating stimulus. We varied the position of the discrepant spatial period information within the standard stimulus presentation. None of the participants reported to have noticed the discrepant periods when being asked after the experiment. But discrepant information contributed to the grating percept, as can be seen from the significant PSE shifts in the expected directions. From PSEs we calculated individual weights of the discrepant stroke for each condition. Our results confirmed our predictions: Weights depended differently on stroke position for the first and the second stimulus. Weights did not significantly change within the first stimulus. But in the second stimulus, a stroke's weight was higher the closer the discrepant stroke was to the first stimulus. Our data are consistent with the assumption that the comparison process during the exploration of the second stimulus becomes - due to decay of the memory trace of the first stimulus - increasingly more variable over time and later strokes are weighted less.

One may wonder whether correlated errors between stroke-specific estimates can alternatively explain the results, as had been the case for other failures of MLE predictions (Oruç, Maloney, & Landy, 2003; Rosas, Wichmann, & Wagemans 2007): Positively correlated errors reduce the effect of an additional estimate on the percept's overall variance as compared to the MLE predictions (Eq. 2). That is, the higher the correlation between the additional estimate and previous estimates, the higher the variance of the final percept. In the case of a sequential, step-by-step integration of correlated estimates, estimates gathered later would correlate more with the previously collected information than earlier estimates, and hence, effectively decrease variance less and obtain less weight in the percept (cf. Oruç et al. 2003). That is, correlated errors

between stroke-specific estimates predict lower weights for later strokes. This prediction applies to both strokes across the first stimulus and strokes across the second stimulus in a trial. However, for the first stimulus we did not observe such a downward trend, rejecting the alternative explanation by correlated errors.

Sensory adaption could be considered as another possibility to explain the data. It was reported that after repeated stimulation sensory adaptation leads to aftereffects by reducing sensitivity (e.g. Thompson & Burr, 2009). Such aftereffects were shown in different aspects of the sense of touch (Kappers & Bermann Tiest, 2015) including the perception of vibration (Lederman, Loomis, & Williams, 1982; Hollins, Bensmaïa & Washburn, 2001). Thereby, the sensitivity should be the more reduced the more stimulations were presented. Sensory adaptation, thus, may predict that information from later strokes is noisier and hence weighted less. However, sensory adaption would predict the same pattern as correlated errors do, namely a general position effect, which applies to the first and the second stimulus. Thus, sensory adaptation can be rejected as an alternative explanation for the observed pattern of weights. Still a possible reducing role of adaptation for the overall variance in longer explorations might deserve further investigation in the future.

Indeed we observed, as expected, no position effect for the first stimulus. But the results on a lack of position effect are not as convincing, as we hoped. Numerically, the line of regression of weight on stroke position for the first stimulus shows an upward trend with high standard errors, which may or may not explain the lack of significance. We conducted another experiment, in that we aimed to replicate the findings and extend them for different numbers of strokes. As importantly, Experiment 3 tests quantitative predictions from a Kalman filter model

of optimal integration under conditions of memory decay during the comparison process, i.e. during exploration of the second stimulus.

## 2.4. Experiment 3

Experiment 3 is meant to generalize the investigations from Experiment 2 to explorations of varying lengths and to compare the results to predictions from a formal Kalman filter model. We manipulated the number of strokes used to explore standard and comparison stimulus. Participants explored each stimulus either with 2, 3, 4 or 5 strokes. Additionally, as in Experiment 2, we varied the position of the discrepant information within the standard stimulus (1st ... Nth position with N being the number of strokes), and the stimulus order (standard presented first vs. second). We measured the PSEs and JNDs for each condition and calculated the weight of the discrepant stroke.

Additionally, we tested in Experiment 3 if our model of a comparison process with memory decay can quantitatively predict the data. Put in a nutshell, the model assumes that estimates from the individual strokes of the first stimulus are integrated to an overall percept, and that during the exploration of the second stimulus estimates from each stroke are compared stroke-by-stroke with the integrated estimate from the first stimulus. The initial integration of the first stimulus estimate is modelled in line with the assumptions of the MLE model. However, importantly, the first stimulus' estimate is affected by memory decay. To account for the comparison process during the exploration of the second stimulus, we used a more complex Kalman filter model of optimal integration.

### 2.4.1. Model

We assume that for each stroke ( $i$ ) of the second stimulus the stroke-specific estimate is compared to the overall estimate from the first stimulus, resulting in a sensory difference value  $\mathbf{D}^{(i)}$ . The posterior estimate of the difference between first and second stimulus after this stroke  $\widehat{\mathbf{D}}^{(i+1)}$  is based on the present sensory difference value  $\mathbf{D}^{(i)}$  and a prior that is given by the difference estimate from the previous stroke  $\widehat{\mathbf{D}}^{(i)}$  (=posterior estimate after *previous* stroke; cf. Shadmehr & Mussa-Ivaldi, 2012):

$$\widehat{\mathbf{D}}^{(i+1)} = \widehat{\mathbf{D}}^{(i)} + \mathbf{k}^{(i)}(\mathbf{D}^{(i)} - \widehat{\mathbf{D}}^{(i)}) \quad (7)$$

That is, the present difference estimate  $\widehat{\mathbf{D}}^{(i+1)}$  is the previous estimate  $\widehat{\mathbf{D}}^{(i)}$  plus the prediction error of the previous estimate  $(\mathbf{D}^{(i)} - \widehat{\mathbf{D}}^{(i)})$  weighted by the Kalman gain  $\mathbf{k}^{(i)}$ . The Kalman gain describes the ratio between the prior variance ( $\mathbf{p}^{(i|i-1)}$ ) and the sensory variance ( $\sigma_{\mathbf{D}^{(i)}}^2$ ). For determining the Kalman gain, it is important to consider that our model is based on multiple comparisons with the first stimulus estimate and thus the first stimulus estimate is included in the computation of each difference estimate. The resultant covariance between prior and sensory estimate has to be taken into account (cf. Oruç et al., 2003, Eqs. 5 & 7):

$$\mathbf{k}^{(i)} = \frac{\mathbf{p}^{(i|i-1)} - \text{cov}(\mathbf{D}^{(i)}, \widehat{\mathbf{D}}^{(i)})}{\mathbf{p}^{(i|i-1)} + \sigma_{\mathbf{D}^{(i)}}^2 - 2\text{cov}(\mathbf{D}^{(i)}, \widehat{\mathbf{D}}^{(i)})} \quad (8)$$

$$\text{with } \mathbf{p}^{(i|i-1)} = \frac{\mathbf{p}^{(i-1|i-2)} * \sigma_{\mathbf{D}^{(i-1)}}^2 - \text{cov}(\mathbf{D}^{(i-1)}, \widehat{\mathbf{D}}^{(i-1)})^2}{\mathbf{p}^{(i-1|i-2)} + \sigma_{\mathbf{D}^{(i-1)}}^2 - 2\text{cov}(\mathbf{D}^{(i-1)}, \widehat{\mathbf{D}}^{(i-1)})} \quad (9)$$

In our model sensory variance of the difference value ( $\sigma_{\mathbf{D}^{(i)}}^2$ ) is the sum of the variance of a one-stroke based estimate ( $\sigma_{\mathbf{N}=1}^2$ ) and the variance of the first stimulus estimate ( $\sigma_{\mathbf{S1}_{\mathbf{N}=j}}^2$ ) modified by memory decay. The variance of the one-stroke based estimate ( $\sigma_{\mathbf{N}=1}^2$ ) was estimated from the corresponding JND in Experiment 1 (considering the transformation from 75%- to



84%- discrimination thresholds). The variance of the first stimulus overall estimate was estimated by  $\sigma_{S1N=j}^2 = \sigma_0^2/j$  (Eq. 2, right), i.e. from the MLE prediction on overall variance as a function of number of strokes ( $N=j$ ) and one-stroke based variance; it was therefore lower the more strokes over the first stimulus were performed (e.g.  $\sigma_{S1N=4}^2 > \sigma_{S1N=5}^2$ ).

Additionally, an effect of memory decay was modelled for the variance of the first stimulus estimate  $\sigma_{S1N=j}^2$ . The rate of the decrease due to memory decay is usually described by a power function of the time  $t$  with a negative exponent (Wixted & Ebbesen, 1991, 1997). Murray, Ward and Hockley (1975) reported such a power function for an experiment that resembles the present one: Two-point thresholds  $T$  at the thumb increased with the prolongation of the time interval  $t$  (in sec) between the first and the second touch by  $T=2.303t^{0.221}$ . The change in thresholds can be directly linked to change in the variance of the individual measurements ( $\sigma^2 = \frac{1}{2}T^2$ ; assuming uncorrelated errors). We modelled memory decay for the variance of the first stimulus estimate as a function of number of strokes over the second stimulus ( $i$ ) with the exponent taken from Murray and colleagues (1975):  $\sigma_{S1N=j(i)}^2 = \sigma_{S1N=j}^2 * i^{0.442}$ . Assuming that the prior for the first stroke on the second stimulus is non-informative (variance set to infinite), we predicted weights of each stroke-specific estimate in the second stimulus.

#### 2.4.2. Participants

Fifteen right-handers, naïve to the purpose of the experiment, were in the final sample (mean age: 25.4 years, range: 20-36 years; 10 females, 5 males). Four subjects had to be excluded from analyses because of problems with the task according to criteria described for Experiment 2.

### 2.4.3. Apparatus, Stimuli, and Procedure

The Apparatus, the configuration of the grating stimuli and the procedure in single trials were identical to those in Experiment 2.

### 2.4.4. Design and Data Analysis

Additionally to *Stimulus order* and *Position*, we varied the *Number of strokes*: Participants applied 2, 3, 4 or 5 strokes per stimulus. As in Experiment 2, we measured PSEs and JNDs using the method of constant stimuli. Each standard was compared 10 times to each of 14 comparison gratings. In addition, in the present experiment we analyzed the movement force and velocities used in each condition.

Table 2.1 gives an overview of the 28 possible combinations of *Number of strokes*, the *Stimulus order* and the *Position*. Two types of standards were used: A period of 4.5 mm could be the discrepant or the dominant information, a period of 6 mm assumed the other role. 24 standard stimuli corresponded to the conditions with more than two strokes, each of which was either presented as first or second stimulus. However, for the two-stroke condition one standard operationalized two different conditions, depending on which information is defined as being dominant. One of the two-stroke standards can be interpreted both as a 4.5 mm dominant stimulus with discrepant information in the second stroke and as a 6 mm dominant stimulus with discrepant info in the first stroke; for the other two-stroke standard it is vice versa. That is, the two-stroke conditions are operationalized by only two standard stimuli, either presented as first or second stimulus. Overall, the experiment consisted of 3640 Trials =  $(24 + 2)$  [standards] x 2 [stimulus order] x 14 [comparisons] x 5 [repetitions] divided into 5 sessions, each lasting about

2.5 – 3 hours. The first sessions started with a training of finger force and velocity similar to Exp. 2.

We determined individual psychometric functions for each standard and in each experimental condition. As in Experiment 2, we calculated weights of the discrepant stroke by taking into account the average PSEs measured in the control conditions of Experiment 2 and restricting individual weights to be within 2 standards deviations from the mean (22 outliers in 420 cases). The individual weights were analyzed by linear contrast analyses over positions separated by *Number of strokes* and *Stimulus order* conditions. We expected that weights for the discrepant stroke in the second stimulus, but not in the first stimulus, systematically decrease with *Position*.

**Table 2.1** Experiment 3: Overview of experimental conditions. Each condition was defined by the *Number of Strokes*, the *Stimulus order* and the *Position*.

Number of strokes	Stimulus order		Position of the discrepant stroke				
2	1	2	1	2			
3	1	2	1	2	3		
4	1	2	1	2	3	4	
5	1	2	1	2	3	4	5

## 2.4.5. Results

### 2.4.5.1. Movement parameters Velocity and Force

In order to check for potential confounds in weight assessment, we tested whether participants systematically varied exploratory force or velocity during the exploration of a stimulus. On average 95% of the movement data of each participant could be used for this analysis. For each *Number of strokes* condition we calculated a separate ANOVA with the within-participant variables *Stroke Position* and *Stimulus order*. We did not find any significant effect of stimulus order on movement force (2 strokes:  $F(1,14)=0.636$   $p=.438$ ; 3 strokes:  $F(1,14)=.811$   $p=.383$ ; 4 strokes:  $F(1,14)=.014$   $p=.907$ ; 5 strokes:  $F(1,14)=2.732$   $p=.121$ ; if necessary  $p$ -value corrected according to Greenhouse and Geisser, 1959) nor on movement velocity (2 strokes:  $F(1,14)=1.150$   $p=.241$ ; 3 strokes:  $F(1,14)=1.161$   $p=.694$ ; 4 strokes:  $F(1,14)=1.029$   $p=.328$ ; 5 strokes:  $F(1,14)=1.698$   $p=.214$ ). Also, there was no significant interaction Stroke Position X Stimulus Order (force: 2 str.:  $F(1,14)=1.902$ ,  $p=.190$ ; 3 str.:  $F(2,28)=2.839$ ,  $p=.113$ ; 4 str.:  $F(3,42)=0.653$ ,  $p=.472$ ; 5 str.:  $F(4,56)=1.211$ ,  $p=.312$ ; velocity: 2 str.:  $F(1,14)=.000$ ,  $p=.992$ ; 3 str.:  $F(2,28)=1.591$ ,  $p=.228$ ; 4 str.:  $F(3,42)=1.724$ ,  $p=.177$ ; 5 str.:  $F(4,56)=1.086$ ,  $p=.372$ ), indicating that differences between the first and the second stimulus in the pattern of stroke-specific weights cannot be due to movement variation.

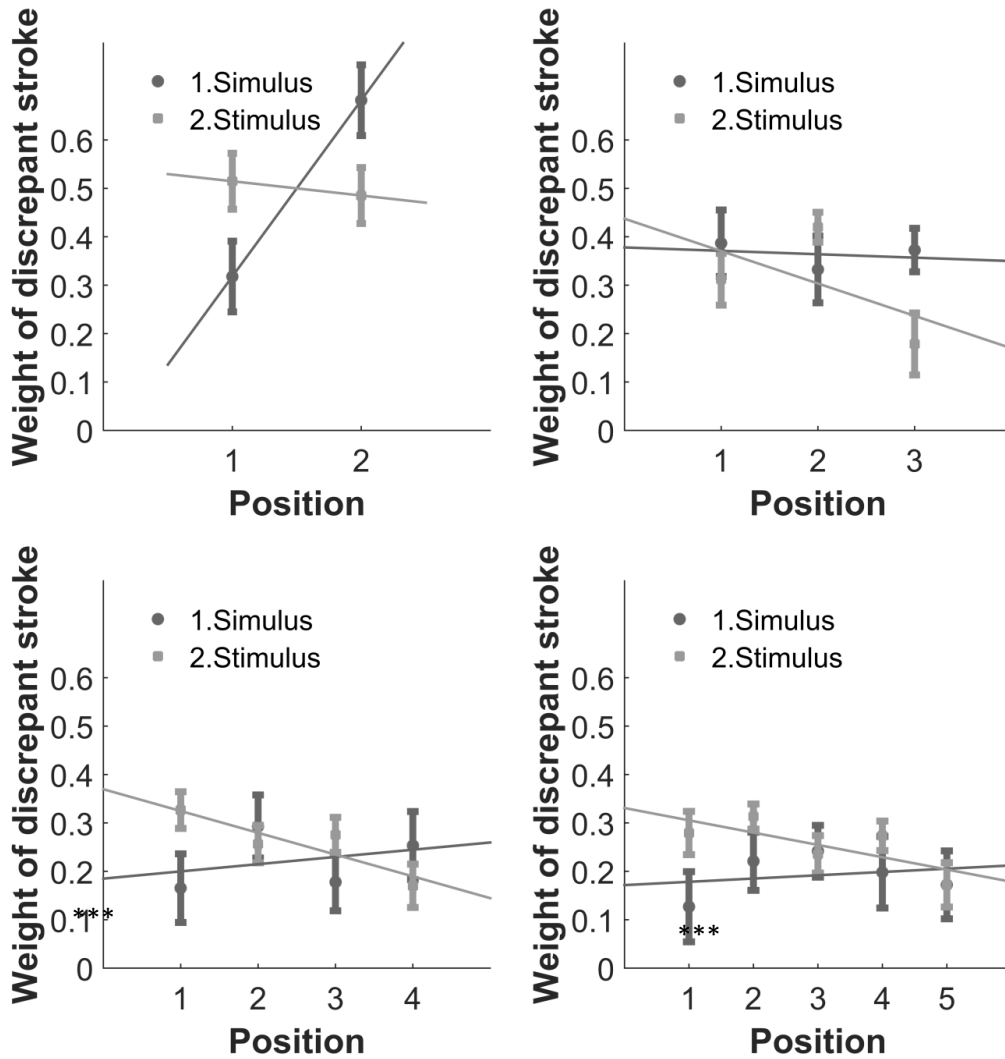
However, a main effect of position can be found for each Number of strokes for velocity (2 str.:  $F(1,14)=7.143$ ,  $p=.018$ ; 3 str.:  $F(2,28)=5.827$ ,  $p=.024$ ; 4 str.:  $F(3,42)=13.924$ ,  $p<.001$ ; 5 str.:  $F(4,56)=10.633$ ,  $p=.001$ ) and force (2 str.:  $F(1,14)=27.987$ ,  $p<.001$ ; 3 str.:  $F(2,28)=13.234$ ,  $p=.001$ ; 4 str.:  $F(3,42)=10.487$ ,  $p=.001$ ; 5 str.:  $F(4,56)=7.584$ ,  $p=.003$ ).

### 2.4.5.2. Weights of discrepant information

The detailed results of the linear contrast analyses of the individual weights can be seen in Table 2.2 and Figure 2.5. Analyses were two-tailed for the first stimulus and one-tailed for the second one, because we expected a position effect only for the second stimulus. As expected for the first stimulus we did not observe significant linear effects of position on the weights in most conditions, except for an increase in the two-stroke condition. For the second stimulus we observed the expected significant linear decrease of weights in the 4- and 5-stroke conditions, and for the 3-stroke condition we observed a corresponding trend. Taken together, these data replicate and extend the findings of Experiment 2. Both experiments offer support for the idea of a different processing for the first and the second stimulus.

**Table 2.2** Experiment 3: Linear trend analysis of the *Position* effect separately for each combination of *Number of strokes* and *Stimulus order* conditions

Number of strokes	Stimulus order Standard ...	<i>F</i>	df	<i>p</i>
2	first	6.213	1,14	.026
	second	0.065	1,14	.401
3	first	0.022	1,14	.885
	second	1.892	1,14	.096
4	first	0.281	1,14	.604
	second	4.642	1,14	.025
5	first	0.014	1,14	.909
	second	5.461	1,14	.018

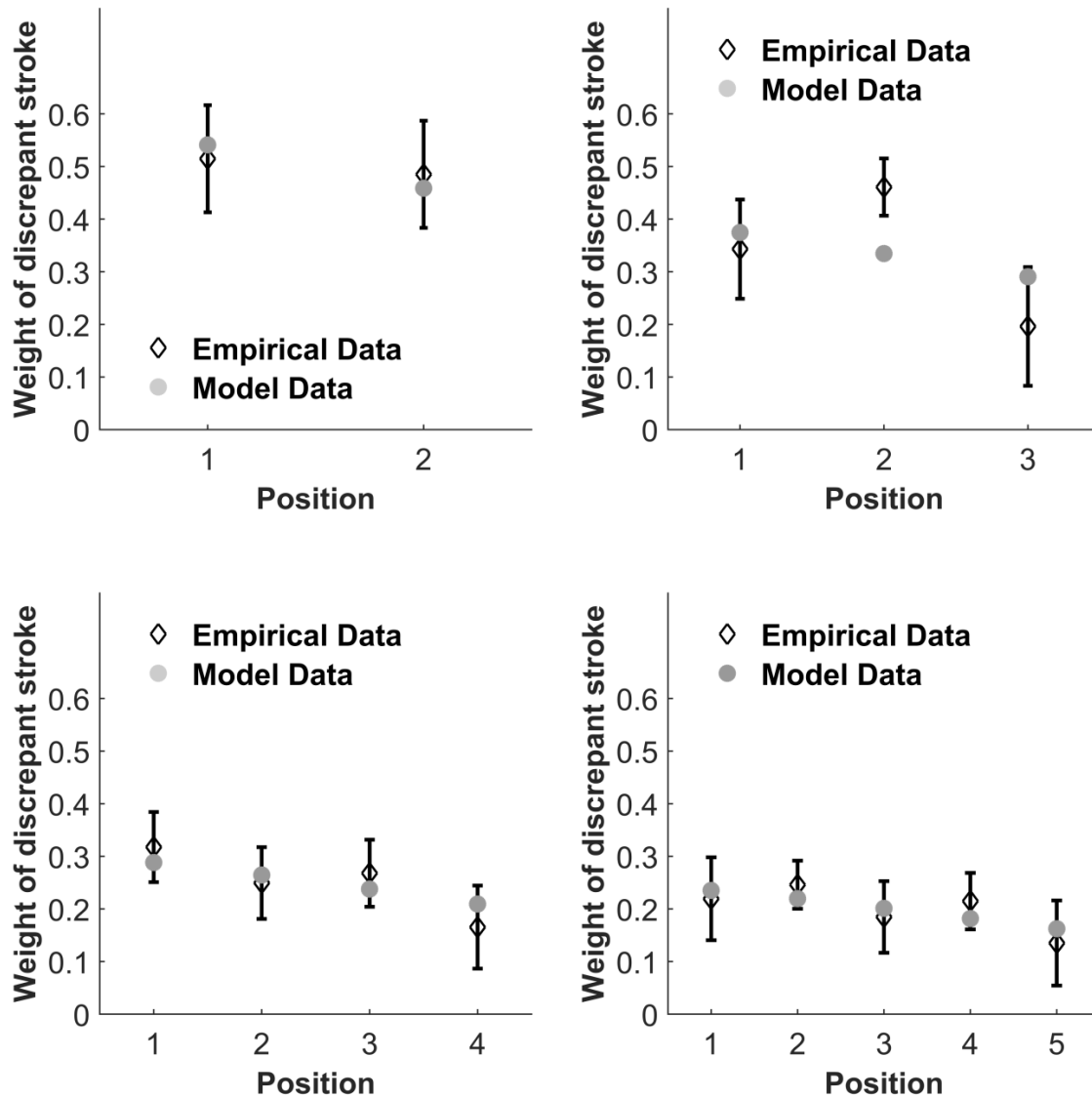


**Figure 2.5.** Exp.3: Average estimated weights of the discrepant stroke and standard error as a function of *Stimulus order* (first vs. second stimulus) and *Position* within the standard, plotted separately for all *Number of strokes* conditions.

#### 2.4.5.3. Model Data vs. Empirical Data

In Figure 2.6 we compare model predictions on the weights with empirical data for the second stimulus. For each combination of *Number of strokes* and *Position* conditions we calculate *t*-tests between the empirical weights and the predicted value. As is the case for the predicted weights, empirical weights were normalized for each *Number of strokes* separately so that averages across all positions sum up to a value of 1. For 13 out of 14 conditions the

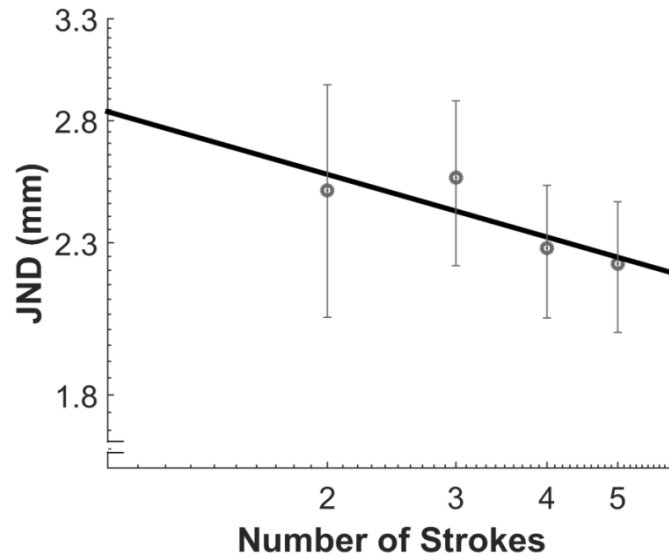
predicted and the measured weights did not differ significantly,  $t(14) \leq |1.374|$ ,  $p \geq .191$ . Only, in the second stroke of the 3-stroke conditions,  $t(14) = 3.722$ ,  $p = .002$ , the empirical weight was higher than expected. Predicted values explained  $r^2 = 0.83$  of the empirical variance between conditions,  $p < .001$ . Overall, empirical data followed model predictions.



**Figure 2.6.** Exp.3: Average empirical (plotted with 95%- confidence intervals) vs. predicted weights for the discrepant stroke in the second stimulus depending on its *Position* within the standard, plotted separately for all *Number of strokes* conditions.

#### 2.4.5.4. JNDs

We averaged the log-transformed (base 10) JNDs across all *Position* and *Stimulus order* conditions with the same number of strokes (Fig. 2.7). The log JND values decreased with an increasing number of strokes in a linear contrast analysis,  $F(1,14)=4.161$ ,  $p=.031$  (one-tailed). The regression of log JND on log *Number of strokes* explained  $r^2 = 0.72$  of the data. The slope of the regression line is  $-0.146$ . As in Experiment 1, this slope not in line with MLE predictions, in that it is significantly different from  $-.5$ ,  $t(14)=4.501$ ,  $p<0.001$ .



**Figure 2.7.** Exp.3: Log-log plot. Log average JNDs and standard errors as a function of log *Number of strokes* collapsed across all *Position* and *Stimulus order* conditions.

#### 2.4.6. Discussion Experiment 3

Experiment 3 replicated and extended the results of Experiment 2 by including different exploration lengths (*Number of strokes*) and comparing the results to model predictions. As in Experiment 2, we found evidence for a different processing of information from the first and the second stimulus. While stroke-specific estimates were rather equally weighted for all strokes



across the first stimulus, weights decreased with the position of the stroke in the second stimulus. Predictions from a Kalman filter model of a comparison process that is affected by memory decay fit the weight data well. The model has no free parameter; the rate of memory decay was estimated from a previous study (Murray et al., 1975). We conclude that in discrimination tasks on sequentially gathered information memory decay affects the comparison process.

## 2.5. General Discussion

The present study addressed the integration of redundant texture signals from sequentially sampled strokes. The integration of simultaneously presented, redundant signals had been successfully described by the MLE model of optimal integration. As expected, the present results show that the assumptions underlying this simple model do not describe the integration of sequentially presented texture information: The MLE assumptions predict a specific rate with which discrimination thresholds decrease with a prolonged exploration over the textures, and it predicts that equally reliable estimates should contribute equally to the percept. We found lower rates of threshold decrease as predicted by the MLE assumptions (Exp. 1 & 3) and unequal weights of estimates from different strokes (Exp. 2 & 3). However, the data can be well explained by an extended model of an optimal observer that we had derived from the literature (Romo et al., 2002; Romo & Salinas, 2003; Hernandez et al., 2010; Metzger et al., 2017; Kalman, 1962): We state that the two stimuli in a trial, when presented sequentially, are not processed in the same way. Information from the first stimulus is integrated in a MLE fashion (with equal weights) into a final estimate. We speculate that the final estimate is transferred to a different structure where it is stored in memory. This memorized estimate from the first stimulus gets noisier over time. Due to this circumstance, information from the second stimulus is

processed differently. For each exploration segment of the second stimulus, a comparison process between the overall first stimulus estimate and the segment-specific second stimulus estimate is performed. The model predicts that the information coming from different strokes of the first stimulus are integrated with equal weights, whereas segment-specific weights should systematically decrease over time for the second stimulus. –As, the comparison process is affected by memory decay and not the integration process, the empirical weights assessed for various exploration lengths are in line with this prediction (Exp. 2 & 3). A Bayesian-type Kalman filter model of the process, which uses a literature based rough estimation of the memory decay and has no free parameter, can quantitatively predict the weights assessed in Experiment 3. Taken together, our experiments help to better understand haptic integration of signals over time. Optimality, in the sense of seeking for the lowest variance of the final percept, is still the aim of our system. However, more complicated system properties, such as memory, need to be taken into account to describe sequential as compared to simultaneous integration processes.

Our result might be surprising given the fact that recent studies on visual perception did find hints for MLE integration of sequential information. For instance, Wolf and Schütz (2015) reported close to MLE-optimal trans-saccadic integration of information. The authors compared weights of presaccadic, peripheral and postsaccadic, foveal signals with predictions of the MLE model. One reason why MLE predicted integration might occur in this case, but not in our study, is the task itself. In the study by Wolf and Schütz (2015) participants had to indicate whether the vertical component of a plaid stimulus was tilted clockwise or counterclockwise. Thus, in contrast to comparing a memorized first stimulus to a sequentially experienced second stimulus, participants compared one sequentially experienced stimulus to a fixed reference. This task,

consequently, did not include memory transfer and storage of a representation of the reference's perceptual estimate, which possibly decays over time. These results may be similar to the integration of information in the first stimulus in a trial within our experiments. That is, the tasks in Wolf and Schütz' (2015) study required a single overall estimate of the stimulus, rather than comparing sequentially gathered information from a (second) stimulus to a memorized and therefore decaying reference.

Other studies do provide examples for perceptual optimization under conditions of memory decay. A recent study on the comparison between a memorized reference stimulus and a comparison stimulus showed that a Bayesian model that includes memory decay can explain the so-called contraction bias (Ashourian & Loewenstein, 2011). In a delayed comparison task, participants compared the visual length of two bars, the first of which was memorized. Participants tended to report the size of the memorized bar to be closer to the overall mean of the used sample of bars than the size of the second bar (= contraction bias). The authors suggest from their data a Bayesian model of optimal processing in that the sample of overall used bars provides a prior for the judgment on the memorized size of the first stimulus, and in that this prior gets weighted higher the more the memorized stimulus representation is affected by memory decay. Their conclusions are in good agreement with our model, in which memory decay is as well assumed to add variance to the memorized representation of the first stimulus. Similarly, in the field of color vision, Olkkonen, McCarthy, and Allred (2014) reported a central tendency bias in a delayed color estimation task, which was also modelled by a Bayesian model including memory decay. In a similar manner, Fassihi, Akrami, Esmaeili, and Diamond (2014) were able to explain performance of humans and rats in a tactile working memory task.

Taken together, it depends on the task, which factors need to be considered in order to achieve optimal perceptual estimates. For some tasks the assumptions underlying the MLE model are sufficient, however in sequential comparison tasks memory decay needs to be taken into account. Other factors may also play a role: Fisher and Whitney (2014) recently suggested that visual perception is ‘serially dependent’, in the sense that it uses both prior information and the present sensory input to inform perception at the present moment. Interestingly, the authors showed in their data that attention is able to modulate the impact of the prior information. Future research focussing on haptic sequential integration may hence also include attention as a potentially modifying factor.

Our proposed model of a comparison process that is affected by memory decay has interesting implications on how participants should ideally explore texture stimuli in a discrimination task, when they are less constrained in their exploratory behaviour. Yet Wismeijer, Erkelens, van Ee and Wexler (2010) described that sensory estimates as predicted by an optimal observer model can predict subsequent visual exploration movements. It has been argued that movements performed in free exploration are aimed to optimize the gathering of sensory information and to enhance task performance (e.g. Kaim & Drewing 2011, Lezkan, Metzger & Drewing, 2017). Given the proposed model, certain exploration strategies should lead to more precise discrimination than other strategies and therefore should be more preferentially performed by the observers. For instance, when participants are free to choose how often they stroke across each of two successively explored texture stimuli, the model would predict that more strokes are conducted across the first than across the second stimulus. The reason is that memory decay is assumed to take place only for the first stimulus estimate during the exploration of the second stimulus. As a consequence, benefit from additional strokes across the second

stimulus is counteracted by memory decay, but not benefit from additional strokes across the first stimulus. To give another example, in completely free exploration, participants might prefer to go back to the first stimulus, when its memory traces gets too noisy and frequent changes between the two stimuli can be expected. It would be interesting to address those points in further research.

It is further noteworthy, that in Experiment 2 the control conditions revealed considerable biases in the perception of the 4.5 mm period stimulus, when it was presented as the second one. As argued previously, we used the average measured values in the control conditions to calculate the weights of discrepant information and therefore the biases did not affect our predictions on the weights. However, here we ask why this bias might have occurred. Karim, Harris, Morley, and Breakspear (2012) described that when participants discriminate two vibrotactile stimuli they perform better when the first stimulus lies between the global mean of all stimuli and the second stimulus. This is known as the ‘time-order effect’ (e.g. Karim et al., 2012; Preuschhof, Schubert, Villringer, & Heekeren 2010). It was suggested that the reason for this observation is a ‘drift’ of neural responses for the first stimulus towards the global mean. We speculate that this effect in combination with a stimulus range effect causes the biases we observe in the control conditions. While we chose an equal spacing of periods between 2 mm and 8 mm, this could be a perceptually not completely symmetric space. If you assume that the standard with the 6 mm period is closer to the perceived global mean than the standard with 4.5 mm, ‘time-order’ effects might explain biases in the perception of the 4.5 mm standard. Interestingly, even this perceptual bias hints to the same conclusion we draw from our main results. That is, in a task of comparing two sequentially presented stimuli the first and the second stimulus are not processed in the same way.

## 2.6. Conclusion

This study asked the fundamental question of how information is integrated over time in the mainly sequentially working haptic sense. Our results show that spatio-temporal integration does take place within haptic perception. However, gains from this integration were lower than we predicted by an optimal integrator model (MLE), which is usually applied to the integration of simultaneously presented information. A closer investigation of the integration process revealed that the processing in our sequential task is likely to be more complex. The perceptual system we describe takes the loss of information due to memory decay into account and counterbalances such decay with weighting this information less over time. We suggest a Bayesian model to describe the perceptual process, which focuses on comparing the two stimuli online in order to produce the least noisy estimate of the difference between the two stimuli.

### 3. Integration of Serial Sensory Information in Haptic Perception of Softness

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Redundant estimates of an environmental property derived simultaneously from different senses or cues are typically integrated according to the maximum likelihood estimation model (MLE): Sensory estimates are weighted according to their reliabilities, maximizing the percept's reliability. Mechanisms underlying the integration of sequentially derived estimates from one sense are less clear. Here we investigate the integration of serially sampled redundant information in softness perception. We developed a method to manipulate haptically perceived softness of silicone rubber stimuli during bare-finger exploration. We then manipulated softness estimates derived from single movement segments (indentations) in a multisegmented exploration to assess their contributions to the overall percept. Participants explored two stimuli in sequence, using 2–5 indentations, and reported which stimulus felt softer. Estimates of the first stimulus's softness contributed to the judgments similarly, whereas for the second stimulus estimates from later compared to earlier indentations contributed less. In line with unequal weighting, the percept's reliability increased with increasing *exploration length* less than was predicted by the MLE model. This pattern of results is well explained by assuming that the representation of the first stimulus fades when the second stimulus is explored, which fits with a neurophysiological model of perceptual decisions (Deco, Rolls, & Romo, 2010).

### 3.1. Introduction

Perception is the process of estimating the properties of our environment. If there are redundant signals from an environmental property, meaning a signal is repeated (sequential redundancy), or there are simultaneous signals in different dimensions (simultaneous redundancy), the property can be better detected (Mulligan & Shaw, 1980; Shaw, 1982; Swets, Shipley, McKey, & Green, 1959; Swets & Birdsall, 1978). Consequently, perception of an environmental property is more reliable with repeated estimates or estimates derived from different senses or cues, as compared to when perception is based on a single estimate. For example, sequential viewing (e. g. Oostwoud Wijdenes, Marshall & Bays, 2015) or touching (e. g. Louw, Kappers & Koenderink, 2005) usually increases perceptual reliability. An object's position and its properties can be estimated more reliably using different senses simultaneously, e. g. when estimating the position of the hand from vision and proprioception (van Beers, Sittig & van der Gon, 1998) or the size of an object from vision and touch (Ernst & Banks, 2002). Also combining different cues from a single sense increases perceptual reliability e. g. estimating the slant of a plane from the texture gradient and the linear perspective (Oruc, Maloney & Landy, 2003).

The integration of redundant information is often modeled as maximum likelihood estimation (MLE, Ernst & Buelthoff, 2004): single estimates are integrated by linear weighted averaging with the weights being proportional to the single estimates' relative reliabilities (Cochran, 1937). Reliability is defined as the inverse of variance  $r = \sigma^{-2}$ .

$$\hat{S} = \sum_{i=1}^n w_i s_i, \text{ with } w_i = \frac{\sigma_i^{-2}}{\sum_{i=1}^n \sigma_i^{-2}}, w_i \geq 0 \text{ and } \sum_{i=1}^n w_i = 1 \quad (1)$$



$\hat{S}$  denotes the combined estimate (i.e., the percept),  $s_i$  the different single estimates,  $w_i$  their individual weights and  $n$  the number of available estimates. If the single estimates are independent Gaussian variables, the combined estimate would have the maximal possible reliability of

$$R_{\hat{S}} = \sum_{i=1}^n r_i. \quad (2)$$

Several studies on the integration of simultaneously available estimates (overview: Landy, Banks & Knill, 2011) support the MLE model for multisensory and cue integration in human perception (e. g. Alais & Burr, 2004; Ernst & Banks 2002; Fetsch, DeAngelis & Angelaki, 2010; Hartcher-O'Brien, Di Luca & Ernst, 2014; Helbig & Ernst, 2007; Hillis, Watt, Landy & Banks, 2004; Moscatelli et al. 2016). Nevertheless, there are also some reports of integration of simultaneous estimates, where perceptual reliability was not maximized or where weights could be changed by feedback without changing reliability (e.g. Cellini, Kaim & Drewing, 2013; Ernst, Banks, & Buelthoff, 2000; Jacobs & Fine, 1999; Rosas, Wagemans, Ernst & Wichmann, 2005; van Beers, van Mierlo, Smeets & Brenner, 2011). There is evidence that multisensory integration also depends on the exploration mode (visual and haptic both parallel or serial vs. visual parallel and haptic serial or vice versa, Plaisier, van Dam, Glowania & Ernst, 2014).

In contrast, studies investigating the mechanisms underlying the integration of sequential estimates from one sense do not yet reveal concordant models. For visual perception of color Oostwoud Wijdenes et al. (2015) found that pre- and postsaccadic estimates were integrated consistent with the MLE model with a higher weight given to the more reliable estimate (derived when the disc was closer to the fovea). Wolf and Schuetz (2015) showed that the orientation of a visually presented grating and the estimate's reliability could be predicted by the MLE model

from the reliabilities of estimates sequentially derived in the periphery and the fovea. Also in haptic perception sequential redundancy is exploited to increase reliability. For example, extended exploration or longer stimulus presentation decreased thresholds in haptic discrimination of surface orientation (Giachritsis, Wing and Lovell, 2009), or in the detection of sine-wave gratings and vibro-tactile stimuli (Gescheider, Bolanowski, Pope and Verrillo, 2002; Louw et al., 2005). However, Drewing, Lezkan and Ludwig (2011) showed for virtual sine-wave gratings that the gain of sequential redundancy was significantly lower than the gain predicted by the MLE model.

A Kalman filter (Bryson & Ho, 1975) could potentially be more appropriate than the MLE model to account for sequential integration of information. The Kalman filter is an optimal model for estimating the state of dynamic linear systems over time. It is a recursive algorithm estimating the current state of a system by combining the current measurement with prior information, maximizing the estimate's reliability. Within the Kalman filter framework sequential integration of sensory estimates can be considered as recursive combination of the current sensory estimate (measurement) with the information obtained from prior sensory estimates. The dynamics of a (one-dimensional) system are predicted in the Kalman filter by a transition function from the previously estimated state  $\hat{s}_{i-1}$  with the estimated noise  $\hat{\sigma}_{i-1}$  to a hypothetical current state:  $s_i = A\hat{s}_{i-1} + \varepsilon_p$  ( $\varepsilon_p$  being the process noise drawn from  $N[0, \sigma_p]$ ). This prediction is combined with the current measurement  $y_i = S + \varepsilon_m$  ( $\varepsilon_m$  being the measurement noise drawn from  $N[0, \sigma_m]$  and  $S$  the true state of the system) by weighted averaging to obtain a new state estimate:

$$\hat{s}_i = \frac{\sigma_m^{-2}}{A^{-2}\hat{\sigma}_{i-1}^{-2} + \sigma_p^{-2} + \sigma_m^{-2}} y_i + \frac{A^{-2}\hat{\sigma}_{i-1}^{-2} + \sigma_p^{-2}}{A^{-2}\hat{\sigma}_{i-1}^{-2} + \sigma_p^{-2} + \sigma_m^{-2}} A\hat{s}_{i-1}. \quad (3)$$

The updated reliability is then given by

$$r_i = r_{i-1} + r_m \text{ with } r_{i-1} = A^{-2} \hat{\sigma}_{i-1}^{-2} + \sigma_p^{-2} \text{ and } r_m = \sigma_m^{-2}. \quad (4)$$

Similar to the MLE model weights that maximize reliability are proportional to the relative reliabilities of the prior information and the measurement. In contrast to the MLE model, the Kalman filter also includes the process noise that influences the prior sensory information and it can be extended to model non-linear systems (Anderson, & Moore, 1979). The Kalman filter was shown to approximate well aspects of state estimation of dynamic systems in human visual perception and learning (e.g. Kwon, Tadin & Knill, 2015; Rao, 1999) and visuomotor behavior (e. g. Burge, Ernst & Banks, 2008; Koerding & Wolpert, 2004). However, sequential integration in the perception of a constant stimulus corresponds to the estimation of the state of a static system (constant state). For the estimation of the state  $S$  of an one-dimensional static system ( $A = 1$ ) with negligible process noise ( $\sigma_p \sim 0$ ),  $n$  iterations of the Kalman filter (Eqs. 3 & 4) result in an final estimate  $\hat{S}$  as given by Eq. 1 and a final reliability  $R_{\hat{S}}$  as given by Eq. 2 in the MLE model. Hence in this case, the estimate and its reliability obtained after  $n$  Kalman filter iterations are identical to the ones obtained from MLE integration of  $n$  estimates.

The question thus remains why and under which conditions in haptic perception sequential redundancy did not result in maximal possible reliability (Eq. 2). For discrimination of virtual gratings in extended exploration Drewing et al. (2011) had predicted maximal reliability under the assumption that the repeated estimates from one sense are equally weighted, because they are all gathered in the same manner and thus have similar reliability. The authors suggested that the observed lower reliability is associated with unequal weighting. Lezkan and Drewing (2014) hypothesized that memory decay might cause unequal weighting of sequential estimates. In haptic perception, the accumulation of sensory information spans longer times than in visual

perception. Due to memory decay, early estimates might become less reliable over time, so that they are weighted less. Lezkan and Drewing (2014) measured the contribution (weight) of every estimate to the discrimination of spatial frequency of two virtual sine-wave gratings (explored successively using 2-5 strokes, each stroke regarded to provide one estimate) by slightly changing spatial frequency during one stroke on the standard. Strokes' weights decreased monotonically as a function of their temporal distance to the comparison stimulus being highest around the time point when participants switched between the stimuli. The findings provide important first hints to the sequential integration during haptic perception: In contrast to simultaneous integration, estimates that were gathered with equal reliability were not equally weighted, and perceptual performance was correspondingly lower than predicted by the MLE model (Eq. 2).

However, the perceptual situation investigated in the study by Lezkan and Drewing (2014) might represent a highly specific case: Only virtual stimuli were used that were explored with a thimble connected to a force feedback device, thereby omitting several cutaneous cues, typically dominating haptic perception of softness (e.g. Bergmann Tiest & Kappers, 2009 for softness). Furthermore, participants could not explore the stimuli in a natural manner, because force and velocity were prescribed. These conditions differ considerably from everyday haptic perception, in that cutaneous information is highly relevant and exploration is hardly constrained. Hence the question arises, whether the results are representative for natural haptic perception. In the present study we investigated the integration of sequential sensory information in haptic perception for naturalistic conditions and stimuli, using softness perception as an example. We used real stimuli (silicon rubber) and constrained the stimulus' exploration only according to its length.

Softness refers to the perception of an object's compliance (ratio between displacement of the object's surface and the force applied to the object). Active exploration of softness usually involves successive manipulation of the object using a stereotypical movement classified as the *Exploratory Procedure of Pressure*, in which the object is repeatedly squeezed between the fingers or palpated with a finger or a tool (Lederman & Klatzky, 1987; Kaim & Drewing, 2011). Active haptic perception of an object's softness could thus be thought of as a multi-segmented exploration, where the movement segments refer to single indentations of the object. A single indentation comprises an increase of finger force up to a peak force, followed by a force decrease down to a local minimum, yielding a pattern of increasing and decreasing deformation of the object by the finger. We considered a single indentation as the basis of a single "indentation-specific" estimate of softness. The combined percept of softness would then be based on the integration of these multiple estimates.

Since in our experiment participant explored real stimuli, whose physical softness was given, we could not present a different stimulus for a single indentation as in Lezkan and Drewing (2014) to assess indentation-specific weights. We developed a paradigm to manipulate perceived softness of real deformable objects during the exploration with bare fingers (Experiment 1). We transmitted subtle external forces to the exploring finger of the participant (Figures 1 and 2) which pressed the finger more into the stimulus (pushing force) or pulled it away (pulling forces). External forces (proportional by factor  $\alpha$  to the forces participants applied themselves) changed perceived softness proportional to  $\alpha$ . Results from Experiment 1 have been presented in a conference article (Metzger & Drewing, 2015), where they were discussed in the context of the cutaneous and kinesthetic integration. We reconsider the results here, because they

are the basis for the following experiments: We used external forces to manipulate softness estimates from single indentations.

In four connected Experiments 2a-d, differing in the length of the exploration (2-5 indentations) we studied the integration of sequential softness estimates during multi-segmented exploration of deformable silicon rubber stimuli. We first investigated how perceptual reliability depends on the number of exploratory movement segments. We hypothesized that perceptual reliability would increase with an increasing number of indentations, but less than predicted by the MLE model (Eq. 2; cf. Drewing et al., 2011).

Second, we studied how estimates from single exploratory segments are weighted in perceived softness. Based on the findings of Lezkan and Drewing (2014), we expected to find the highest weights of indentation-specific estimates around the time point when participants switched between the stimuli in order to compare them, and that weights would decrease with increasing temporal distance to this time point. The MLE model predicts equal weights  $w_i$  for the integration of estimates gathered with equal reliabilities.

## **3.2. General Methods**

### **3.2.1. Participants**

Participants were right-handed (with the exception of one), naïve to the purpose of the experiments, volunteered to participate, and were reimbursed for their time. No participant reported sensory or motor impairments of the index finger of the dominant hand, which we confirmed by measuring a two-point discrimination threshold lower than 3 mm on this finger (Johnson & Phillips, 1981). In total 70 participants took part in the experiments; 10 participants were excluded from the analysis (six due to misdetection of indentations in more than 5% of

trials (see *Data analysis*, Experiments 2a-d); two due to repeated loss of connection between the finger and the force-feedback device during external force transmission); two due to reporting in the post-experimental survey that the restrictions imposed by our setup strongly impeded the exploratory behavior). The main characteristics of the final sample are listed in Table 3.1. More participants were recruited for Experiments 2c-d, because subtler effects in weights were expected with longer explorations. The study was approved by the local ethics committee LEK FB06 at Giessen University and was in line with the declaration of Helsinki from 1964. Written informed consent was obtained from each participant.

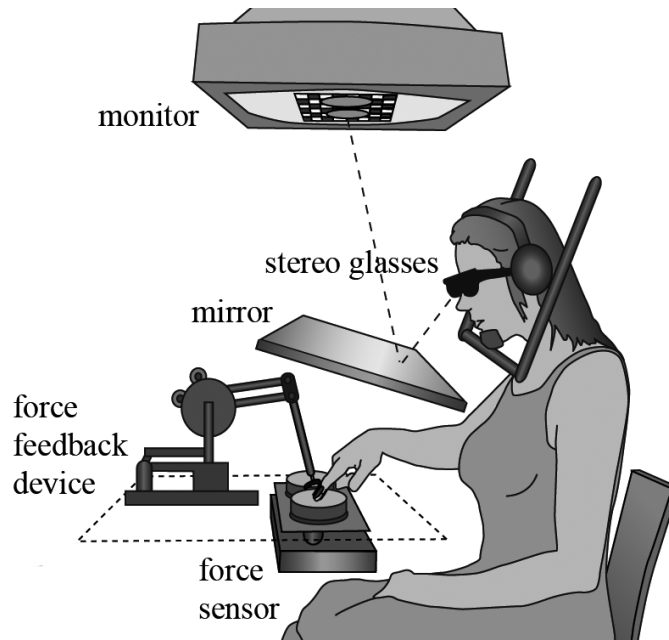
**Table 3.1** Main characteristics of the final sample.

Experiment	Participants	Mean age	Age range	Female/Male	Duration (h)
1, 1 indentation	10	23.8	19-29	4/6	5
2a, 2 indentations	10	24.3	19-27	6/4	2.5
2b, 3 indentations	8	26.9	21-32	4/4	4
2c, 4 indentations	13	24.5	21-29	9/4	5
2d, 5 indentations	19	25.3	21-35	12/7	6

### 3.2.2. Apparatus and Setup

The experiments were conducted at a visuo-haptic workbench (Fig. 3.1), which displayed haptic stimuli by a PHANToM 1.5A haptic force feedback device, and 3D visual stimuli using a 22"-computer screen (120 Hz, 1280x1024 pixel) viewed via stereo glasses indirectly through a mirror from 40 cm viewing distance. The mirror enabled spatial alignment of visual and haptic displays and prevented participants from seeing their hand when touching the stimuli. Force feedback was limited to the transmission of subtle external forces during the exploration of real

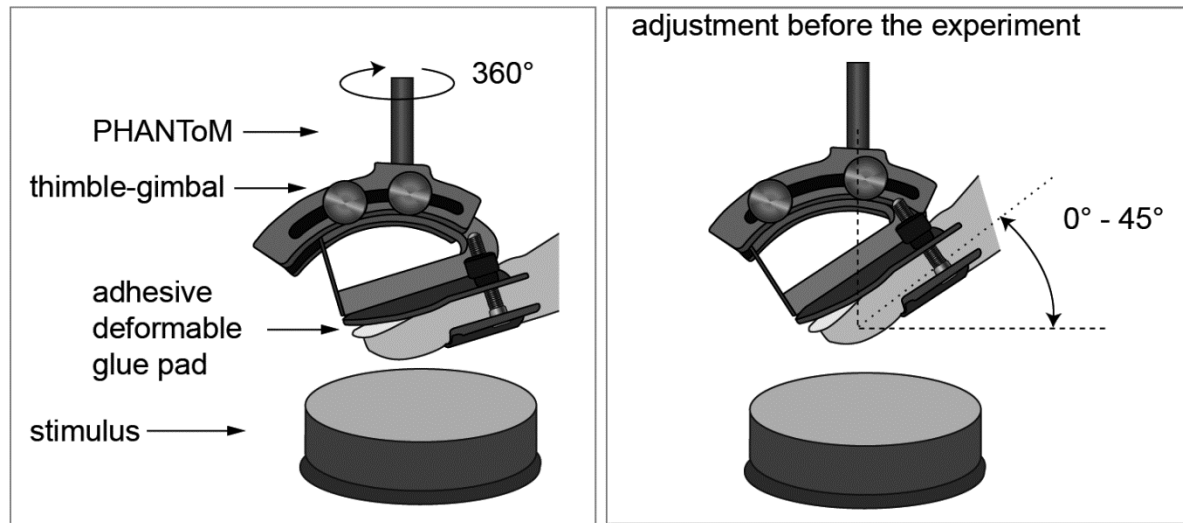
stimuli. Two rubber stimuli were placed side-by-side in front of the participants on a force sensor (produced by ME-Messsysteme GmbH) consisting of a bending beam load cell (LCB 130) and a measuring amplifier (GSV-2AS, resolution 0.05 N, temporal resolution 682 Hz) to record exerted forces. Participants touched the stimuli with the index finger of their dominant hand using a downward directed movement. The finger was connected to the PHANToM arm. The visual 3D scene comprised a schematic representation of the finger (sphere of 8 mm diameter) and the two stimuli. Visual information was used only to guide participants through the experiment. Importantly, no visual information about the finger movement and stimulus compliance was presented when the stimuli were touched (force > 0.1 N). The head was fixated by a chin rest.



**Figure 3.1.** Visuo-haptic workbench. Real stimuli were placed in front of the participant on the force sensor next to each other (distance 2 cm). A visual representation of the stimuli was displayed on the screen and viewed via stereo glasses. The head of the participant was stabilized by a head and a chin rest. The index finger of the dominant hand was connected via a custom-made adapter to the PHANToM, which was used to measure the position of the finger and to apply external forces during the exploration. White noise was presented via headphones to mask sounds from the motors of the PHANToM.



A custom-made gimbal-like adapter was used to connect the participant's index finger to the PHANToM (Fig. 3.2). It was designed to have no vertical degrees of freedom to ensure the transmission of forces and to allow (despite this restriction) natural and comfortable exploration of the stimuli. The adapter left the finger pad uncovered and was adjusted to the preferred inclination of the finger between  $0^\circ$  and  $45^\circ$  before the experiment, by rotating the main gimbal of the adapter, which was then fixed by two screws during the experiment. We used a circular design for the adapter to ensure that the direction of external forces as well as the calibrated zero-position of the PHANToM would not change with inclination. To exclude finger movement independent of the adapter, the dorsal side of the finger was affixed to the adapter by adhesive deformable glue pads (Pritt Multi-Fix). The weight of the adapter was counterbalanced with a constant upward force (0.2 N) produced by the PHANToM. While attached to the PHANToM participants were able to move freely in a  $38 \times 27 \times 20$  cm workspace.



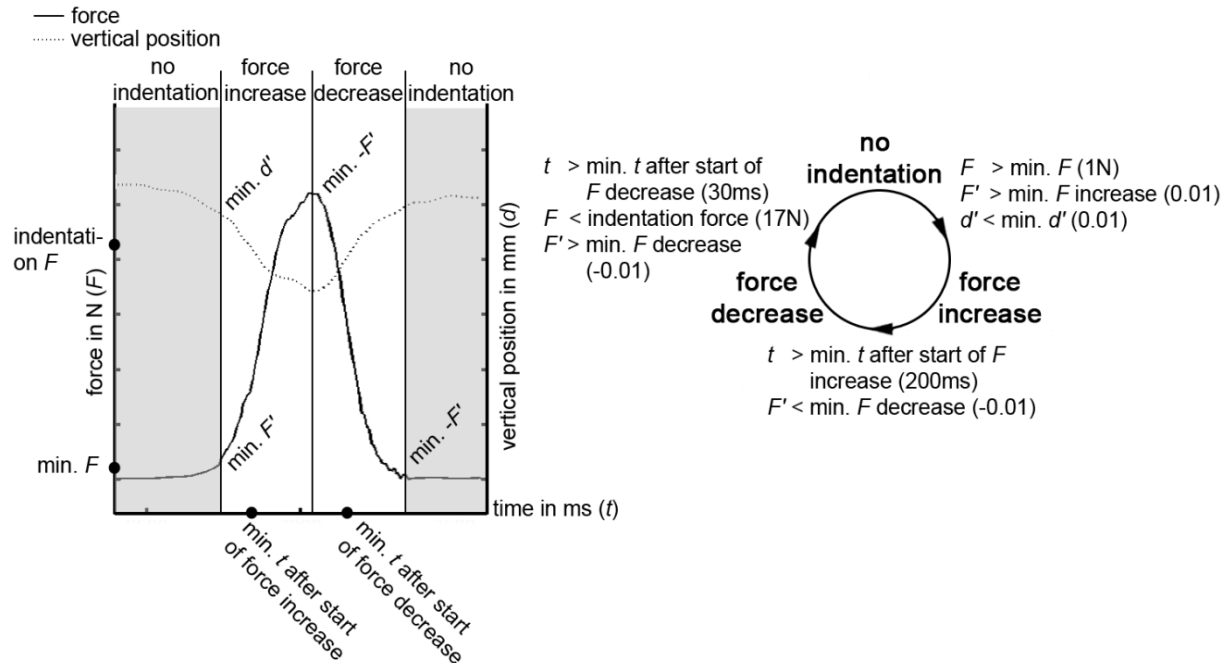
**Figure 3.2.** Adapter to connect the index finger of the participant to the PHANToM. The adapter was designed to leave the finger pad uncovered and to ensure the transmission of forces, by restricting the vertical degrees of freedom. Preferred vertical inclination between  $0^\circ$  to  $45^\circ$  was adjusted before the experiment. Due to a circular design the direction of the external force and the calibrated zero-position was unchanged by the adjustment. The adapter was additionally affixed to the dorsal side of the finger by adhesive deformable glue pads.

Via the adapter external forces were transmitted by the PHANToM to the index finger vertically, either pushing the finger into the stimulus orthogonal to the stimulus' surface or pulling it out of the stimulus. The amounts of external force were fixed fractions  $\alpha$  of the force applied by the participant. The total vertical force was measured every 3 ms with the force sensor. We calculated the force applied by the participant by subtracting the external force transmitted at the previous time point. To avoid amplification of noise produced by the force sensor (causing vibrations), external forces were calculated based on the force average from the last 15 ms. External forces were transmitted only during one indentation of the standard stimulus, i.e., in Experiment 1 during the single performed indentation and in Experiments 2a-d during one of the indentations.

The algorithm to detect and count the indentations was developed and trained using samples of trajectory data (force and vertical position) from free softness explorations (described in Lezkan & Drewing, 2015). The algorithm distinguished between three states in the temporal course of exploratory movements:

1. The state without indentation.
2. Force increase and downward directed vertical displacement.
3. Force decrease and upward directed vertical displacement.

These states alternated circularly as long as the participant explored the stimulus and were detected using different threshold combinations of time, force, vertical position, and derivatives of force and vertical position (Fig. 3.3). When a full cycle of these states was completed, one indentation was counted. The beginning of "force increase" marked the beginning of the indentation and the end of "force decrease" marked its end.



**Figure 3.3.** Detection of indentations. Depicted are the force (solid line) and vertical finger position (dotted line) during a single indentation of a stimulus in Exp. 1 as a function of time. The thresholds (absolute values and first derivatives) used to detect the indentation are symbolically indicated by black dots in the axes and by text inside the plot. The right part outlines schematically how these thresholds were used to distinguish the different states (min. = minimum/minimal). The states are depicted in bold font. The circle indicates in what order the states changed. Conditions for the change from one state to another are listed between the corresponding two states.

In the beginning of a trial the state was set to "no indentation". If a minimal force (1N, measured by the force sensor below the stimulus, Fig. 3.1) was reached and minimal increase in force (0.01) and decrease in vertical position (-0.01) were detected, the state changed to "force increase". If after a minimal time from the beginning of the indentation (200ms) the force minimally decreased again (-0.01), the state changed to "force decrease". Finally, if after the minimal time following the onset of "force decrease" (30ms) the force fell below 17N and stopped to decrease (force derivative  $> -0.01$ ), the indentation was considered to be terminated ("no indentation") and the next cycle could begin. The thresholds used by the algorithm were

optimized to produce less than 5% misses (absent or wrong detection of an indentation) as compared to careful visual inspection.

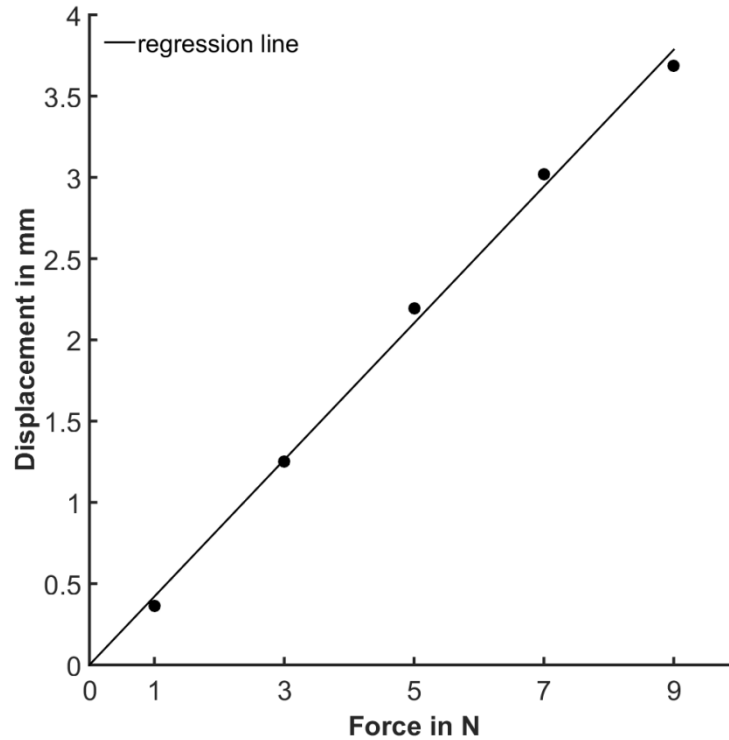
If the indentation was the one to be manipulated, transmission of external force started with the beginning of the indentation. To prevent sudden on- and offsets at the indentation' beginning and end the fraction of participants' forces used to calculate external forces linearly increased to  $\alpha$  or decreased to 0 (respectively) within 30 ms.

A custom-made software (C++) controlled the experiment, collected responses, and recorded finger positions and reaction forces. White noise presented via headphones masked possible sounds from the PHANTOM's engines when transmitting external forces.

### **3.2.3. Softness Stimuli**

The stimuli were made from two-component silicon rubber solution (AlpaSil EH 10:1), which was mixed with varying amounts of a diluent (polydimethylsiloxane, viscosity 50 mPa·s) to obtain different compliances. The solution was poured into cylindrical plastic dishes (75 mm diameter x 38 mm high) avoiding the formation of air pockets, to obtain flat surfaces without any discriminable differences in texture. After the stimuli were completely cured, compliance was measured using the experimental apparatus but replacing the finger-adapter at the PHANTOM arm by a flat-ended cylindrical probe of 1 cm<sup>2</sup> area ('standard finger'). The probe was repeatedly pressed into the stimulus using sufficiently high forces (15-25N), to warrant that enough data was sampled in the analyzed force range (0-9 N). The compliance was calculated as the slope of the regression line, fitted to the measured displacement-force traces (example plot in Fig. 3.4). For analysis we used only the trajectories caused by the increase of force, to exclude hysteresis effects during the decrease of force. Possible biases from non-uniform data sampling due to

manual indentation of the stimuli were reduced by calculating the mean displacement in 2N steps for bins of  $\pm 0.4$  N. For further details and discussion on the measurement method see Kaim and Drewing (2011).



**Figure 3.4.** Compliance measurement. A force-displacement function of an exemplar stimulus as used in our Experiments. The average displacements calculated for every 2N steps for bins of  $\pm 0.4$  N are plotted as black solid dots. The regression line with the slope corresponding to the compliance of the stimulus is plotted as a black line.

We produced two sets of rubber stimuli, each consisting of one standard and ten comparison stimuli. As standards we used one rather hard (0.32 mm/N) and the other rather soft (0.67 mm/N) stimulus. In each set half of the comparisons had increasingly lower and the other half increasingly higher compliance as compared to the standard. The compliance difference between two neighbored comparison stimuli was about 1/2 Weber fraction (0.03 mm/N step for the hard and 0.05 mm/N step for the soft set) and the range covered by the comparisons was about 2.5 Weber fractions in each direction. Different Weber fractions of about 20% and 15%

were used for the hard and the soft stimulus sets respectively (values taken from Kaim & Drewing, 2011). To reduce the traces of usage we produced each stimulus in two similar versions and alternated them. The compliance values of the stimuli are listed in Table 3.2.

**Table 3.2** Compliances of the silicone rubber stimuli.

Set	Compliance (mm/N)										
Hard	0.16	0.19	0.23	0.26	0.29	0.32	0.36	0.39	0.43	0.46	0.49
Soft	0.41	0.47	0.52	0.56	0.62	0.67	0.72	0.77	0.82	0.87	0.92

### 3.2.4. Design

#### 3.2.4.1. Experiment 1

The experimental design comprised two within-participant variables: *Compliance of Standard*  $c \in [0.32, 0.67] \frac{mm}{N}$  and the fraction of *External Force*  $\alpha \in [-.16, -.11, 0, .11, .16]$ , resulting in 10 conditions. We measured individual Points of Subjective Equality (PSE) of the manipulated standard stimulus as compared to non-manipulated comparison stimuli for each condition. For that purpose, we used a Two-Interval Forced Choice (2IFC) task combined with a 1-Up-1-Down staircase paradigm. We also estimated individual Just Noticeable Differences (JND) from fitted psychometric functions. In Experiment 1 each stimulus was indented once.

#### 3.2.4.2. Experiments 2a-d

The Experiments 2a-d differed by the *Exploration length*, as instructed by the number of indentations of each stimulus,  $N \in [2, 3, 4, 5]$ . The experimental design of each Experiment 2a-d

comprised the two within-participant variables *Number of Intervening Indentations* ( $0, \dots, N-1$ ) and the fraction of *External Force*  $\alpha \in [-.16, 0, .16]$ . The compliance of the standard was always  $c = 0.67$  mm/N. An external pulling or pushing force was applied during a single indentation of the standard stimulus or was not applied at all. We distinguished between different indentations by their distance to the exploration of the comparison stimulus, as expressed by the *Number of Intervening Indentations*. For example, when the standard was explored first the standard's last indentation had the minimum distance (0 intervening indentations) to the exploration of the comparison and when it was explored second, its first indentation had the minimum distance. The order in which the standard and the comparison were presented was balanced and randomized. Each Experiment 2a-d comprised  $2*N$  conditions with external forces and one baseline condition without. Again, we measured individual PSEs for each standard stimulus using a 2IFC softness discrimination task and a 1-Up-1-Down staircase paradigm. From the PSEs we calculated the weights of single indentation-specific estimates. To assess the gain of sequential redundancy we estimated for each Experiment 2a-d JNDs from fitted psychometric functions.

### 3.2.5. Procedure

There were up- and downwards directed staircases. In the first trial of the downwards directed staircase the standard was paired with the comparison stimulus of highest compliance in the set. The upwards directed staircase started with the comparison stimulus of lowest compliance. The comparison for trial  $j$  in a staircase depended on the participant's response in trial  $j-1$  of this staircase. If the comparison had felt softer (harder) than the standard, the next comparison in the staircase was less soft (hard). If the calculated comparison was out of the

range of the staircase, the same comparison was presented again in the next trial. The estimation of the PSE and JND by one staircase was considered terminated after 10 reversals (changes of direction in the staircase because participants changed their judgment from softer to harder and vice versa), which were reached on average after 18.43 trials ( $SD = 1.67$ ).

Each of the five experiments was split into two sessions, which were completed on two days within one week, except for Experiment 2a which was completed on the same day. In each session the estimation of the PSE and JND of each condition was completed by one upward and one downward directed staircase. There were thus in total four staircases, two per condition and session. Each session consisted of blocks in which the current step of each staircase was presented once in random order (number of trials = number of conditions\*2). Toward the end of the session, the number of trials in one block decreased, because staircases were increasingly terminating. The sessions were interspersed with pauses (1 min every 45 trials, about every 15 min). In the first session participants completed a practice session prior to the experiment consisting of 8 trials to familiarize them with the setup and the task. After the last session participants completed a survey in which they reported whether they noticed differences between the trials, which technique they used to compare the softness of the two stimuli, and how they experienced the experiment overall.

In the beginning of each trial the stimulus to be touched first (standard or comparison) was displayed on the computer screen (left or right). A tone presented via the headphones signaled the participant to start the exploration. Participants were instructed to touch each stimulus in its center, which was visually rendered as a cross on the stimulus representation. Depending on the design of each experiment (1, 2a-d) participants were instructed how many times to indent each stimulus. The standard and the comparison stimuli were always indented the



same number of times. As soon as the first stimulus was touched, the second stimulus appeared in the visual scene and after its exploration, participants reported which stimulus felt softer by moving their finger to one of the two virtual decision buttons displayed above the stimuli. They did not receive any feedback about the correctness of their response. If participants used more or less indentations than instructed, the trial was repeated later in the block. Between trials, participants moved their finger to an indicated position in the corner of the 3D-scene to wait until the experimenter had manually changed the stimuli. The position (left, right) of the standard was randomized by the computer program.

### 3.2.6. Data Analysis

#### 3.2.6.1. Psychometric Functions

In both Experiments 1 and 2a-d in order to assess PSEs and JNDs, we calculated for each participant, each condition and each comparison stimulus the percentage of trials in which it was perceived to be softer than the standard. These values, combined for all comparisons composed the individual psychometric data, to which we fitted cumulative Gaussian functions using the `psignifit4` toolbox (Schuett, Harmeling, Macke, & Wichmann, 2016). From the fitted psychometric functions, we estimated the PSE as the 50% discrimination threshold and the JNDs as the 84% discrimination threshold, corresponding to the standard deviation of the cumulative Gaussian function (Helbig & Ernst, 2007). The goodness of fit of the psychometric functions was assessed by comparing the measure of *deviance* ( $D$ ) to the critical  $\chi^2$  value for 10 comparisons,  $\chi^2_{10;95\%} = 18.31$  (Wichmann & Hill, 2001). *Deviance* is the log-likelihood ratio between the full model (one parameter for every observation) and the fitted model (achieved by maximum likelihood) - the smaller the *deviance*, the better the fit.

We estimated PSEs using psychometric functions instead of averaging over compliances at reversals, in order to eliminate the influence of trials in which the manipulation of force was not warranted and to be able to analyse the data separately for the cases that the standard was explored first or second. Estimates from both methods are highly correlated ( $R = 0.95$ ).

### 3.2.6.2. Experiment 1

We assumed that external forces (calculated as the fraction  $\alpha$  of force applied by participants) would proportionally increase (pushing forces,  $+\alpha$ ) or decrease (pulling forces,  $-\alpha$ ) perceived softness ( $\hat{c}_m$ ) as compared to perceived softness without external forces ( $\hat{c}_0$ ; Metzger & Drawing, 2015):

$$\hat{c}_m = (w_f \alpha + 1) \hat{c}_0 . \quad (5)$$

with  $w_f$  being the extent by which external forces are translated into a perceptual change. To calculate  $w_f$  we performed linear regressions of individual PSE shifts with external forces relative to the PSE without external force ( $\frac{\hat{c}_m - \hat{c}_0}{\hat{c}_0}$ ) on  $\alpha$ . According to Eq. (5) the relative PSE shift caused by external force is a linear function of  $\alpha$  (cf. Landy, Maloney, Johnston & Young, 1995):

$$\frac{\hat{c}_m - \hat{c}_0}{\hat{c}_0} = w_f \alpha . \quad (6)$$

with  $w_f$  being the slope. We expected the slope to be positive and used a one-tailed  $t$ -test to test this hypothesis. Two-sided  $t$ -tests were used to analyze the regression intercepts and to compare the regression parameters between the *Compliance of standard* conditions. To verify that external forces do not affect perceptual reliability, we additionally assessed individual JNDs for each *External Force* condition and performed a one-way repeated measures ANOVA.

### 3.2.6.3. Experiments 2a-d

In order to verify that the manipulation of perceived softness was successful in Experiments 2a-d, i.e., that external force was transmitted in the target segment and only in the target segment, force applied by the participant and external force were visually inspected for every trial. Trials in which the manipulation was not successful were excluded for the fit of psychometric functions (total of 0.9% trials). Participants for whom more than 5% of trials had to be excluded were excluded from the analysis.

To analyze perceptual reliability we assessed individual JNDs for each *Exploration length* (1-5 indentations, Experiments 1,2a-d), by averaging over the *External Force* conditions in both Experiments 1 and 2 and additionally over the *Number of Intervening Indentations* conditions in Experiments 2a-d. Individual JNDs were entered in a one-way ANOVA with the between participant factor *Exploration length*. To test whether perceptual reliability decreased with increasing length of the exploration, we performed a trend analysis using linear contrasts. We wanted to analyze whether the JNDs decreased as predicted by the MLE model. According to Eq. 2 integration of  $N$  statistically independent estimates with the same variance  $\sigma^2$  results in a variance of  $\frac{\sigma^2}{N}$  for the combined estimate, which predicts that the JNDs, which are proportional to  $\sqrt{\sigma^2}$  (Ernst & Banks, 2002), decrease with the number of indentations  $N$  by the factor of  $N^{-1/2}$  (Quick, 1974; Drewing et al., 2011). We log-transformed the JNDs and the total number of indentations in order to linearise the relationship, fitted a linear regression model to this data and compared the decrease in JNDs to the predicted decrease which corresponds to a slope of -0.5 in of the regression function.

In our experiments JNDs were estimated from psychometric data sampled with the 1-Up-1-Down staircase. Simulations show that JNDs are proportionally underestimated in similar cases (Leek, Hanna & Marshall, 1992). We replicated the simulation of Leek et al. (1992) for the estimation of JNDs with our 1-Up-1-Down staircase and found a small proportional bias of 12%. However, a proportional bias in the JND estimates might change the intercept but not the slope of the analyzed decrease of JNDs with the extension of the exploration, because we perform it on log-transformed data. Nevertheless, due to this proportional distortion caution is advised when generally comparing JNDs estimated from a 1-Up-1-Down staircase to JNDs estimated with more appropriate methods (e.g. constant stimuli).

For each condition in Experiments 2a-d we estimated individual PSEs. To confirm that the manipulation of perceived softness was successful, we entered the PSEs in ANOVAs with the within-participant factor fraction of *External Force*, separately for each Experiment 2a-d.

From the PSEs we calculated individual indentation-specific weights  $w_i$  for each indentation  $i$  and each *Exploration length* (2-5 indentations, Experiments 2a-d). We assumed that the overall percept (as assessed by the PSE) was the result of a weighted linear combination of indentation-specific estimates (Eq. 1) and that indentation-specific estimates of non-manipulated indentations equal the perceived softness without external force  $\hat{c}_0$ . According to the results of Experiment 1, external forces transmitted during the exploration, shifted perceived softness following Eq. (6). In a multi-segmented exploration, the manipulation of a single indentation  $i$  would then shift the overall percept  $\hat{c}_{mi}$  relatively to  $\hat{c}_0$  by:

$$\frac{\hat{c}_{mi} - \hat{c}_0}{\hat{c}_0} = w_i w_f \alpha . \quad (7)$$

To assess  $w_i w_f$  we performed a linear regression of the relative PSE shift  $\frac{\hat{c}_{mi} - \hat{c}_0}{\hat{c}_0}$  on  $\alpha. w_f$  (0.3) was estimated from the results of Experiment 1 as the average of the factors  $w_f$  for rather soft and rather hard stimuli.

To confirm that the weights sum up to 1 as predicted by Eq. (1) we performed a  $t$ -test on individual weight sums against one. To analyze whether the weights decreased with the *Number of Intervening Indentations*, we performed linear regressions of the weights on the number of intervening indentations, for each participant and exploration length and computed a  $t$ -test of individual slopes against 0.

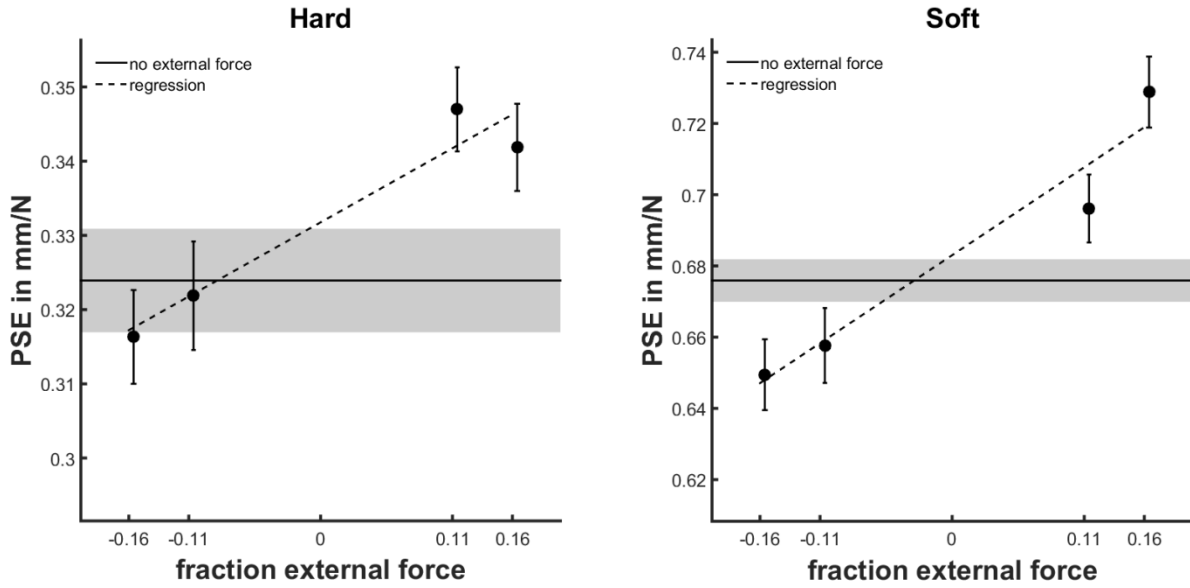
We additionally investigated whether the weight of each estimate depended on whether the stimulus was explored first or second. For this purpose, we estimated the PSEs, using only trials in which the standard was the first or the second stimulus (respectively) and repeated the analysis reported above. Additionally, we analyzed for each exploration length whether the pattern of weights differed between the first and the second stimulus (interaction *Number of Intervening Indentations X Presentation of the Standard* as first vs. as second stimulus in two-way ANOVA) and whether the decrease of weights with the number of intervening indentations depended on the length of the exploration (one-way ANOVA on the slopes of the weights with between-participant factor *Exploration Length*). We did this analysis only for the second stimulus, because only there we found a decrease of weights.

### 3.3. Experiment 1

#### 3.3.1. Results

Participants did not report in the surveys that they noticed any differences between the trials. Thus, it can be assumed that they were not aware of external forces. For all external force

conditions, we observed a shift in the PSEs in the predicted direction: to a softer percept with pushing external forces and to a harder percept with pulling external forces. In Figure 3.5, the PSEs with and without force manipulation are plotted as a function of  $\alpha$  (fraction of force participants applied themselves used to calculate external forces).



**Figure 3.5.** Average PSEs (black dots) with standard errors as a function of the fraction of external force separately for the soft and the hard standard. The average PSE without external forces is plotted as a solid black line. The respective standard error is indicated by the grey area. Additionally regression lines are plotted as black dotted lines.

The average regression slopes ( $w_f$ , Eq. 6) were significantly positive for both standards: hard:  $t(9) = 4.80$ ,  $p < .001$ ; soft:  $t(9) = 5.93$ ,  $p < .001$  (one-tailed tests). The intercepts were not significantly different from zero for both, the hard,  $t(9) = 1.18$ ,  $p = 0.268$  and the soft,  $t(9) = 0.95$ ,  $p = 0.365$  standards. The regression functions were  $\frac{\hat{c}_m - \hat{c}_0}{\hat{c}_0} = 0.28 * \alpha + 0.03$  for the hard standard and  $\frac{\hat{c}_m - \hat{c}_0}{\hat{c}_0} = 0.33 * \alpha + 0.01$  for the soft standard (dashed black lines in Fig. 3.5). Paired

$t$ -tests on individual slopes and intercepts showed no significant difference in the average slope,  $t(9) = -0.72$ ,  $p = .489^1$ , nor in the average intercept,  $t(9) = 0.74$ ,  $p = .476$ , between the hard and soft conditions.

The one-way repeated measures ANOVA on the JNDs did not reveal a significant effect of the within-participant factor *External Force*,  $F(4,36) = 0.22$ ,  $p = 0.928$ , indicating that external forces did not change perceptual reliability.

### 3.3.2. Discussion

Force feedback has been previously used for virtual and augmented softness (Biggs & Srinivasan, 2002; Jeon & Choi 2009, 2011). However, the effect of external forces had not yet been studied for the exploration of compliance stimuli with bare fingers. In Experiment 1, we showed that haptically perceived softness of deformable silicon rubber stimuli can be manipulated during the exploration with bare fingers. Perceived softness was changed by transmission of subtle external forces (calculated as a fraction of the forces  $\alpha$  participants exerted themselves). PSEs shifted as a linear function of  $\alpha$ . The same stimuli were judged to be softer when pushing forces were transmitted, and judged to be harder with pulling forces. We argued that the linear relationship between  $\alpha$  and the resulting PSE shift reflected the exclusive perturbation of the force estimate provided by the kinesthetic system and the efference copy (Metzger & Drewing, 2015). As kinesthetic afferent subsystem we subsume the receptors in the muscles and tendons and the efference copy of the motor command (Wolpert & Flanagan, 2001) whereas mechanoreceptors innervating the skin are referred to as the cutaneous afferent

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<sup>1</sup> Please note, average slopes were erroneously reported to be significantly different for the soft and the hard standard in Metzger & Drewing, 2015.

subsystem. It is likely that the kinesthetic force receptors and the efference copy only inform about self-produced forces (Jones, 1986). Hence, if assuming further that the kinesthetic and the cutaneous subsystem provide separate softness estimates which are integrated with constant weights (Eq. 1), the slope ( $w_f$ ) in the regression function (Eq. 6) corresponds to the weight of the kinesthetic estimate.

However, the impact of external forces might have been not as exclusive. The two estimates (cutaneous and kinesthetic) might not have been perfectly disentangled. For instance the change in contact area as sensed by the cutaneous afferent subsystem could have been also interpreted as displacement of the finger (Moscatelli et al, 2016). It is also possible that external forces triggered resistance forces (similar to resistance forces reported for the ocular system, Stark and Bridgeman, 1983), resulting in an additional efference copy, which would have reduced the impact of external forces on the kinesthetic estimate. Furthermore, averaging and ramping in the calculation of external forces (cf. *Apparatus and setup*) introduced small asynchronies and nonlinearities of external forces with respect to participants' forces possibly modulating the perceptual effect (cf. impact of delays in softness perception; Di Luca, Knoerlein, Ernst & Harders; Knoerlein, Di Luca & Harders, 2009; Leib, Karniel & Nisky, 2015; Pressman, Welty, Karniel & Mussa-Ivaldi, 2007). Here, we used the effect of external forces on perceived softness, and the average extent  $w_f$  (0.3, Eq. 6) to which  $\alpha$  is translated into a perceptual difference in order to study the integration of sequential information in Experiments 2a-d.

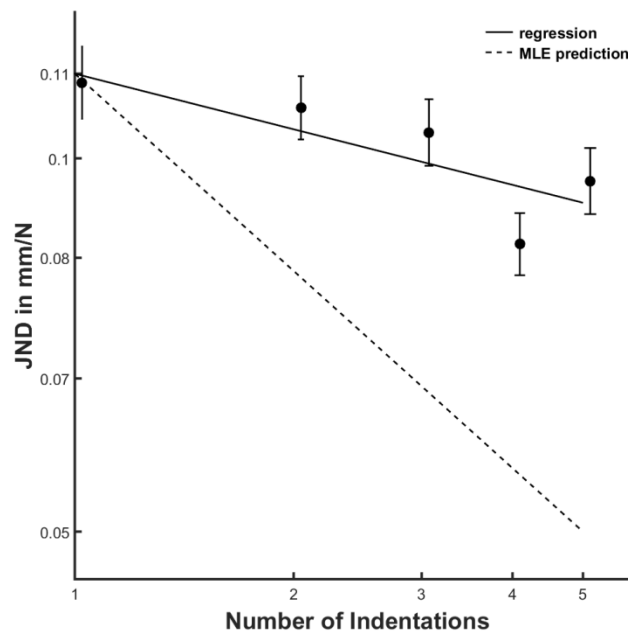
### **3.4. Experiments 2a-d**

#### **3.4.1. Results**



### 3.4.1.1. Psychometric Functions

Overall, the participants' responses were well fit by cumulative Gaussian functions: The *deviance* values were below the critical  $\chi^2_{10;95\%} = 18.31$  in more than 99% of all fitted psychometric functions. When splitting the data into the sets where the standard was explored as the first or as the second stimulus, the *deviance* values were still below the critical  $\chi^2$  values in more than 95% of the psychometric fits in these datasets.



**Figure 3.6.** Average JNDs and standard errors as a function of the Number of Indentations in Log-Log space. The regression line is plotted as a solid line and the dashed line indicates integration yielding maximal possible reliability.

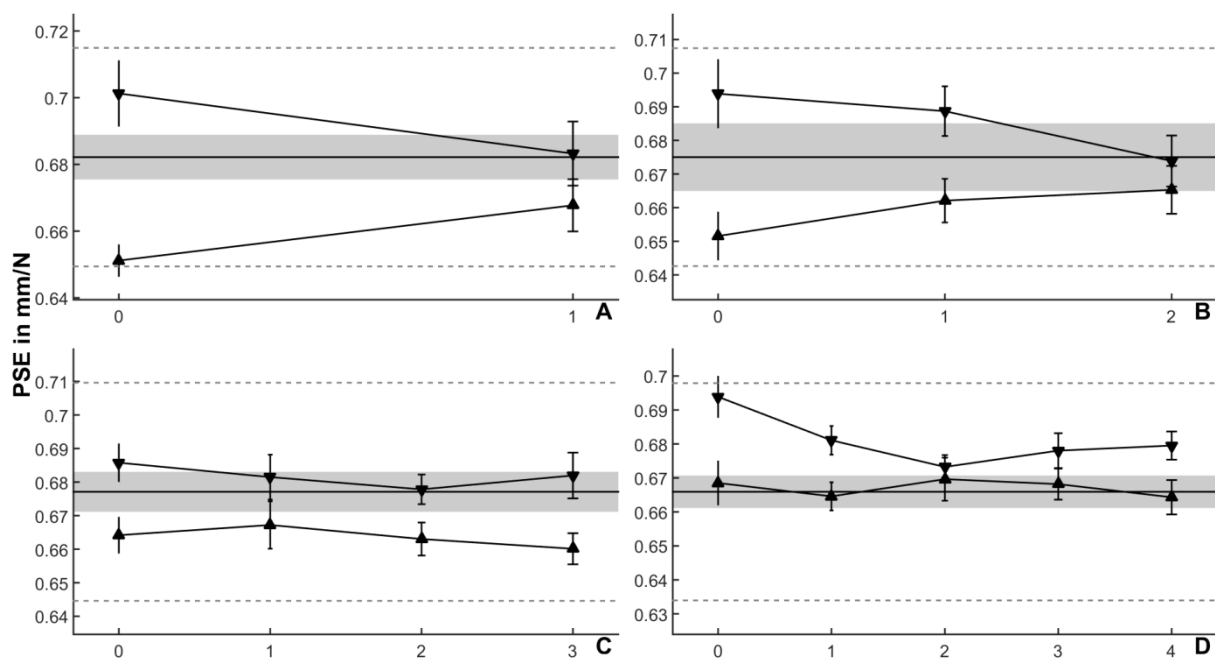
### 3.4.1.2. JNDs

The one-way ANOVA on the JNDs revealed a significant main effect of the between participant factor *Exploration length*,  $F(4,55) = 3.27$ ,  $p = 0.018$  and the trend analysis confirmed that the JNDs linearly decreased with an increasing number of indentations,  $F(1,55) = 7.89$ ,  $p = .007$  (Fig. 3.6). Averages and standard errors of logarithmized JNDs are plotted as a function of logarithmized exploration length (number of indentations) in Figure 3.6. The slope of the linear

regression function (solid line) was  $-0.141$ . The 95% confidence interval of the slope, ranging from  $-0.884$  to  $-0.048$ , did not include the value of  $-0.5$  predicted by the MLE (dotted line), indicating a shallower decrease of JNDs with increasing length of the exploration as compared to the prediction of the MLE.

### 3.4.1.3. PSEs

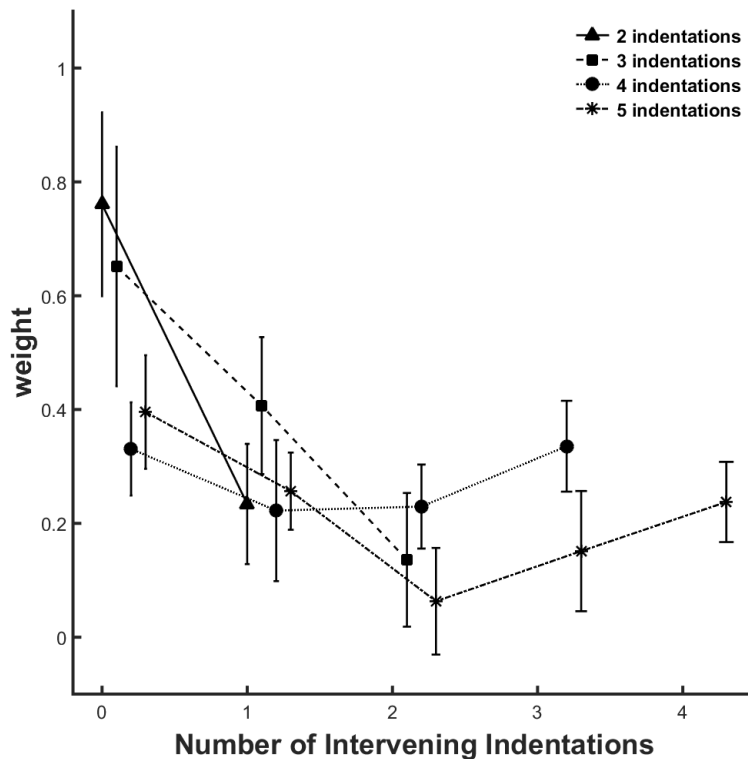
For each Experiment 2a-d average PSEs for each fraction of external force transmitted in each indentation are plotted in Figure 3.7. As expected from the results in Experiment 1 overall the pushing external force shifted the PSEs to a softer percept, and a pulling external force shifted it to a harder percept. The separate one-way ANOVAs revealed a significant main effect of *External Force* in all Experiments 2a-d (all  $p$ 's  $< .008$ ), indicating successful manipulation of perceived softness.



**Figure 3.7.** PSE-shift as a function of external force and the number of intervening indentations. The perceived softness is plotted separately for each Experiment 2a-d (exploration lengths of 2-5 indentations) as a function of the number of intervening indentations to the comparison. The mean values are plotted as black and individual measurements as grey triangles. Average and individual PSEs as well as the standard error are plotted for both external force conditions

(pushing force and pulling force, downward and upward pointing triangles respectively). For each length of the exploration average perceived softness in the condition without external forces is plotted as a solid line. The respective standard error is indicated by the grey area. Additionally, the two grey dotted lines indicate the two PSEs, which would result if the manipulation of one indentation would entirely determine perceived softness (maximal possible shift, according to the effect of manipulating a single-indentation exploration in Experiment 1). This value could have been reached if the softness estimate of one indentation would be weighted by 1.

#### 3.4.1.4. Weights

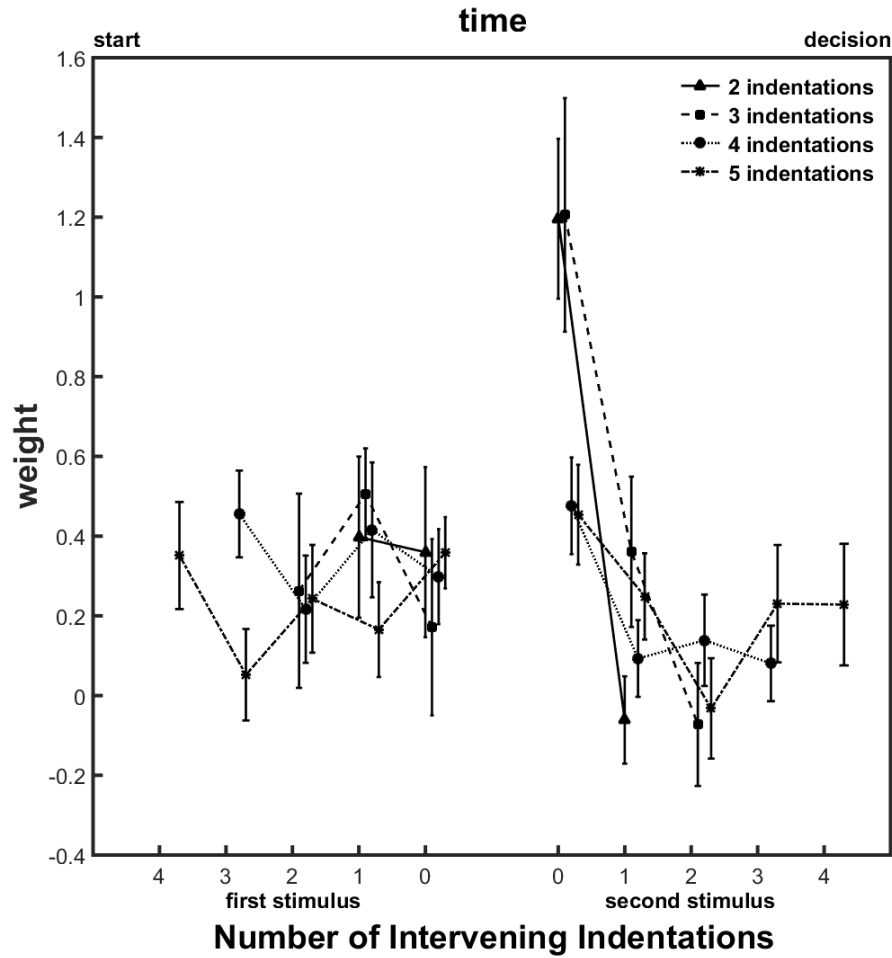


**Figure 3.8.** Weights of the estimates derived from single indentations as a function of their temporal distance to the comparison stimulus. The average weights of the estimates and their standard errors are plotted separately for each length of exploration.

The average weights are plotted as a function of the number of intervening indentations to the comparison, separately for each length of the exploration (Experiments 2a-d) in Figure 3.8. A  $t$ -test showed that (consistent with Eq. 1) for none of the exploratory lengths ( $N$ ) the average sum of the weights was significantly different from 1 (all  $p$ 's  $> 0.5$ ). The average slope of the regression of weights on the number of intervening indentations was significantly negative for

the exploration lengths of 2 indentations,  $t(9) = -4.96$ ,  $p < .001$  and 3 indentations,  $t(7) = -3.23$ ,  $p = .015$  but not for 4 indentations,  $t(12) = .06$ ,  $p = .95$  and 5 indentations,  $t(18) = -2.09$ ,  $p = .051$ .

In Figure 3.9 the weights of indentation-specific estimates are plotted separately for the first and the second stimulus. In both cases the sum of the weights was not significantly different from 1 for all exploration lengths (all  $p$ 's  $> 0.2$ ). The ANOVA on individual weights with the within-participant factors *Number of Intervening Indentations* and *Presentation of the Standard* (as first vs. as second stimulus) revealed a significant interaction for the exploration lengths of 2 indentations,  $F(1,9) = 36.07$ ,  $p < .001$ , 3 indentations,  $F(2,14) = 10.07$ ,  $p = .002$ , was at the edge of significance for 4 indentations,  $F(3,36) = 2.81$ ,  $p = .053$  and not significant for 5 indentations,  $F(4,72) = 1.06$ ,  $p = .385$ , indicating differences between the first and the second stimulus in the pattern of weights for the shorter exploration lengths. When the standard was explored first the slopes of linear regressions of the weights on the *Number of Intervening Indentations* were not significantly different from 0 for all exploration lengths: 2 indentations,  $t(9) = 0.23$ ,  $p = .820$ ; 3 indentations,  $t(7) = 1.19$ ,  $p = .274$ ; 4 indentations,  $t(12) = 0.84$ ,  $p = .417$ ; 5 indentations:  $t(18) = -0.35$ ,  $p = .733$ . When the standard was explored as the second stimulus, the slopes were significantly negative for 2 indentations,  $t(9) = -9.35$ ,  $p < .001$ , 3 indentations,  $t(7) = -4.53$ ,  $p = .0003$ , and 4 indentations  $t(12) = -3.03$ ,  $p = .010$  but not for 5 indentations  $t(18) = -1.22$ ,  $p = .240$ . A one-way ANOVA on the slopes of the weights in the exploration of the second stimulus with the *Exploration length* as the between-participant factor revealed that the slopes were affected by the *Exploration length*,  $F(3,46) = 49.65$ ,  $p < .001$ . A trend analysis showed that the slopes increased with the decreasing exploration length,  $F(1,46) = 134.48$ ,  $p < .001$ .



**Figure 3.9.** The weights of the estimates from single indentations on the first and the second stimulus separately as a function of their distance to the comparison stimulus and time. The average weights of estimates from single indentations of the first and the second stimulus and their standard errors are plotted separately for each length of the exploration. Time is depicted in arbitrary units.

### 3.4.2. Discussion

As predicted, JNDs in softness discrimination decreased with an increasing length of the exploration. This finding demonstrates that participants were able to increase perceptual reliability by accumulating information about softness over time, and is in concordance with earlier reported redundancy gains as a result of spatiotemporal extension of the exploration (Drewing et al., 2011; Giachritsis et al., 2009; Lezkan & Drewing, 2014; Louw et al., 2005).

Also as expected, the decrease in the JNDs with increasing exploration length was significantly smaller than would have been predicted by the MLE model ( $N^{0.14}$  vs.  $N^{0.5}$  for  $N$  indentations). Drewing et al. (2011) and Lezkan and Drewing (2014) found similarly flat decreases of JNDs ( $N^{0.12}$ ,  $N^{0.15}$ ) with increasing length of the exploration of virtual gratings. Hence, we can extend the conclusion that the integration of sequential information in haptic perception does not follow the MLE model, to a naturalistic task.

To approach the question, why sequential information was not integrated according to the MLE model, we assessed the weights of softness estimates derived from single exploratory segments (i.e., indentations). In agreement with previous observations on the perception of virtual gratings (Lezkan & Drewing, 2014), we found that the weights of indentation-specific estimates decreased significantly as a function of the indentation's distance to the comparison - at least for the short explorations comprising 2-3 indentations. Distinguishing between the indentation-specific weights on the first and the second stimulus in the 2IFC task, we found that the estimates from indentations of the first stimulus were weighted approximately equal, and that only the estimates gathered during the exploration of the second stimulus were weighted unequally, decreasing with increasing distance to the comparison stimulus (significant for explorations comprising 2-4 indentations). We did not find a significant decrease in weights over time for the exploration of the second stimulus comprising 5 indentations. Smaller effects in weights were expected with an increasing number of indentations (weights sum to 1), thus the differences between the weights might have been too small to be measured. We conclude that in the natural integration of sequential haptic information, softness estimates from different movement segments of the exploration of the second stimulus are unequally weighted, at least for explorations comprising less than 5 indentations.

The question arises why observers did not use all of the information provided by the repeated exploration of the stimulus. Estimates with correlated noises do not provide as much information as statistically independent estimates (Oruc et al., 2003). However, correlations between signal estimates do not predict that estimates with similar reliabilities are integrated with unequal weights, as we find for the integration of information on the second stimulus' softness.

Unequal weights of estimates derived in the same sense on the same environmental quality by repeated exploration (comparable in length to a typical haptic exploration [ $\sim 2$ s]) were also observed in several studies on summary statistics (review: Hubert-Wallander & Boynton, 2015), which addressed the ability of humans to estimate the mean value of serially presented visual cues (e.g. mean size of a dot that changed size over time). Some of these studies observed so-called *recency effects* (late information is weighted higher; Cheadle et al., 2014; Toscani, Zdravković & Gegenfurtner, 2016) others observed *primacy effects* (early information is weighted higher; Drugowitsch, Moreno-Bote, Churchland, Shadlen & Pouget, 2012). Whereas recency effects cannot explain the pattern of our results, a primacy effect could be responsible for higher weights of early estimates of the second stimulus' softness.

For primacy effects it is hypothesized that early information is weighted higher, due to increasing costs of sampling and processing of information. In our experiments participants were instructed to indent each stimulus a fixed number of times. It is possible that in order to reduce the costs and effort of sampling and processing, participants had decided which stimulus felt softer before the end of the exploration of the second stimulus. At the same time, it is a feasible assumption that resources were not saved during the exploration of the first stimulus, because the difficulty of the decision was unknown at this time point. From such a strategy, equal weights

during the exploration of the first stimulus and a decrease of weights during the exploration of the second stimulus over time might be explained. However, this explanation does not fit with observations on the muscular effort that participants spend over the time course of the exploration: participants significantly increased peak force in their last indentation as compared to all previous indentations of the first  $t(49) = -9.14, p < .001$ , as well as the second stimulus,  $t(49) = -4.76, p < .001$  (paired  $t$ -tests comparisons of peak forces averaged over indentations  $1, \dots, n-1$  and peak forces in the  $n$ -th indentation).

As already outlined, in the introduction for the integration of information over time a Kalman-filter approach might be more appropriate than the MLE. Remember, that for the estimation of a static variable the Kalman-filter approach yields the same estimate and the same reliability as the MLE model, if the process noise is negligible. However, unequal weights of estimates could be expected in our experiment if the process noise were large. According to Eq. (3) high process noise would bias the estimate towards the current sensory measurement in every iteration. In our experiment where we manipulated always one of the estimates this would result in higher weights if the manipulated estimate was acquired later in the exploration. However, we instead observed a decrease of weights towards the end of the exploration and only in the exploration of the second stimulus. Thus, high process noise cannot explain the pattern of weights we found in our experiment.

Given different patterns of weights of indentation-specific estimates of the first and the second stimulus, it might be assumed that there are different underlying mechanisms in information processing for these two stimuli. There is indeed an important difference - participants could compare the softness of both stimuli only when they explored the second stimulus. Deciding which stimulus is softer requires them to keep the perceived softness of the



first stimulus in memory while they explore the second stimulus. Romo, Hernández and Zainos (2004) studied the neural correlates of such perceptual decisions. Monkeys were trained to compare two vibrotactile stimuli with frequencies  $f1$  and  $f2$ , which were sequentially presented to the fingertips, and to report which stimulus had higher frequency. The authors recorded single neurons in the ventral premotor cortex (VPC).

The VPC receives input from the sensory areas and sends projections to motor areas (Godschalk, Lemon, Kuypers & Ronday, 1984; Matelli, Camarda, Glickstein & Rizzolatti, 1986; Luppino, Murata, Govoni & Matelli, 1999; Lu, Preston & Strick, 1994). Its neurons exhibit both sensory (Rizzolatti & Luppino, 2001; Graziano, Hu & Gross, 1997; Graziano, Reiss & Gross, 1999) and motor (Gentilucci, Fogassi, Luppino, Matelli, Camarda & Rizzolatti, 1988) related response properties, and inactivation of VPC impairs sensorimotor tasks (Fogassi, Gallese, Buccino, Craighero, Fadiga & Rizzolatti, 2001). Therefore, the VPC is thought to likely be involved in the mechanisms that link sensory events with actions (Romo et al., 2004).

Romo et al. (2004) found neurons in the VPC which encoded  $f2$  and two other populations representing the decisions  $f1 < f2$  and  $f1 > f2$ . Yet other neurons which the authors labeled "partially differential neurons", encoded  $f1$  during the presentation of the first stimulus and were modulated by  $f2$  afterwards. However, there were no neurons coding  $f1$  during the presentation of the second stimulus. The question arose how the difference between the frequencies of the two stimuli was computed.

On the basis of this work, Deco et al. (2010) suggested a synaptic mechanism to model the activity of the "partially differential neurons" and their role in decision making. They proposed that the memory of  $f1$  is realized by short-term synaptic facilitation of the "partially differential neurons". The phenomenological model of short-term synaptic facilitation is based

on residual calcium accumulated during the firing of the cells increasing the probability of transmitter release (Mongillo, Barak & Tsodyks, 2008). This means that as long as  $f1$  is presented, recurrent connections between the selective neurons are strengthened. When  $f2$  is presented, the activity of these selective neurons depends on the synaptic history and on  $f2$ . Deco et al. (2010) proposed that the activity of these neurons might represent the sum of  $f1$  and  $f2$ , from which the difference between  $f1$  and  $f2$  can be read out by comparing it with the activity of neurons representing  $f2$ . This difference might then be the input to a standard attractor based-decision-making network comprising competing neuronal populations representing the decisions  $f1 < f2$  and  $f1 > f2$ .

Our observations on information processing in a comparison of haptic softness fit well with the model of perceptual decision making proposed by Deco et al. (2010). If we assume that for softness discrimination there are "partially differential neurons" in the VPC or an analogous area, they would encode the softness of the first stimulus  $c1$  during its presentation. Our results suggest that in this case, the gathered information equally contributes to the overall percept. This might be implemented by e. g. computing the mean over the activity of neurons in lower areas, which show a tuning to certain softness values (possible model in Knudsen, Lac & Esterly, 1987; Metzger & Drewing, 2016). When the second stimulus with softness  $c2$  is presented, the "partially differential neurons" would reflect the sum of  $c1$  and  $c2$  which would be compared to the activity of the neurons encoding  $c2$ . Since the short-term memory of  $c1$  is implemented by synaptic properties of "partially differential neurons", it decays over time. Accordingly, the estimates from the indentations in the beginning of the exploration of the second stimulus would be weighted higher, because they can reliably be compared to the estimated softness of the first stimulus. Furthermore, also the observation that weights decreased less rapidly in a longer

exploration is consistent with the synaptic model of perceptual decisions. If the memory of  $cI$  is implemented as calcium based synaptic facilitation of the "partially differential neurons", it could be expected that in a certain range, longer explorations facilitate the neurons more than shorter ones (Deco et al., 2010; Mongillo et al., 2008). Thus the decay of the memory of  $cI$  after the exploration of the first stimulus is more rapid the shorter the exploration.

Taken together, the model of perceptual decision making by Deco et al. (2010) can well explain the observed pattern of unequal weights during softness discrimination. We correspondingly suggest that our observation of sequential integration with unequal weighting leads back to the the decay of the representation of the softness of the first stimulus in memory, which is stronger the longer the stimulus is explored.

### 3.5. General Discussion and Conclusions

In the present study we showed that haptically perceived softness can be manipulated using subtle external forces. The value of perceived softness can be shifted to softer or to harder percepts by pushing or pulling forces. For the multi-segmented exploration of softness, we found that the redundant information is not being exploited according to the MLE model. Unequal weights of indentation-specific estimates of the second stimulus are most likely the reason for the lower reliability gain than predicted by the MLE. The results are well explained by a model of synaptic dynamics in a perceptual decision task (Deco et al., 2010), that attributes our findings to decay of the memory about the first stimulus during the discrimination task. Noise introduced by memory effects is considered neither in the MLE nor in the Kalman filter model. These models in their simplest form assume constant measurement noise (Eq. 1 and 3), which might change over time. However, in an extended Kalman filter model further assumptions on the sources of

noise e.g. memory decay could be included to model the integration of estimates of the second stimulus' softness. For this purpose it is necessary to determine the relevant factors influencing memory decay (e.g. does it progress with time or with acquisition of information about the second stimulus?). Our results further indicate that also decision making processes might be involved in this kind of information integration, so a combination of an information integration model (e.g. MLE/Kalman filter) with decision making demands might be required. Such model of the integration of serially sampled information might then represent a theoretically optimal integration in the sense of exploiting *actually* available information in a decision making task.

## **4. Active Haptic Exploration of Softness: Indentation Force is Systematically Related to Prediction, Sensation and Motivation**

*A similar version of this manuscript is currently under review (after second revision):*

*Lezkan, A., Metzger, A., & Drewing, K. (under review). Active haptic exploration of softness: indentation force is systematically related to prediction, sensation and motivation. Frontiers in Integrative Neuroscience.*

Active finger movements play a crucial role in natural haptic perception. For the perception of different haptic properties people use different well-chosen movement schemes (Lederman & Klatzky, 1987). The haptic property of softness is stereotypically judged by repeatedly pressing one's finger against an objects' surface, actively indenting the object. It has been shown that people adjust the peak indentation forces of their pressing movements to the expected stimulus' softness in order to improve perception (Kaim & Drewing, 2011). Here, we aim to clarify the mechanisms underlying such adjustments. We disentangle how people modulate executed peak indentation forces depending on predictive versus sensory signals to softness, and investigate the influence of the participants' motivational state on movement adjustments. In Experiment 1, participants performed a 2AFC softness discrimination task for stimulus pairs from one of four softness categories. We manipulated the predictability of the softness category. Either all stimuli of the same category were presented in a blocked fashion, which allowed predicting the softness category of the upcoming pair (predictive signals high), or stimuli from different categories were randomly intermixed, which made prediction impossible (predictive signals low). Sensory signals to softness category of the two stimuli in a pair are gathered during exploration. We contrasted the first indentation (sensory signals low) and last

indentation (sensory signals high) in order to examine the effect of sensory signals. The results demonstrate that participants systematically apply lower forces when softer objects (as compared to harder objects) are indicated by predictive signals. Notably, sensory signals seemed to be not as relevant as predictive signals. However, in Experiment 2, we manipulated participant motivation by introducing rewards for good performance, and showed that the use of sensory information for movement adjustments can be fostered by high motivation. Overall, the present study demonstrates that exploratory movements are adjusted to the actual perceptual situation and that in the process of fine-tuning, closed- and open-loop mechanisms interact, with varying contributions depending on the observer's motivation.

#### **4.1. Introduction**

Hand movements are a fundamental part of haptic perception. In a natural exploration process, haptic sensations are generated by active hand movements (Gibson, 1962). The way people naturally move their hands depends on what object property they are interested in (Lederman & Klatzky, 1987). Imagine two possible situations: First, you want to test how ripe a mango is. Second, you want to know whether a blouse is made out of silk. In order to explore in these two situations you would probably apply two fundamentally different movements. The ripeness of a mango is probably best judged by its softness. Softness is a central dimension in haptic perception (Bergman Tiest & Kappers, 2006) and refers to the subjective impression of how compressible and deformable an object is. In order to explore softness people typically perform a specific movement scheme: they apply a normal force to the surface with their fingers, indent the object (Lederman & Klatzky, 1987). This movement scheme is systematically used only for softness perception and *not* for the exploration of other object properties. However,

people do not only choose appropriate movement schemes, they also seem to adjust individual movement parameters to the perceptual situation. In the case of softness, it was found that higher peak forces were used for the first indentation when stimuli were expected to be hard as compared to soft (Kaim & Drewing, 2011). Here we aim to clarify the mechanisms underlying such fine-tuning. We study whether indentation forces are systematically adjusted to gradually varying softness values, and in particular, we investigate the contribution of predictive signals, sensory signals, and motivation to the fine-tuning of force over the course of a natural exploration.

Previous research found that movement parameters are adjusted in haptic exploration for various tasks. Specific movement parameters, like force, velocity, or direction, matter for different tasks. Tanaka, Bergman Tiest, Kappers and Sano (2014), for instance, reported that participants vary their normal force, scanning velocity, and break times depending on the roughness of objects. Some other studies also described how movement adjustments may influence perception (e.g., Drewing, 2012; O'Malley & Goldfarb, 2002; DiLuca, 2011). With regard to softness perception, it was reported that (especially for hard stimuli) higher indentation forces can improve softness discrimination (Srinivasan & LaMotte, 1995; Kaim & Drewing, 2011). Kaim and Drewing (2011) described a corresponding fine-tuning of the peak force in the first indentation for a discrimination task. Two interesting results were reported. First, participants exerted a higher peak force in the first indentation in a trial, when they predicted that the stimulus pair would be hard in contrast to soft. Without predictions, no difference was found between the initial peak force used for hard and soft stimuli. Second, in an additional experiment participants were instructed to indent with either less or more force than they used spontaneously. When participants indented hard stimuli with *less* force, their ability to

discriminate them diminished, whereas *more* force did not improve discrimination performance. Taken together, this study suggests that people adjust indentation force based on predictive signals, and that these adjustments can improve softness perception.

The reported indentation force adjustments were only analyzed for two categories of softness. Additionally, only the first indentation was investigated, and a role for sensory information in force adjustments was neglected. However, natural exploration goes far beyond the previously investigated first indentation. People tend to repeat movements, because a single touch seems not to generate sufficient sensory signals to reach a decision (Klatzky & Lederman, 1999). This means that in natural exploration, sensory information about the stimulus is accumulated and may also be used for further movement control. Here, we aim to consider the entire process of softness exploration and the determinants of force adjustments over the course of the exploration. Therefore, we test whether indentation force adjustments occur not only based on prediction (predictive signals) but also based on sensation (sensory signals).

When the entire exploration process was considered previously, exploration movements were reported to change systematically over the course of the exploration. Lederman and Klatzky (1990) showed a corresponding two-stage exploration in haptic object identification. First, participants applied general exploration procedures, like grasping and lifting, which allowed them to obtain some initial (yet imprecise) information about a variety of properties. Secondly, a specific exploratory procedure was used- typically one that was associated with a property that is highly informative for the explored object. Thus, people qualitatively adjusted their exploration behavior in the second stage based on previously gathered sensory information. Some studies also reported adjustments of individual movement parameters, for instance, of speed and force to an unpredictable surface curvature (Weiss & Flanders, 2011). Another example is the study of



Saig, Gordon, Assa, Arieli, and Ahissar (2012), in which the authors reported online adjustments of specific movement parameters for a localizing task with artificial whiskers. The authors showed that, rather than repeating the same movements all over again, movement parameters converged during the task to a steady state. Training on the task resulted in changes of the hand velocity, which was connected to better performance. This is to say, sensory signals gathered during the exploration led to adjustments of motor variables. Our study investigates whether in the natural exploration of softness a similar closed sensorimotor control loop is involved, in which – besides predictive signals – sensory signals also affect movement parameters.

That is to say, we speculate that movement parameters are influenced by feedforward processes via predictive signals; and by feedback processes via sensory signals (cf. Wolpert, 1997). Predictive signals are available before any interaction with the object and are, for instance, based on previous experiences or on vision. Sensory signals are gathered during the exploration. Therefore, later in the exploration process, more sensory signals are available (Lezkan & Drewing, 2018). We propose that the sensory signals from initial movements are taken into account as feedback and, thus, that they influence upcoming motor commands, which will generate further sensory signals until a decision on the to-be-judged property is reached (i.e., softness). Consequently, later in the exploration process, movements are assumed to be better tuned to fit object characteristics (here called “online adjustments”) based on sensory signals. This is similar to ideas of ‘Iterative Learning Control’ incorporated in control theory, where repetitiveness is used for control optimization (Chen, Moore & Ahn, 2012). Note also that the acquisition of sensory signals may vary substantially, as people are able to decide how many movements they perform. The more exploratory movements are performed, the more sensory signals are generated, and the more reliable the sensation will be (e.g., Lezkan & Drewing, 2018;

Quick, 1974; Gescheider, Berryhill, Verrillo, & Bolanowski, 1999). Although additional exploratory movements can add sensory signals, they are also associated with additional movement costs. In consequence, there is a trade-off between benefits of additional movements (more reliable sensation) and their movement costs (effort). It has been suggested that the rewarding nature of the performed movement determines where the balance between movement costs, in terms of effort, and benefits from additional movements, in terms of additional sensory signals, is found (Todorov & Jordan, 2002; Todorov, 2004). The rewarding nature of a task can be also rephrased as the motivation to perform the task (Beckmann & Heckhausen, 2006). So far most of the evidence for the fact that higher energetic effort is spent when the task motivation (i.e., its' rewarding nature) is higher comes from studies on eye movements (Schütz, Trommershäuser, & Gegenfurtner, 2012; Takikawa, Kawagoe, Itoh, Nakahara, & Hikosaka, 2002; Xu-Wilson, Zee, & Shadmehr, 2009). We assume that in free haptic exploration, motivation influences the participant's effort, and thus the gathering and subsequent influence of sensory signals, in a similar way. Higher motivation should lead to the willingness to spent more effort in order to generate more sensory signals. Therefore, we suggest that increased motivation will lead to an increased impact of sensory signals. In particular, Experiment 1 investigates whether and in how far sensory and predictive signals lead to the adjustments of indentation force. Experiment 2 tests if effects of sensory signals are moderated by motivation.

## **4.2. Experiment 1**

On every trial, two deformable silicone stimuli were discriminated according to their softness. Stimuli were defined by the physical correlate of softness, namely compliance, which is the relationship between a physical force applied to an object and the resulting deformation of

the object's surface. We used four different softness categories ('soft'  $\sim 0.7$  mm/N, 'medium soft'  $\sim 0.4$  mm/N, 'medium hard'  $\sim 0.2$  mm/N or 'hard'  $\sim 0.1$  mm/N). Both stimuli of each pair were from the same softness category and differed only by 15-20% in their exact compliance.

We studied the influences of predictive signals on movement control by manipulating the presentation order. Hence, within one experimental block, all stimulus pairs could either be from the same softness category, which implicitly induced prior knowledge of the softness category of the upcoming stimulus pair (predictive signals high) or from all four categories (predictive signals low). Extending Kaim and Drewing (2011), we used more than two categories of softness, and tested whether movement adjustments systematically follow the softness category. We expected systematic adjustments of force with respect to object softness: Peak forces should be systematically adjusted towards higher forces when it can be predicted that stimuli will be harder. Specifically, when subtracting peak forces based on low predictive signals from peak forces based on high predictive signals, we expected linearly increasing values with harder categories.

We further investigated force adjustments based on sensory signals. We focused on the first (sensory signals low) and the last (sensory signals high) indentations during each trial, because those indentations represent the two extremes of the availability of sensory signals. We expected that indentation forces would be systematically adjusted between the first and the last indentation, which would correspond to the feedback influence of sensory signals (low vs. high sensory signals, respectively). Specifically, difference values, produced by subtracting peak forces based on low sensory signals from peak forces based on high sensory signals, should show a systematic increase for less soft categories.

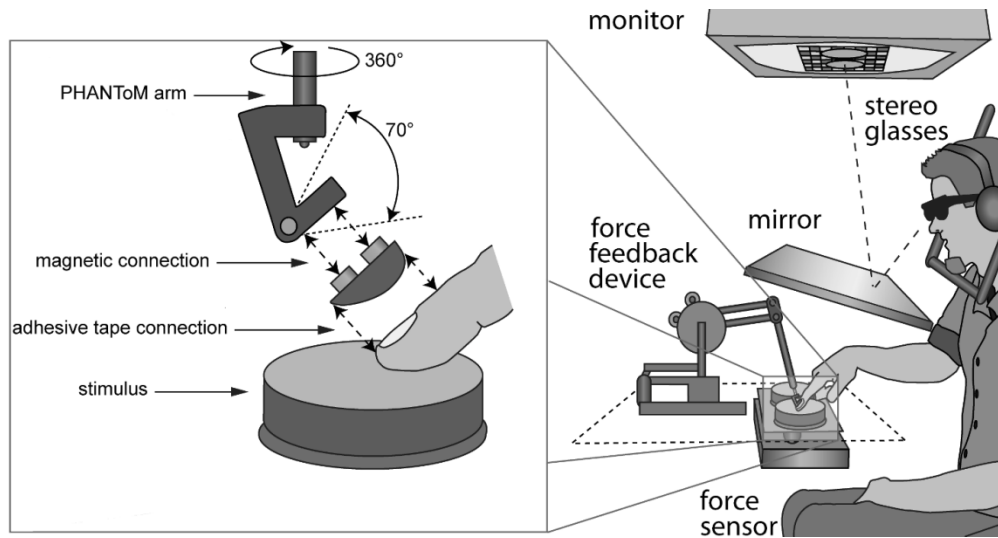
#### **4.2.1. Material and Methods**

#### **4.2.1.1. Participants**

The sample consisted of one left-handed and fifteen right-handed participants (mean age: 24.9 years, range: 19 – 33 years; 8 females). Participants from both experiments were naïve to the purpose of the experiment and were reimbursed for participating. All participants had no sensory or motor impairments or recent injuries of the right index finger, and had a two-point discrimination threshold of 2 mm or less for the right index finger. Methods and procedures of both experiments were approved by the local ethics committee LEK FB06 at Giessen University, which were in accordance with the ethical standards of the 2008 Declaration of Helsinki. Participants gave written informed consent.

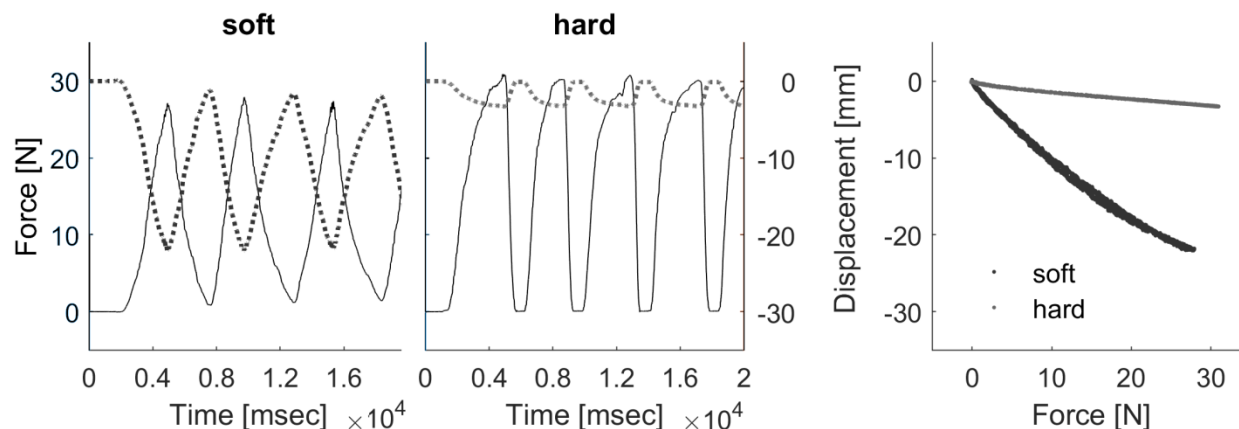
#### **4.2.1.2. Apparatus and Stimuli**

Participants sat in front of a custom-made visuo-haptic workbench (Fig. 4.1), which comprised a PHANToM 1.5A haptic force feedback device, a force sensor (682 Hz, resolution: 0.05 N), and a 22" computer screen (120 Hz, 1024 x 1280 pixels). A head and chin rest limited head movement. Participants saw the screen via stereo glasses and a mirror, which prevented them from seeing their hand or the stimuli. The right index finger was connected to the PHANToM via an adapter for the fingernail (Fig. 4.1). In order to make kinesthetic and tactile signals available, we used double-sided adhesive tape and an adapter, which left the finger pad bare. The PHANToM measured finger positions. The force sensor, consisting of a measuring beam (LCB 130) and a force amplifier (GSV-2AS) was placed below the stimuli. Custom software controlled the experiment, collected responses, and recorded force and position data at recording intervals of 3 ms.



**Figure 4.1.** Setup. Stimuli were visually represented on a monitor and seen through a mirror and stereo glasses. Rubber stimuli were placed on a force sensor next to each other. The right index finger was connected to the PHANTOM via an adapter.

Participants touched two real compliance stimuli placed side by side in front of them. We produced custom-made silicone rubber discs (diameter: 75 mm; height: 38 mm) by mixing a two-component silicone rubber mold material (Alpa Sil EH 10:1) with adjusted amounts of silicone oil (polydimethylsiloxane). The final stimulus set contained compliances between 0.12 mm/N and 0.88 mm/N. Compliances were defined as the slope of the regression line, fitted to vertical surface displacement produced by a mechanical ‘standard finger’ for forces between 0 and 9 N. The ‘standard finger’ was a flat-ended cylindrical probe (1 cm<sup>2</sup> area-- for details on compliance measurement, Kaim & Drewing 2011). Figure 4.2 shows deformation of a stimulus from the ‘soft’ and the ‘hard’ category for ‘standard finger’ exploration with peaks up to 30 N, which is the average range of peak forces in natural exploration. As it can be seen in the figure, the deformation of stimuli from both extreme categories (‘soft’ and ‘hard’) does not saturate within this range, which excludes full compression as a possible discrimination clue.



**Figure 4.2.** Deformation behavior of example ‘soft’ and ‘hard’ stimuli with ‘standard finger’ exploration up to 30 N. The curves for both categories that all stimuli in our range would not reach full compression for typical peak forces (Kaim & Drewing, 2011).

Stimuli were grouped into four softness categories. Each category consisted of a standard stimulus and two comparison stimuli: ‘hard’ (standard [s]: 0.14 mm/N, comparisons [c]: 0.12 mm/N & 0.15 mm/N), ‘medium hard’ (s: 0.21 mm/N, c: 0.18 mm/N & 0.24 mm/N), ‘medium soft’ (s: 0.37 mm/N, c: 0.29 mm/N & 0.46 mm/N), or ‘soft’ (s: 0.74 mm/N, c: 0.62 mm/N & 0.88 mm/N). The compliance differences between the stimuli of a stimulus pair were at least three times smaller than compliance differences between stimuli of different categories. The comparisons of each compliance category were chosen to differ approximately by one JND (just noticeable difference) from the standard. The calculations were based on interpolations from Weber fractions for harder (21.2 %) and softer (13.5 %) stimuli reported in Kaim and Drewing (2011).

Stimuli were displayed on the screen as three-dimensional (3D) cylindrical discs in a virtual 3D scene. Position and size of the ‘visual’ stimuli corresponded to those of the real objects. Outside the stimulus area, the current finger position was visible as a sphere (8 mm diameter). No visual feedback about stimulus compliance was provided; the finger representation disappeared when the stimulus was touched ( $> 0.1$  N force).

#### 4.2.1.3. Design and Procedure

In each trial, a stimulus pair, which comprised a standard and a comparison stimulus, was explored. We manipulated two within-participant variables: Softness Category of the stimulus pair (hard, medium hard, medium soft, soft) and Presentation Order (predictive signals high vs. low) of pairs within one block. For the manipulation of Presentation Order either all stimulus pairs of a block were taken from the same softness category (blocked condition: predictive signals high), or from all four categories (random condition: predictive signals low). In each block of the blocked condition, only the two pairs from the same softness category were presented. Therefore, a prediction of the softness category of the upcoming stimulus pair was possible (predictive signals high). In each block of the random condition, all eight stimulus pairs were presented. Therefore, no prediction of the softness category of the upcoming stimulus pair was possible (predictive signals low). We analyzed data from two Exploration Moments (first indentation: sensory signals low vs. last indentation: sensory signals high).

The experiment consisted of four sessions. Each session comprised four blocks of 96 trials (1536 trials in total) and was conducted on a different day. Per session, either only blocks from the blocked, or from the random condition, were presented. After balancing which stimulus was left (standard or comparison), each of the four combinations (stimulus pair  $\times$  positioning) was randomly repeated 24 times in a block of the blocked condition. For the random blocks, we balanced the positioning of the standard, and made sure that each combination was repeated six times in a block. Additionally, we balanced between participants which condition they started with in the first session. In the following sessions, the two conditions alternated from session to session. The order of softness categories in a blocked session was counterbalanced across

participants according to a Latin square and stayed the same for the two blocked sessions of one participant.

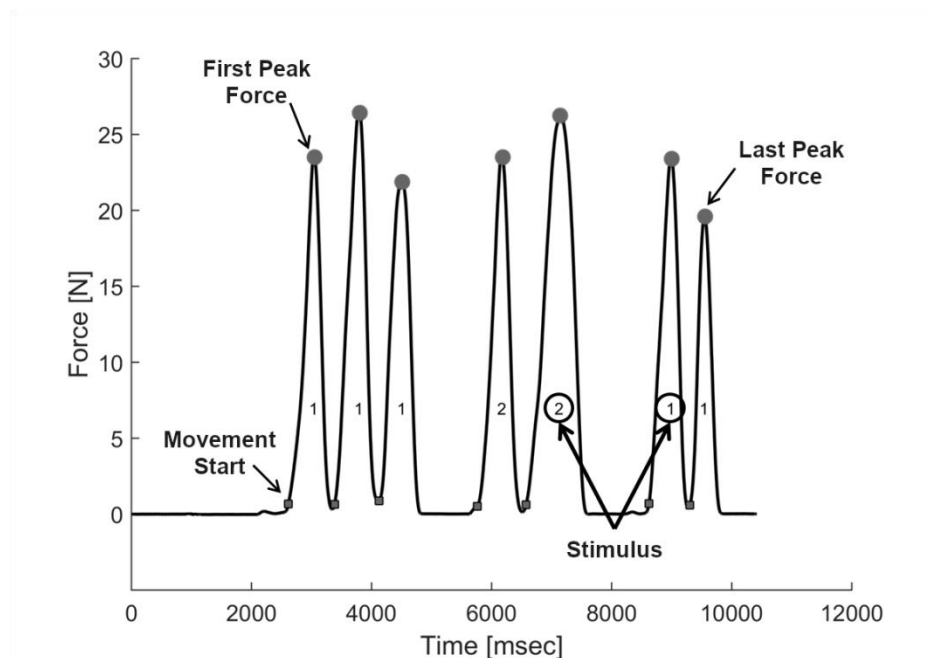
On each trial, participants performed a two alternative forced-choice (2AFC) discrimination task, judging which stimulus was softer. A cross indicated the center of the stimulus to be touched. Only the left or the right stimulus was presented on the screen before the first touch, which indicated which stimulus to explore first. Participants were free to perform as many indentations as they wanted, and to switch between left and right stimuli at any point in time. No immediate feedback about the correctness of the answer was given. However, at the end of each session, the percentage of correct trials was shown, so that participants would be motivated to perform equally well in all sessions.

#### **4.2.1.4. Data Analysis**

We analyzed the first and last indentations performed on the stimulus pair for each trial (Fig. 4.3). We focused on the peak indentation forces, which play an important role in softness perception (Srinivasan & LaMotte, 1995; Tan, Durlach, Beauregard & Srinivasan, 1995). Peak forces were defined as the forces for which the derivative of force over time changed from positive to negative. Force signals were previously smoothed by a moving-averaging window with a kernel of 45 ms. We restricted the time interval between two peaks to be at least 180 ms in order to exclude finger shaking or movement pauses. We calculated average individual peak forces for the first and last indentations per experimental condition (Presentation Order  $\times$  Softness Category). To test for systematic effects, we used a linear contrast analysis of differences produced by predictive signals (predictive signals low vs. predictive signals high) as well as those produced by sensory signals (sensory signals low vs. sensory signals high). This is



to say, we calculated for each softness category the difference in peak forces between blocked and random sessions (effect of predictive signals) as well as between the first and last indentations (effect of sensory signals). Those difference values were tested in linear contrast analyses, in which the linear combination of mean values for softness category is tested against '0'. We expected that difference values produced by the effect sensory signals as well as those produced by the effect of sensory signals systematically increase for less soft categories. Because we have well-defined directed hypotheses about the linear contrasts for the effect of sensory signals and the effect of predictive signals, we used one-tailed tests. Two-tailed tests were used for all the other reported statistics.



**Figure 4.3.** Example trial for exploration of one stimulus pair. As it can be seen, participants were free to indent the stimuli and switch between the two stimuli of a pair, as often as they wished. The difference between the last first peak indentation force is the measure of the effect of sensory signals.

## 4.2.2. Results

### 4.2.2.1. Task Performance and Number of Indentations

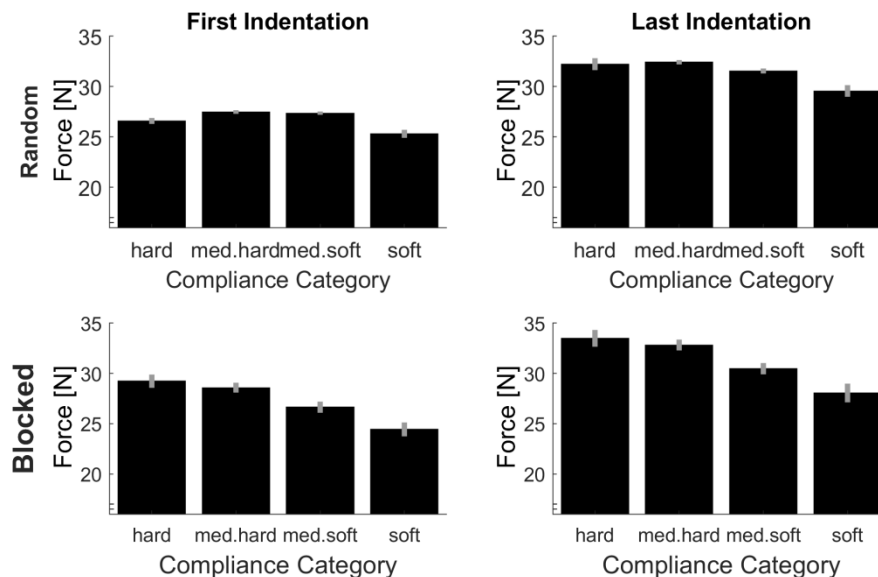
On average, participant accuracy was approximately 92%. Individual values ranged between 81% and 98%. Performance was significantly higher when predictive signals were high (blocked condition: 93.2 %) than when predictive signals were low (random condition: 90.8 %),  $t(15) = 3.17$ ,  $p = .006$ . This performance enhancement in the blocked condition as compared to the random condition was present independent whether participants started their first session with the random,  $t(7) = 2.47$ ,  $p = .043$ , or the blocked condition,  $t(7) = 3.63$ ,  $p = .008$ . Additionally, in a between-participant comparison, the number of indentations was significantly correlated with discrimination performance ( $r = 0.62$ ,  $p = .01$ ). Hence, participants who explored the stimulus with more indentations had a better performance on average. Overall, participants performed 6.1 indentations per stimulus pair on average, which was more than the minimum of 2 indentations that would have been necessary to do the task. The individual average ranged from 2.5 to 14.1 indentations. The average number of indentations was not significantly different between the random (6.3) and the blocked (5.8) Presentation Order,  $t(15) = -1.33$ ,  $p = .20$ .

### 4.2.2.2. Peak Forces

Average peak forces per experimental case are plotted in Fig. 4.4. On the upper left of this figure, the peak forces in the first indentation (low sensory signals) within the random condition (low predictive signals) are plotted, which constitutes the baseline, for which signals on softness category as much reduced as possible. Importantly and as should be the case, in this baseline, there is no systematic increase of peak forces for softer objects,  $t(15) = 1.64$ ,  $p = .122$  (linear contrast analysis., two-tailed). Therefore, the difference values which we calculate in the

following indicate meaningful adjustments. In other words, higher difference values indicate that higher absolute peak forces were used. First, we computed linear contrast analyses of the effects of predictive signals (differences in peak force between blocked/ high predictive signals and random/ low predictive signals condition, see Fig. 4.5a). For the linear contrast, the linear combination of mean values for each softness category was tested against '0' with a one-sided  $t$ -test. As expected, there was a significant linear contrast over the Softness Categories for one-sided testing,  $t(15) = 3.00$ ,  $p = .005$ , indicating that participants strived to systematically use lower peak forces for softer objects and higher peak forces for harder objects, when softness could be predicted. We then calculated linear contrast analyses based on the effects of sensory signals (differences in peak force between last indentation/ high sensory signals and first indentation/ low sensory signals, see Fig. 4.5b). Here, the expected linear combination of mean values over the Softness Categories was not statistically significant and showed only a trend in the predicted direction,  $t(15) = 1.24$ ,  $p = .088$ , one-sided.

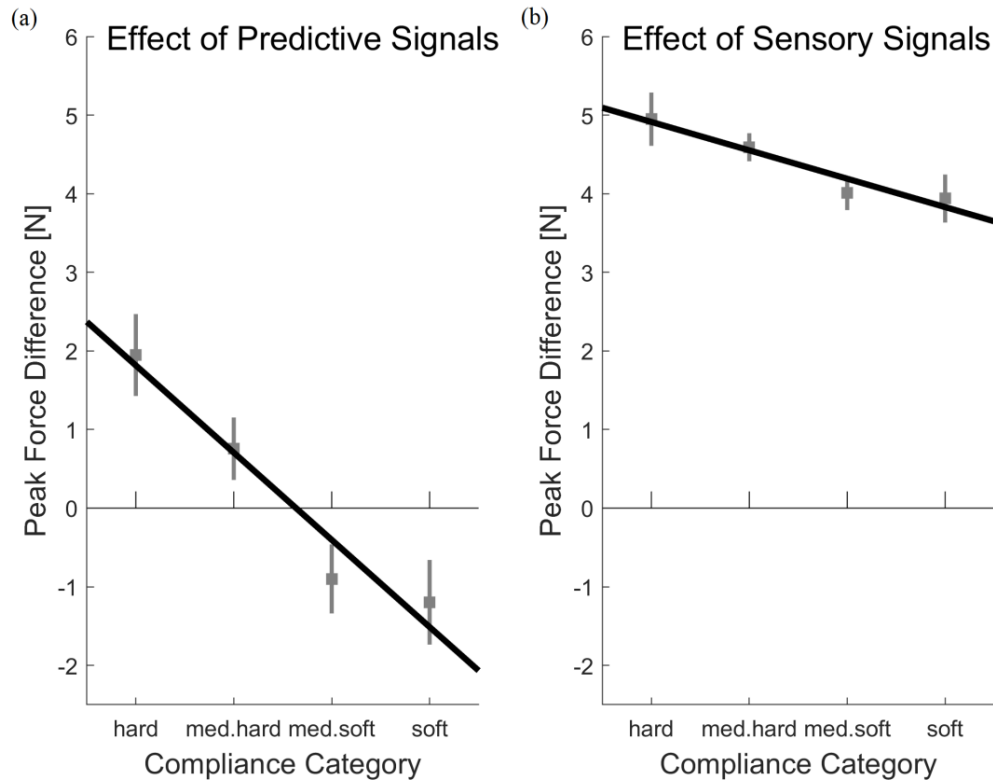
However, we performed an additional analysis of the movement adjustments based on sensory signals. Similarly to Saig et al. (2012), we calculated coefficients of variation in peak force (standard deviation normalized by the mean) for the first and the last indentation. In agreement with Saig et al. (2012), we found a significant decrease in the coefficient of variation, i.e. a convergence of movement parameters to steady values, when we compared peak forces in the first and the last indentations ( $t(15) = 1.94$   $p = 0.036$ , one-sided). That is, although there is only a trend for adjustment in peak forces based on sensory signals, the convergence to steady movement parameters might indicate that sensory signals had at least some effect on movement control.



**Figure 4.4.** Average peak indentation forces for each condition. Error bars are indicating within-participant standard errors (Morey, 2008).

#### 4.2.3. Discussion Experiment 1

We investigated the influence of predictive and sensory signals on the control of peak forces during softness exploration. We found systematic influences of predictive signals. Participants strived to systematically use lower peak forces for softer objects and higher peak forces for harder objects, when softness could be predicted. This result is in agreement with the existing literature on active movement control (e.g., Wing & Lederman, 1998; Johansson & Westling, 1988; Kaim & Drewing, 2011). Based on the finding that using higher peak forces for hard stimuli enhances discrimination performance (Kaim & Drewing, 2011), we can conclude that the observed movement adjustments optimize movements. We were additionally able to show that the effect of predictive signals is systematic in that it depends on the softness category in a linear fashion.



**Figure 4.5.** Differences in peak forces produced by (a) predictive or (b) sensory signals. (a) Peak force differences produced by predictive signals were calculated by subtracting values of the random (predictive signals low) conditions from values of the blocked (predictive signals high) conditions. The black line represents a linear contrast of peak force difference on softness category (hard; med. hard; med. soft; soft). (b) Peak force differences produced by sensory signals were calculated by subtracting values of the first indentation (sensory signals low) from the values of the last indentation (sensory signals high). Again, the black line represents a linear contrast on softness category. Error bars indicate within-participant standard errors (Morey, 2008).

The expected influence of sensory signals was not significant. In the present study, we observed only a tendency to use lower forces for softer objects based on sensory signals. The follow-up question is, how can we explain the finding that predictive signals had a clear influence on motor control, whereas the relevance of sensory signals was not evident? First, we can consider possible difference in the measurement of the effect of predictive and sensory signals. The effect of sensory signals was measured within one trial (last indentation vs. first indentation) while the effect of predictive signals was measured between sessions (blocked

condition vs. random condition). Potentially when comparing force measurements between separate sessions estimates of an effect are likely to be noisier than when comparing two force measurements within one trial of a session. However, this would predict a higher power to detect effects of sensory signals as compared to effects of predictive signals, whereas we found a significant effect of predictive but not sensory signals. Thus these methodological considerations cannot explain the difference between sensory and predictive signals. However, the literature on motor control might provide an explanation. The most prominent theory of motor control states that our motor system functions like an optimal controller. In the idea of an optimal controller it is suggested that the system uses all available signal sources, but weights those signals that are more reliable more heavily (e.g., Saunders & Knill, 2004). This is the same principle that theories of optimal signal integration describe for perception (Ernst & Banks, 2002). In order for one source of signals to show a major effect on movement control, it has to be sufficiently reliable to be weighted heavily in the computation. Consequently, it may be that in our experiment, the reliability of sensory information was not sufficient to warrant a significant effect on movement control. In active touch, sensory information gains reliability with extension of exploration; the more movements performed, the more sensory signals are generated, and the more reliable the sensory information overall will be (Lezkan & Drewing, 2018). Therefore, it seems possible that our participants did not explore with the necessary extension to generate sufficient sensory signals.

The fact that people do not necessarily use a maximum number of movements for a task was previously explained in movement control literature (Todorov & Jordan, 2002; Todorov, 2004) by the additional energetic effort every extra movement costs. It was suggested that movement costs (in terms of effort) are counterbalanced with the rewarding nature of the

performed movement. This means that higher energetic costs should only be spent if they increase the reward. Corroborating these notions, research from visual perception indicates that the expectation of reward impacts eye movements. When rewarded, saccades (especially longer saccades) had higher peak velocities and shorter latencies in monkeys and humans (Schütz, Trommershäuser, & Gegenfurtner, 2012; Takikawa, Kawagoe, Itoh, Nakahara, & Hikosaka, 2002; Xu-Wilson, Zee, & Shadmehr, 2009). This is evidence for a link between higher energetic effort and expected reward in visual perception. We speculate that similarly our participants might not have gathered sufficient sensory signals because they were not expecting higher reward for high perceptual performance. In Experiment 2, we investigate the influence of motivational factors. In the present case, we refer to the rewarding value of a task as the motivation to perform it (Beckmann & Heckhausen, 2006). We investigate whether motivation influences the effort spent for exploration movements in haptic perception. In particular, we assume that high reward (yielding high motivation) increases the gathering of sensory signals and the online adjustment of movement.

### **4.3. Experiment 2**

We manipulated motivation via the possibility to win money with each correct response in half of the experiment (motivation part) and pretending that the system does not work in the other half (demotivation part). Participants performed a 2AFC softness discrimination task among stimulus pairs from either the soft (0.61 - 0.73 mm/N) or the hard (0.15 - 0.16 mm/N) category. With higher motivation, we expected more pronounced adjustments of peak force based on sensory signals. Thus, motivation should moderate the effect of sensory signals on movement adjustments. Specifically, we expect a statistically significant linear contrast when

calculating the differences between the two motivation conditions in the effect of sensory signals (i.e., the peak force differences between the first and the last indentation) for each softness category. Please note, in the 2x2 design the expected linear contrast is equivalent to the interaction effect in a standard ANOVA.

### **4.3.1. Material and Methods**

#### **4.3.1.1. Participants**

Sixteen participants (10 female; mean age: 25.6 years, range: 20 – 32 years) entered in the final sample based on a successful manipulation of motivation. For fourteen other people, who filled in the questionnaire, we were not able to manipulate motivation as intended. The a-priori defined inclusion criterion was that motivational values (i.e., the points achieved in the motivational questionnaire) in the motivational part were higher than motivational values in the demotivation part. Therefore, participants, who did not meet this criterion, were not part of the main analysis. Participants were compensated by 24-32€ (29€ on average). The compensation was calculated from a fixed value (12 €) for the demotivation part of the experiment, plus the monetary equivalent of the achieved points in the motivation part with a fixed bonus (in total 12-20 €, 17 € on average).

#### **4.3.1.2. Apparatus and Stimuli**

The apparatus and setup were identical to Experiment 1. In each softness category, the standard was paired with one of two comparisons ('soft': 0.61, 0.67, 0.73 mm/N; 'hard': 0.152, 0.156, 0.162 mm/N). Compliance differences of the two comparison and the standard were either easier or more difficult discriminate. We chose stimuli in adaptive piloting procedure (duration: 30-45 minutes per participant). Thirteen participants (who were not part of either of the main



experiments) explored stimulus pairs of either both or one of the softness categories. We changed the stimuli of a pair across participants until at least two participants showed a performance of approximately 90% for one pair and 80% for the other pair of the same softness category.

#### **4.3.1.3. Design and Procedure**

Motivation (motivation vs. demotivation) and Softness category (hard vs. soft) were manipulated as within-participant variables. The manipulation of motivation restricted us to a single-session design. Given the single-session design we did not manipulate presentation order as a within-participant variable, because it was not the focus of this experiment to look for interactions of predictive signals with motivation. The presentation order was approximately balanced between the participants in the final sample (nine blocked, seven random), but not further analyzed, because this design does not provide sufficient statistical power for these analyses. As in Experiment 1, a 2AFC softness discrimination task was used. Visual cues were similar to Experiment 1, except for an additional screen to inform participants about gaining monetary rewards.

The experiment consisted of one session with four blocks of 112 trials (448 trials in total), and breaks were given between blocks. The total experiment took about three hours. In each block, the eight stimulus pair combinations were repeated fourteen times. Stimulus pair combinations were defined by the compliances of the stimulus pair and the positioning (standard left vs. right). Two successive blocks constituted the motivation part and two other successive blocks constituted the demotivation part. We approximately balanced the order of conditions between the participants in the final sample (nine started with the motivation condition, seven started with the demotivation condition). All participants were instructed to consider the

experiment as a game, in which they can gain points. Before the start of the exploration, a screen indicated how many points (50 or 100) could be gained with a correct response (randomly associated to half of the trials each). Whenever the participant accumulated 1000 points, an additional euro was gained. Thus, based on the pilot data, we estimated that participants accrued 1€ every 18 trials. Visual and auditory feedback was given one to three trials after gaining an additional euro. This gaining rule was only true for half of the experiment (two subsequent blocks; motivation part). For the other half of the experiment, we pretended that the reward system stopped working and we had to reimburse participants with the conventional payment (demotivation part). We induced demotivation in this way, because a not working system implies that a reward will be expected but not given. Losing the expected reward should be weighted more than not being rewarded (cf. Kahnemann & Tversky, 1974; Crespi, 1942) and we wanted to maximize the difference between the two within-participant motivation conditions as much as possible. This ‘error’ was presented by the system displaying a zero for the points in each trial. For participants who started with the demotivation part, we pretended that the only person able to fix this ‘error’ was not reachable at first. However, after the first experimental part (demotivation), this person came back and was able to fix the ‘problem’ so that the second half was conducted with the possibility to win money (motivational part). For the other half of participants, the experiment worked as instructed in the first half of the session. After the second break, the ‘error’ appeared. Again, no one who could fix it was reachable and the second part of the experiment did not allow participants to gain points (demotivation).

#### **4.3.1.4. Motivational Questionnaire**

In order to ensure the manipulation, a motivational questionnaire was given to participants after each experimental half. The questionnaire was constructed by adapting two

questionnaires that access task motivation and adding four items that capture the social desirability bias (used for distraction and individual correction (cf. below)). The basis for the motivational questionnaire was the following two surveys: PMI (“Potsdamer Motivationsinventar”, Rheinberg & Wendland, 2002), originally used to measure task-specific motivation values in a school environment, and the PANAVA scale (PA: positive activation, NA: negative activation, VA: valence) which measures one’s mental state while performing a task (Schallberger, 2000).

To measure social desirability, we chose four items from the German SDS-E scale of social desirability (items 7, 8, 17, 22; Lück & Timaeus, 2014), which would not stand out if added to the PMI scale. Our adapted PMI scale included all ten items from the original PMI, in which we only modified task-specific expressions, like ‘mathematical task’ into ‘this task’. The responses were given on Likert-type items, which could be rated from “does apply” (1) to “does not apply” (5). Two examples are: “I wish I did not have to perform this task” and “Performing this task has positive effects on my mood”. The PANAVA scale asks how the participant felt “directly before starting a trial”. Assessments were done on a seven-step scale between two adjectives, representing opposite poles of one dimension. Four items captured positive activation (awake vs. tired; full of energy vs. shiftless; energetic vs. inert; excited vs. bored); two items measured valence (happy vs. unhappy; satisfied vs. unsatisfied). These six items are positively related with motivation. The other four items measured negative activation (relaxed vs. stressed; good-humored vs. upset; calm vs. nervous; carefree vs. worried), which is negatively related to motivation. The questionnaires were rated after each experimental part (motivation vs. demotivation). For each item’s response, the associated values were read out as points. For each questionnaire, a range between the minimum and maximum sum of points was defined (PMI:

min.10, max. 50; PANAVA: min.-22, max. 38, note: NA only contributes negative points) and transformed in percentages between the minimum (0%) and maximum (100%) sum of points. An uncorrected motivation score was calculated by averaging these two motivational values from the two scales for each experimental part. Additionally, to improve the validity, individual motivation scores were corrected by the social desirability score. As a corrected motivation score, we used the residuals of a linear regression of uncorrected motivation scores on social desirability, which is common practice in several scales as the MMPI (Lubin, 1957; Paulhus, 1981).

#### **4.3.1.5. Data Analysis**

We estimated the exhibited energetic effort of the exploration in one trial by the sum of peak forces over all indentations performed in this trial. Additionally, we calculated individual peak forces per condition and the effects of sensory signals on peak force, as described in Experiment 1. Because we have directed hypotheses about the effect of motivation on the task performance, the energetic effort and the linear contrast produced by sensory signals we used one-tailed tests for these analyses.

### **4.3.2. Results**

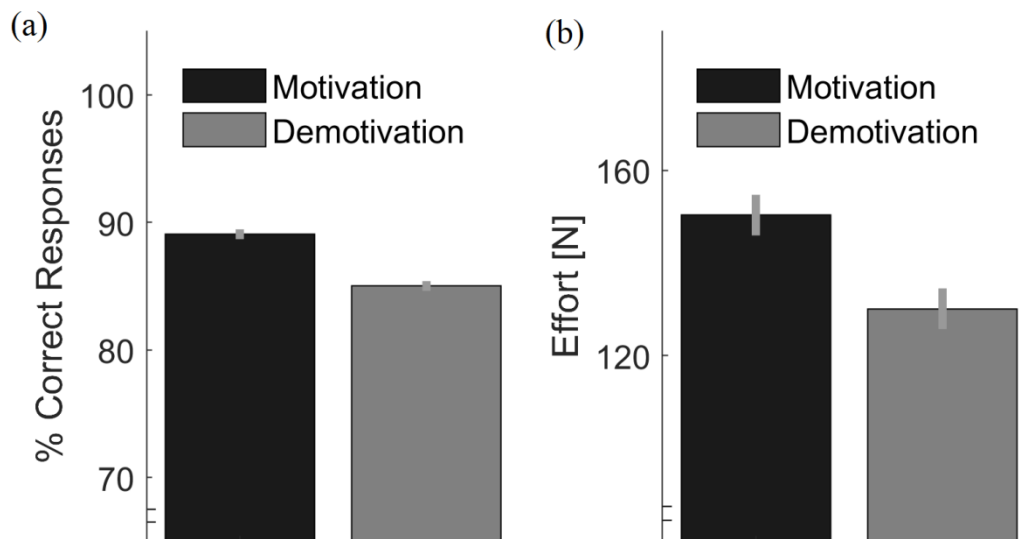
#### **4.3.2.1. Questionnaire**

On average, participants in the final sample reported 39.5 % (SD = 12.5 %) from the maximal points they could achieve in the motivational questionnaire in the demotivation part and 49.1 % (SD = 7.7 %) in the motivation part. This difference between the motivation conditions was statistically significant,  $t(15) = -4.89$ ,  $p < .001$ . Additionally, differences in motivational values between the motivation conditions in the subgroup that started with the motivation

condition were not significantly different from the difference values in the other subgroup,  $t(14) = 1.61$ ,  $p = .320$ . The data from participants, that we excluded based on the questionnaire are fully consistent with our hypothesis: As it is to expect from the not successful manipulation, their data showed no differences in performance, effort or movement adjustments between the conditions.

#### 4.3.2.2. Task Performance and Energetic Effort

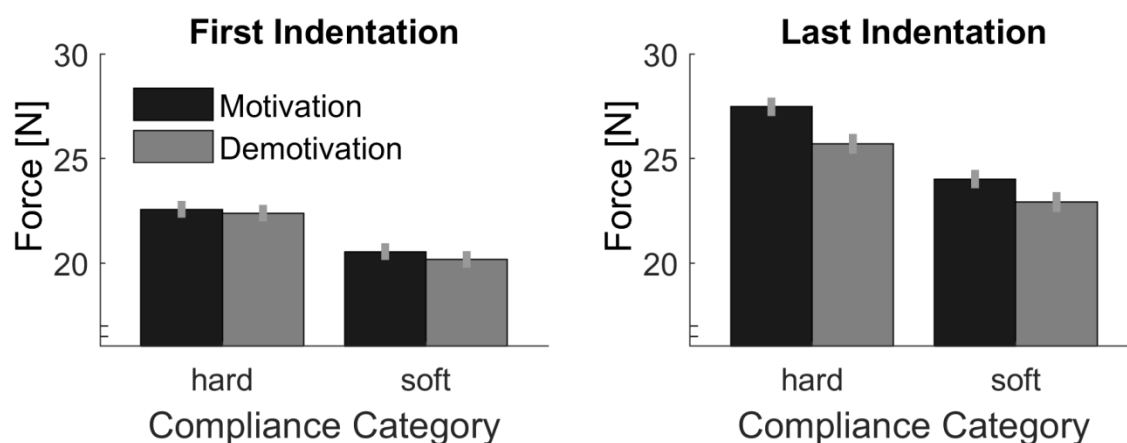
We calculated individual percentages of correct answers (Fig. 4.6a). We analyzed whether Motivation significantly increased performance with a one-sided t-test (after rationalized arcsine transformations of the individual proportional data). We found a significant effect of Motivation,  $t(15) = 4.43$ ,  $p < .001$  with 88.9 % (SD = 5.7 %) correct answers in the Motivation condition vs. 85.3 % (SD = 7.6 %) in the Demotivation condition. Further, values of energetic effort (Fig. 4.6b) were tested in the same way. As expected, we found a significant effect of Motivation in one-sided testing,  $t(15) = 2.06$ ,  $p = .029$ .



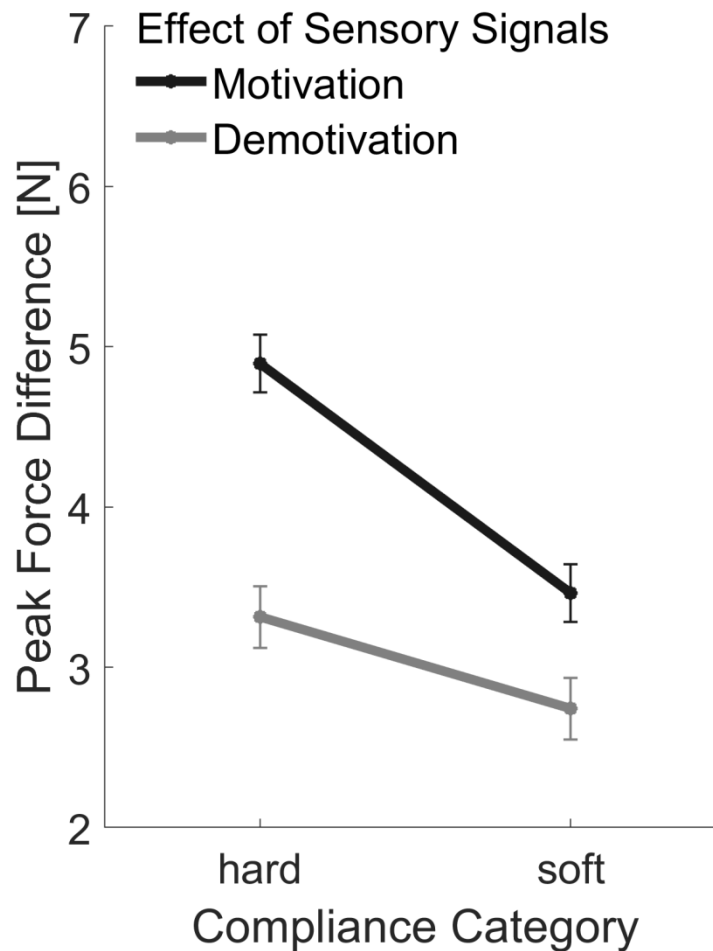
**Figure 4.6.** (a) Performance, as measured by the percentage of correct responses, plotted separately for motivation vs. demotivation and hard vs. soft softness category. (b) Estimate of effort per trial based on the sum of peak forces from all indentations of one trial. Error bars indicate within-participant standard errors (Morey, 2008).

#### 4.3.2.3. Peak Forces and Motivational Effects on Adjustments to Sensory Signals

Peak forces are plotted in Figure 4.7. As in Experiment 1, we calculated the difference between the first and the last peak forces in each trial in order to assess effects of sensory signals (Fig. 4.8). First we computed, the linear contrast analyses, of mean force difference values over the Softness Categories with a one-sided t-test. The linear contrast analyses over both Motivation conditions, which represents the overall adjustments to sensory signals, revealed a statistically significant effect,  $t(15) = 2.71$ ,  $p = .016$ . More importantly, we calculated the linear contrast on the differences in mean values between the two Motivation conditions, which revealed a significant interaction between Motivation and the linear contrast on Softness Category in the one-sided test,  $t(15) = 2.25$ ,  $p = .020$ . This result supports our hypothesis, that effects of sensory signals were higher in the motivation part. That is to say, peak force adjustments based on sensory signals were higher with higher motivation.



**Figure 4.7.** Average peak indentation forces for each condition. Grey bars represent the demotivation part and black bars the motivation part. Error bars indicate within-participant standard errors (Morey, 2008).



**Figure 4.8.** Differences in peak forces produced by sensory signals. The peak force differences were calculated by subtracting values of the first indentation from the values of the last indentation. Error bars indicate within-participant standard errors (Morey, 2008).

In order to test whether adjusted movements based on sensory signals were moderated by the experimental half, we performed the same analyses as previously but with experimental half (instead of motivation) as the moderator. Therefore, we calculated the linear combination of the differences in force difference values between the two experimental half and tested it with a two-sided t-test against '0'. The experimental half, was not a significant moderator of the effect of sensory signals,  $t(15) = 1.24$ ,  $p = .235$ .

### 4.3.3. Discussion Experiment 2

The motivational manipulation influenced the exploration process as expected: When motivated, participants adjusted movements based on sensory signals more profoundly as compared to when being demotivated. Additionally, participants spent more energetic effort for the exploration and performed better when motivated.

Our participants started the experiment with either the motivation or the demotivation condition which we approximately counterbalanced (9 to 7). One could ask whether this slight disproportion in favor of the participants who started in the motivation condition might have caused the effect. That is to say, did the experimental half influence movement adjustment instead of the motivation condition? As we did not find a significant moderation of the effect of sensory signals by the experimental half, our results speak against the experimental half as a possible confound in our data set.

An increase of the effect of sensory signals, as produced in the motivation condition, could be either due to the availability of more sensory signals or to a higher weighting of sensory signals in motor control. The present results show that participants not only improve motor adjustment, but also show better perceptual performance and generate more sensory signals when being motivated. Therefore, in our case, changes in online adjustment of movements are more parsimoniously explained by the acquisition of more sensory signals. Although, the acquisition of additional sensory signals seems to rule out the up-regulation as an alternative explanation in our experiment, previous literature has reported conditions under which sensory signals gain or lose influence on motor adjustment without any change in their availability (e.g., Jakobson and Goodale, 1991; Knill, Bondada, & Chhabra, 2011). For instance, Knill et al. (2011)



demonstrated that, after a perturbation of the visual feedback, participants corrected their pointing movements more if the accuracy demands of the task were greater.

#### **4.4. General Discussion**

We investigated whether peak indentation forces are adjusted based on predictive or sensory signals to softness category, in natural exploration. Participants systematically used higher peak force for harder objects when they were informed about the softness by predictive. Interestingly, self-generated sensory signals in Experiment 1 had a less clear impact on movement adjustments (if any) than predictive signals. We reasoned this to be due to a lack of motivation to generate sufficient sensory signals. Thus in Experiment 2, we manipulated the motivation to do the task in order to modulate the effect of sensory signals. When participants were motivated, they adjusted their peak forces significantly to the sensed softness. We associated this with the generation of additional sensory signals, because participants also spent more energetic effort for exploration when motivated. This was additionally indicated by an improved perceptual performance. Taken together, this study provides evidence that softness exploration constitutes a closed sensorimotor loop, where prediction, sensation, and motivation are relevant determinants of movement control.

In our experiments, we showed that when participants adjusted their peak force more precisely to the object they also generated more sensory signals. In previous work, we additionally showed that perception gets more precise with more generated sensory signals (Lezkan & Drewing, 2018; Metzger, Lezkan & Drewing, 2018). In sum, accumulating sensory signals seems to improve the precision of movement and perception. Therefore, we propose that in natural softness exploration, a strong links exist between sensory signals and following

movements. We believe that the softness estimates used for motor control are similar to softness estimates used for perception. However, there is a long-standing debate on whether sensory signals are used in the same manner when being processed for action versus for perception (Milner & Goodale, 1992; Smeets & Brenner, 2006). Interestingly, Leib, Karniel, and Nisky (2015) described for a task, similar to our own, a dissociation between the use of sensory signals for movement control and for perception. In their experiment, participants explored the stiffness of virtual elastic force fields using a tool. When the force feedback was delayed, participants underestimated the stiffness, meaning that perception did not discount the temporal delay. In contrast, their grip forces, with which they were holding the tool, were adjusted to the force feedback delay. However, in that study, not only the use of sensory signals differed between perception and action, but also the tasks for which the sensory signals were used: The motor task involved keeping a stable grip, while the perceptual task required estimating the stiffness of an object. Thus, the motor control required information about the time course of feedback force in order to program grip forces that warrant a stable grip. In contrast, for the perceptual task force feedback and position feedback had to be combined into an estimate of stiffness. Thus, the dissociation observed in Leib et al. (2015) might be caused by the differences between the perceptual and the motor task, rather than a differential use of the same signals (cf. Smeets & Brenner, 2006). In the present study, sensory signals have been used for the same basic task, namely to derive a softness estimate. Future experiments are required to test our assumption that softness estimates used in perception and for motor adjustment are indeed highly linked.

Based on our observations, we can summarize several observations about movement control in natural exploration: Exploratory movements seem to be executed with the aim of enhancing performance. When possible, our motor system uses predictions to lower movement

costs. Additional exploration movements are performed when perceptual performance is not yet at the target level. However, this active sensory gathering is moderated by motivation. Thus, our results may be taken to suggest that the aim of motor control is to change the internal state to be more rewarding. This can happen internally by a better perceptual representation or externally by reward. If so, motivation could be understood as a driving mechanism in the motor control system. So far, this is rather a hypothesis which we derive from our results and which should be investigated in future.

In our study we tried to systematically clarify the mechanisms underlying movement control for softness exploration. However, more research is needed in order to understand whether the described mechanisms can be generalized to other natural exploration behaviors. Understanding general mechanisms of movement control in natural exploration might also be useful to help in cases, when these mechanisms do not work. Several links between abnormalities in the sensorimotor mechanisms and psychological dysfunctions have been suggested. In a recent study, Mosconi, Mohanty, Greene, Cook, Vaillancourt, and Sweeney (2015) reported that patients with an autism spectrum disorder show impairments in feedforward as well as in feedback processes of sensorimotor control. Additionally, Shadmehr, de Xivry, Xu-Wilson, and Shih (2010) discussed the relation between diseases of the reward system, such as Parkinson's disease or schizophrenia, and movement control. The authors suggest, similar to our conclusions, that rewards are driving motor signals and see these diseases in the context of a discounting of rewards, which can be achieved with motor commands. Our study offers a first step in understanding the role of motivation in motor control for natural exploration movements. Further systematic research about factors influencing motor control may not only help to understand natural exploration behavior, but also diseases of the movement system.

Apart from the investigated factors, which seem to be indispensable for a functioning motor control, our data allows to speculate which additional variables may influence motor control in natural softness exploration. One interesting observation is that participants did not use a fixed order of indentations for the two stimuli. In the last indentation before giving a response, participants touched disproportionately more often the stimulus, which they were about to choose (Experiment 1: 75.74%; Experiment 2: 72.68%). Similar behavior of fixating the object right before choosing it was also reported for vision (Krajbich Armel, & Rangel, 2010; Manohar & Husein, 2013). In the haptic modality, Mitsuda and Yoshioka (2015) described that participants tended to sample last the object they reported to be more preferable to the other object. This behavior could reflect attention or decision making processes. One possibility is that participants perform the last movement to reaffirm their choice based on the sensory signals gathered up to that point.

Additionally, we observed an unexpected general effect of the exploration moment (last vs. first indentation) on peak forces. In the last indentation, peak forces increased in comparison to the first indentation (Experiment 1:  $t(15) = -3.81$ ,  $p = .002$ ; Experiment 2:  $t(15) = -3.99$ ,  $p = .001$ ). This increase happened gradually, given that it was also reflected in the middle indentation. One possible explanation is that through perceptual adaptation to force, the softness sensitivity diminished. Every indentation is associated with a force profile on the finger tip, which varies over time and space. The adaptation to pressure was one of the first characteristics described for mechanoreceptors (Nafe & Wagoner, 1941; Zigler, 1932; Johnson, 2001). Adaptations on a neural basis are reflected in changed perception (Cohen & Viereck, 1993). Consequently, repeated indenting within static contact with the object might lead to diminished neural responses, and thus, reduced sensation during softness exploration. On the other hand,

increases in contact force between finger and stimulus were previously observed to scale population responses upwards (Goodwin, Browning, & Wheat, 1995). Thus, increasing indentation force might be a way to counteract declining neural response due to adaptation. That is to say, increasing indentation force could be a reasonable strategy to counteract negative effects of such perceptual adaptation. However, this is mere speculation at this point and further research is needed. Taken together, we assume that although prediction, sensation, and motivation have a high impact on movement control in natural exploration, there are likely further impact factors, including bottom-up factors like adaptation, or top-down factors, like decision-making. In order to build a model of natural motor control, several of those factors have to be further investigated.

#### **4.5. Conclusion**

This study provides new and important insights in movement control within unconstrained haptic softness exploration. Participants applied systematically lower forces in the exploration of softer objects when the softness category was predictable, or previously experienced within the exploration of this stimulus. Based on this finding, softness exploration can be understood as a sensorimotor control loop containing a feedforward process based on predictive signals, and a feedback process, based on sensory signals. The roles of the feedforward and feedback processes seem to change during the exploration. While the existence of a feedforward process influences movement control during the entire exploration process, the feedback process gains importance as more sensory feedback is gathered over time. Our findings highlight the role of motivation as a moderator of feedback processes. Increased motivation led to an increase in motor adjustments based on sensory signals. Overall, such a system seems to

aim for the most effective way to perform a task. Movements are chosen as appropriately as possible at a given point in time. Energetic effort of the movements is kept low in order to achieve an aimed performance.

## 5. Interdependences between Finger Movement Direction and Haptic Perception of Oriented Textures

*A similar version of this manuscript is currently under review (after second revision):*

*Lezkan, A., & Drewing, K. (under review). Interdependences between finger movement direction and haptic perception of oriented textures. PLOS ONE.*

Although the natural haptic perception of textures includes active finger movements, it is unclear how closely perception and movements are linked. Here we investigated this question using oriented textures. Textures that are composed of periodically repeating grooves have a clear orientation defined by the grooves. The direction of finger movement relative to texture orientation determines the availability of temporal cues to the spatial period of the texture. These cues are absent during movements directed in line with texture orientation, whereas movements orthogonal to texture orientation maximize the temporal frequency of stimulation. This may optimize temporal cues. In Experiment 1 we tested whether texture perception gets more precise the more orthogonal the movement direction is to the texture. We systematically varied the movement direction within a 2-IFC spatial period discrimination task. As expected, perception was more precise (lower discrimination thresholds) when finger movements were directed closer towards the texture orthogonal as compared to in parallel to the texture. In Experiment 2 we investigated whether people adjust movement directions to the texture orthogonal in free exploration. We recorded movement directions during free exploration of standard and comparison gratings. The standard gratings were clearly oriented. The comparison gratings did not have a clear orientation defined by grooves. Participants adjusted movement directions to the texture orthogonal only for clearly oriented textures (standards). The adjustment to texture

orthogonal was present in the final movement but not in the first movement. This suggests that movement adjustment is based on sensory signals for texture orientation that were gathered over the course of exploration. In Experiment 3 we assessed whether the perception of texture orientation and movement adjustments are based on shared sensory signals. We determined perceptual thresholds for orientation discrimination and computed ‘movometric’ thresholds from the stroke-by-stroke adjustment of movement direction. Perception and movements were influenced by a common factor, the spatial period, suggesting that the same sensory signals for texture orientation contribute to both. We conclude that people optimize texture perception by adjusting their movements in directions that maximize temporal cue frequency. Adjustments are performed on the basis of sensory signals that are also used for perception.

## **5.1. Introduction**

Imagine entering a room with the lights turned off. In order to perceive the world around you with your sense of touch, you would probably move your hands and explore. The way you would move your hands will depend on the things you encounter. In other words, hand movements generate haptic sensations (Gibson, 1962) and exploratory movements depend on the object property of interest (Lederman & Klatzky, 1987). Recent studies described the mutual influence of movement and sensation in haptic perception of location, softness, and roughness (Saig, Gordon, Assa, Ariali, & Ahissar, 2012; Lezkan & Drewing, 2015; Tanaka, Bergman Tiest, & Kappers, 2014). Our study investigates the interaction between movement and sensation in natural exploration of oriented texture. In three experiments, we test whether people optimize the perception of oriented textures by adjusting the direction of exploratory movements based on sensory signals for texture orientation. Experiment 1 tests whether there is a systematic influence



of movement direction on the precision of perceiving the spatial period of oriented textures. Experiments 2 and 3 investigate whether sensory signals for texture orientation influence the control of movement directions, first by studying whether movement direction is adjusted to the orientation of the explored texture (Experiment 2), and then by investigating whether sensory signals that underlie the perception of texture orientation are also used in the adjustment of movement direction (Experiment 3).

Texture perception by touch is multidimensional and people can describe multiple facets of a surface texture including roughness, coarseness, jaggedness, spatial element density, or configuration (Lederman, Thorne, & Jones, 1986). However, texture perception has often been investigated using rather simple textures such as periodic grooved gratings, which can be defined by their spatial period (e.g., Sathian, 1989), and most researchers have asked for roughness judgments (e.g., Cascio & Sathian, 2001; Lederman & Taylor, 1972; Drewing, 2016). However, several others also asked for a more direct spatial period judgment (e.g., Morley, Goodwin, & Darian-Smith, 1983; Gamzu & Ahissar, 2001; Nefs, Kappers, & Koenderink, 2002; Zhang, Mariola, Stilla, Stoesz, Mao, Hu & Sathian, 2005). Results from both tasks suggest that haptic perception of such aspects of the structure of textures is based on spatial and temporal cues (Gamzu & Ahissar, 2001; Weber, Saal, Lieber, Cheng, Manfredi, Dammann, & Bensmaia, 2013). Spatial cues are the kind of information we can get from skin deformation after pressing a textured surface against the skin without permitting lateral movement (e.g., Hollins & Risner, 2000). The neural coding of spatial cues, as shown in roughness perception, is strongly based on the spatial pattern of activation of the slowly adapting afferents (SA1; Weber et al., 2013). Temporal cues arise from movement over a textured surface and refer to the changes of signals over time, i.e. vibrations (e.g., Klatzky & Lederman, 1999). Those vibrations are mainly coded

by rapidly adapting (RA) and Pacinian (PC) afferents, as also shown in the perception of roughness (Weber et al., 2013). Although, in natural situations, textures are typically explored with lateral movements (Lederman & Klatzky, 1987), it has been previously discussed how much movements can actually enhance perceptual precision (at least for certain kind of textures; Lederman, 1974; Johnson & Hsiao, 1994). For fine textures, movements seem to be crucial; roughness discrimination was reported to be seriously impaired without the temporal cues produced by movements (Hollins, Bensmaia, & Roy, 2002). In contrast, the roughness of coarse textures was reported to be highly distinguishable by static touch alone (Hollins & Risner, 2000). Nevertheless, there is evidence that even for coarse textures, as well as for most natural surfaces, spatial cues are combined with temporal cues (Cascio & Sathian, 2001; Weber et al., 2013). Gamzu and Ahissar (2001) demonstrated the advantage of temporal cues. For their frequency ( $=1/\text{spatial period}$ ) discrimination task, poor haptic performers were able to improve by changing movement velocity as a strategy, which accentuated temporal cues. Similarly, Lamb (1983) showed that when exploration generates temporal cues, the precision of texture perception can be increased. In his study, textures, which incorporated stripes of raised dots, were passively moved against the participant's finger. The spacing between stripes was either modified perpendicular to the movement track or along the movement track. After the sequential presentation of two textures, participants reported in which of the two textures the spacing between stripes was modified. Performance was better for manipulations along the movement track than perpendicular to it. This can be attributed to the added temporal cues in the case of variations along the movement track. These two reported studies indicate that not only movements (or the lack of them) but also the specific movement parameters matter. More precisely, the study of Gamzu and Ahissar describes an influence of movement velocity on perception and Lamb's

study describes an influence of direction of passive movement between the skin and the surface. For oriented textures, movement direction is systematically linked to temporal cue frequency. Therefore, if temporal cues matter in active touch, movement direction should impact the perception of the spatial period of the texture. To our knowledge, however, there exists no study that investigated the influence of movement direction in active touch on perceptual precision and did so by systematically varying movement direction.

Assuming that there is one movement direction that leads to the best perceptual precision, it can be referred to as the optimal movement direction. But do humans utilize this optimal movement direction in free exploration? Freely chosen movements used in active exploration were suggested to aim for maximization of sensory information gain (e.g., Najemnik & Geisler, 2005; Klatzky & Lederman, 1999). As a matter of fact, in visual research, the orientation of depicted textures was found to influence eye movement direction (Wexler & Ouarti, 2008; Wismeijer, Erkelens, van Ee, & Wexler, 2010; Wismeijer & Gegenfurtner, 2012). For haptic softness and shape perception, it has been demonstrated that participants enhance the precision of perception through motor control (Kaim & Drewing, 2011; Drewing, 2012). For roughness perception, Tanaka, Bergman Tiest, Kappers, and Sano (2014) observed that participants adjust normal force, scanning velocity, and break times in ways that seem effective for different tasks and explored stimuli. Along these lines, Nefs, Kappers and Koenderink (2002) reported that applied contact force increased with line frequency of gratings and suggested that this might have improved perception in the task. However, these two studies on texture perception have not assessed whether movement adjustments actually optimize perceptual precision, neither did they investigate movement direction.

The objective of the current study is to investigate the interdependence between sensation and movements in the perception of texture spatial period. Our hypothesis is that humans adjust their movement direction when exploring oriented textures in order to optimize perceptual performance, and that they do so based on sensory signals for texture orientation. Our textures are defined by periodic parallel grooves; they are orientated by the groove orientation. For these oriented textures, movement direction and temporal cues are systematically linked. Finger movements in the direction of the texture orientation do not produce temporal cues to the spatial period of the texture. Finger movements directed orthogonally to the texture orientation produce temporal cues with maximal frequency. The more movement directions are shifted from the texture orthogonal (i.e., the direction along which a grating modulates), the lower is the temporal frequency of stimulation. Therefore, the temporal frequency also differs less between textures with different spatial frequencies, which probably yields less precise estimates of spatial frequency. By prescribing the movement direction on oriented textures, Experiment 1 systematically investigates the impact of movement direction on the perception of spatial period of textures. We expect that perceptual precision is enhanced when movements are directed orthogonally to the texture. Experiments 2 and 3 test whether participants use sensory signals for texture orientation in order to optimize movement directions.

In Experiment 2, we investigate adjustments of movement direction over different strokes of the exploration process. Any adjustment of movement direction can only be based on the sensory signals gathered during the exploration process, when no prior knowledge is given. Thus, movement direction will only be adjusted after sufficient sensory signals for texture orientation are available. The integration of sensory signals can extend over several movements (Henriques & Soechting, 2005), and, because sensory signals are accumulated haptic perception

becomes more precise with extended exploration (Lezkan & Drewing, 2018). Hence, we expect that only in the late strokes, at the end of natural exploration movement, are directions adjusted to optimize temporal cues (i.e., towards the texture orthogonal). Note that a previous analysis of part of the data of Experiment 2 has been pre-published in a conference paper (Lezkan & Drewing, 2016). However, here a considerably improved analysis of movement data has been used, so that the present results have not been previously published.

In Experiment 3, we investigate whether adjustments of movement direction and the perception of texture orientation rely on a common basis, namely shared sensory signals for texture orientation. In vision, numerous studies have investigated how far underlying sensory signals are shared by eye movement control and perception. These studies compared perceptual precision to eye movement precision as derived from psychophysical and ‘oculometric’ functions, respectively (e.g., Watamaniuk, & Heinen, 1999; Stone & Krauzlis, 2003; Gegenfurtner, Xing, Scott, & Hawken, 2003). Here, we construct ‘movometric’ functions based on the exploratory behavior, which allow for the direct comparison between the precision of motor adjustments and the perception of texture orientation. We expect that the precision of perception and movement vary with the same factor, namely texture period.

## 5.2. Experiment 1

Experiment 1 investigates the impact of movement direction on the perception of texture period. Haptic texture stimuli were 3D printed (Stratasys Objet 30 Pro). All gratings were cylindrical discs with a groove pattern following a sine-wave function on top of the surface. Participants stroked once over each of two gratings in a pair and judged which one had a higher spatial frequency ( $=1/\text{spatial period}$ ). We used a PHANToM force-feedback device to restrict

finger movements to specific directions by defining exploration tunnels (orientation:  $0^\circ$ ,  $30^\circ$ , or  $60^\circ$ ). The movement direction relative to the texture orthogonal was manipulated ( $0^\circ$  vs.  $45^\circ$  vs.  $90^\circ$  shifted from the texture orthogonal). The orientation of the textures relative to the body was varied systematically depending on the exploration tunnel orientation and the movement direction relative to the texture orthogonal. For each of the relative movement directions we measured the just noticeable difference (JND) of the textures' spatial period. Based on the decreasing availability of temporal cues, we predict a systematic increase in JNDs (i.e., discrimination thresholds assessing perceptual precision) with higher shifts from orthogonal movement direction.

### **5.2.1. Methods and Materials**

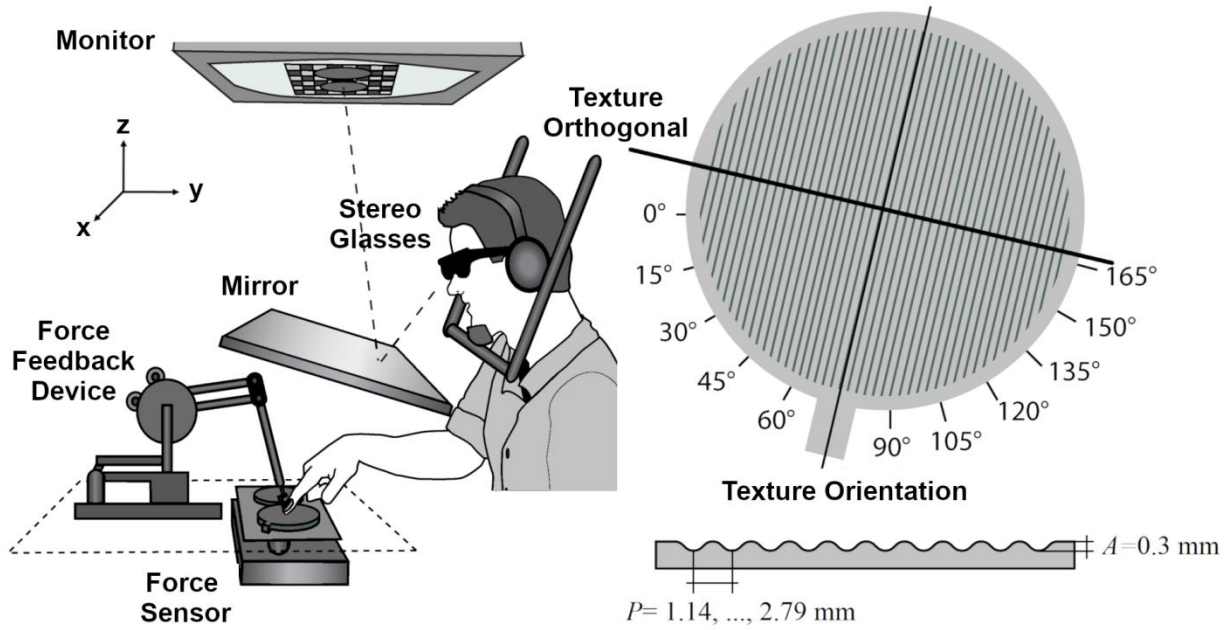
#### **5.2.1.1. Participants**

The sample was composed of sixteen right-handed participants aged 19 - 29 years (11 females). All participants were naïve to the purpose of the experiment and were paid for participating. Nobody reported recent injuries of the right index finger or sensory or motor impairments. All had a two-point discrimination threshold of 3 mm or lower at the finger pad of the right index finger. In all three experiments, the reported methods and procedures were approved by the local ethics committee (LEK) of FB 06 at Giessen University (approval number: 2013-0021). Participants gave written informed consent. The study was conducted in accordance with the ethical standards laid down in the 2008 Declaration of Helsinki.

#### **5.2.1.2. Apparatus and Stimuli**

Participants sat in front of a visuo-haptic setup (see Fig. 5.1). The setup contained a PHANToM 1.5A haptic force feedback device, force sensor (682 Hz, resolution: 0.05 N) and a 22"-computer screen (120 Hz, 1024 x 1280 pixel). Circular grating stimuli were presented next

to each other placed on the force sensor, which measured the finger force applied to the stimuli. Participants looked on the computer screen through stereo glasses and a mirror (40 cm viewing distance in total). Due to this mirror, participants were not able to see the real stimuli or their hand. Additionally, the setup allowed for a spatial alignment of the 3D-visual representation with the haptic display. In the virtual 3D-scene stimuli were displayed as three dimensional cylindrical discs with a border. This visual representation did not present the texture pattern or its orientation. The participant's finger position was visible as a small sphere (8 mm diameter) when moving outside the stimulus area. We connected the right index finger to the PHANToM via an adapter, which was attached by double-faced adhesive tape to the nail. This setup allowed for free finger movements having all six degrees of freedom in a  $38 \times 27 \times 20 \text{ cm}^3$  workspace. However, here we used the PHANToM device to restrict finger movements to follow a predefined direction within the exploration tunnel and to measure finger position. Exploration tunnels were defined by a 16 mm wide path across the texture's surface, where the PHANToM device displayed no force. Outside this exploration tunnel, forces  $F$  (in  $N$ ) were presented that drove the finger back to the exploration tunnel, and increased by a square function with the finger's distance  $D$  (in  $mm$ ) to the tunnel's border ( $F = \sqrt{2} D^2 / 441 \text{ mm}^2/N$ ). The exploration tunnel was displayed by a cuboid on top of the stimulus in the 3D-visual representation. In order to provide stable 3D vision, the participants head was stabilized by a chinrest. Custom-made software controlled the experiment, collected responses, and recorded the data from the force sensor and the PHANToM with recording intervals of 3 ms. We used headphones and ear plugs to mask sounds from haptic exploration.



**Figure 5.1.** Sketch of setup and stimulus. Stimulus location, shape and the exploration tunnel contour were visually represented on a monitor and were seen through a mirror and stereo glasses. The participant's right index finger was connected to the PHANTOM via an adapter. The PHANTOM measured the finger position and restricted the movement to a predefined exploration tunnel. Both real grating stimuli were placed in the same orientation next to each other on a force sensor.

Haptic gratings were created with the OpenSCAD software and 3D printing. The 3D printer (Objet 30 Pro, Stratasys Ltd., United States) builds drop-wise arbitrary 3D objects from 3D digital data (photopolymer material: VeroClear; build resolution: 600 x 600 x 1600 dpi (x-, y-, z-axis)). The grating discs were 4 mm high (z-axis) with a texture diameter of 90.7 mm (total diameter with border: 100.7 mm). A grip (10 x 5 mm) indicated the texture orientation for the experimenter (Fig. 5.1). The height of the texture  $z$  followed a sine-wave function with the peak amplitude ( $A$ ) of 0.3 mm (see Equation 1). The advantage of sine-wave stimuli is that they consist of only one spatial frequency component (Loomis & Lederman, 1986). The standard stimulus had a period ( $P$ ) of 1.78 mm. We created 25 comparison gratings with periods between 1.14 and 2.79 mm, with an approximate step size of  $0.016 \cdot \log(P)$ . The spatial period of grooves was chosen so that they would be big enough to fall in the range of macrostructures ( $\geq 1$  mm) and



small enough to lie in the range where manipulations of spatial period are in a monotonic relationship to perceived roughness ( $\leq 3$  mm; Klatzky, Lederman, Hamilton, Grindley & Swendsen, 2003; Drewing, 2016).

$$z = \frac{1}{2}A \sin \frac{2\pi x}{p} + \frac{1}{2}A \quad (1)$$

### 5.2.1.3. Design and Procedure

Participants explored a stimulus pair consisting of one standard and one comparison stimulus in each trial. They judged which of the two had a higher spatial frequency, as this is more intuitive to judge than the spatial period. We explained spatial frequency as the number of experienced (i.e., felt) grooves over a certain distance. Note that textures included 40-80 ridges that were typically explored within less than a second (movement speed  $\sim 10$  cm/s); therefore, counting of individual ridges is likely impossible. Stimuli with a longer period have lower spatial frequencies. We randomized which of the two stimuli was presented on the left side. During each trial, both stimuli of the stimulus pair were placed in the same orientation (example for one stimulus in Fig. 5.1). The orientation of the stimulus pair was determined by a) the variable orientation of the exploration tunnel which was randomly chosen to be  $0^\circ$ ,  $30^\circ$ , or  $60^\circ$ , and b) the presented level of the within-participant variable shift of movement direction from the texture orthogonal ( $0^\circ$  vs.  $45^\circ$  vs.  $90^\circ$ ). We measured just noticeable differences (JNDs) in terms of the discrimination of spatial period as a function of movement direction shift from the texture orthogonal. The lower the JNDs the better discrimination performance, that is to say the higher the perceptual precision. JNDs were assessed by the 75% discrimination threshold using the Best PEST adaptive staircase procedure (Lieberman & Pentland, 1982) combined with the two-interval forced-choice task. In this method, the next comparison stimulus is chosen by an

algorithm, which takes in to account previous responses for this condition. More precisely, the algorithm chooses the comparison with the maximum likelihood of being the threshold. In this way, the information gain in each step is maximized, which makes this method optimal in order to fasten threshold determination. The procedure came to an end after 45 trials per staircase. The final maximum-likelihood estimate in each staircase estimated the JND. For each condition, one upper and one lower staircase were implemented starting with the 2.79 and 1.14 mm, respectively. The trials from all 6 staircases were randomly interleaved. In order to practice the task and the movement restrictions through the exploration tunnel, participants performed 4 trials of each staircase prior to the experiment.

At the beginning of each trial a blank three dimensional cylindrical disc with a border indicated the location of the first stimulus (randomly assigned to the left and the right stimulus of the stimulus pair). Additionally, a cuboid on top of the stimulus displayed the exploration tunnel (orientation:  $0^\circ$ ,  $30^\circ$ , or  $60^\circ$ ). A dot, which was randomly assigned to be either on the left end ( $0^\circ$ ,  $30^\circ$ , or  $60^\circ$ ) or the right end ( $180^\circ$ ,  $210^\circ$ , or  $240^\circ$ ) of the exploration tunnel, indicated on which point the exploration should start. The visualization served to guide the participant through the trial without giving any information about textural structure or texture orientation. Participants were instructed to move from one point on the stimulus border to another through this ‘tunnel’ and they couldn’t see their hands moving during this time. After the participant stroke once over the texture within the exploration tunnel, the visualization of the second stimulus appeared. Exploration tunnel, shift from orthogonal, and starting point were identical for both stimuli of a pair. After one stroke over each stimulus, participants decided which of the two textures had a higher spatial frequency by pressing virtual buttons rendered by the PHANToM.

#### 5.2.1.4. Data Analyses

The data for each participant consisted of upper and lower JNDs for each of the three movement direction shifts from the texture orthogonal. In order to calculate JNDs for each movement direction shift, we averaged the corresponding upper and lower JND estimates. These values were entered into an ANOVA with the within-participant variable, Direction Shift of movement from the texture orthogonal ( $0^\circ$  vs.  $45^\circ$  vs.  $90^\circ$ ). We tested our hypothesis of a systematic monotonic increase in JNDs with higher Direction Shift by performing a linear contrast analysis on the direction-specific JNDs. Further, we calculated planned paired one-sided *t*-tests to analyze whether the contrasts between individual conditions reflect the increase in JNDs with higher Directional Shift.

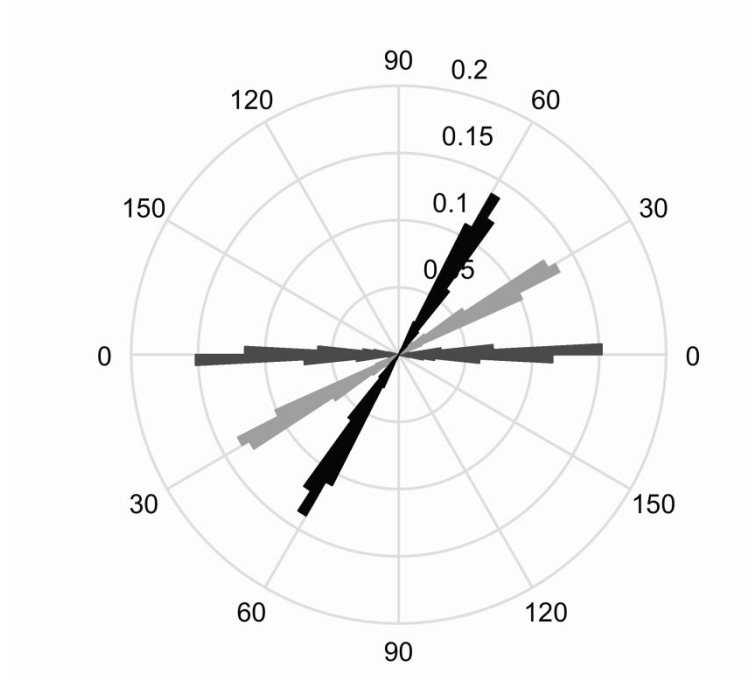
Additionally, in order to check for the manipulation of the exploration tunnel, we analyzed the exploratory movement data. We extracted the direction of one stroke over each stimulus within each trial and averaged over the two strokes of a trial. Strokes were analyzed from exploratory parts of the movement, when the finger was touching the stimulus area with at least 0.1N of force for at least 200 msec. We detected strokes as continuous movements either from one texture border to another or between two movement turns, which we extracted by zero crossings in the 1st order derivatives of the x- or y-position over time. Stroke detection algorithms were considerably improved in comparison to a previous conference article on Exp. 2 (Lezkan & Drewig, 2016), as follows: First, in order to exclude that curved movements will be detected as movement turns, we only included those zero crossings for which the 1st order derivative changed by more than 0.01 rad. Second, we increased the precision of measuring movement endpoints: In case the z-position of a movement turn was an outlier based on the exploratory part of the movements for this trial, stroke endpoints were defined as the closest

positions within the 95%-confidence interval of z-positions. In case several strokes over one stimulus were detected by the algorithm (which might occur due to movement pause or slip) we analyzed only the stroke with the longest duration. We included only trials in this analysis for which we were able to extract strokes from the movement data for both stimuli of a trial (94%).

## 5.2.2. Results

### 5.2.2.1. Movement Data

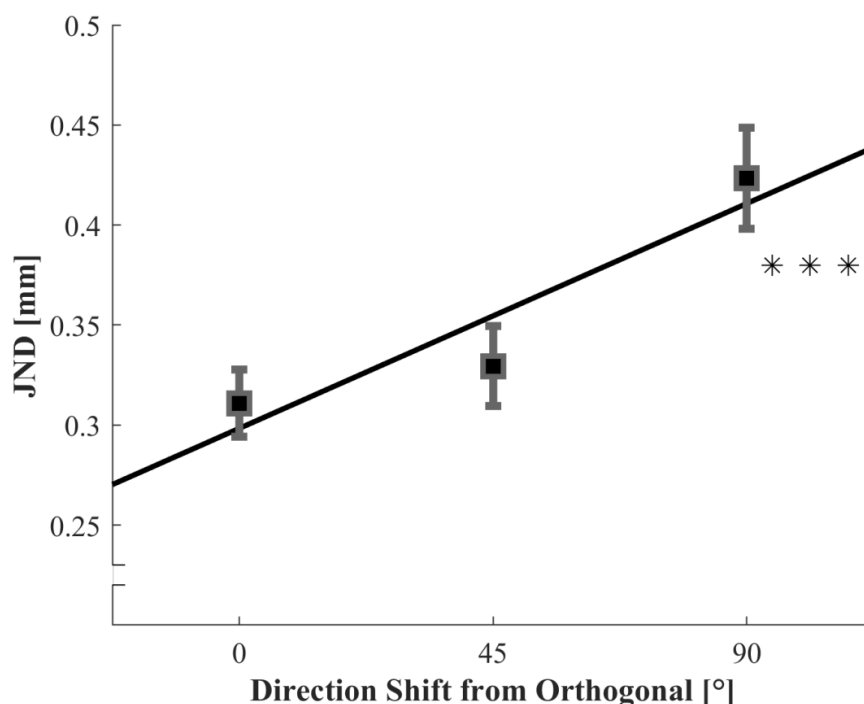
We plotted the movement directions from all participants and all trials in a circular histogram (see Fig. 5.2). The different colors represent trials with different exploration tunnels. As can be seen from the graph, movements followed the aimed direction with little spread.



**Figure 5.2. Movement directions.** Circular histogram (bin size 3°) of all trials and participants for different exploration tunnels. Movement direction for trials with the exploration tunnel of 0° are plotted in dark gray, light grey stands for the 30°, and black for the 60° exploration tunnel. The numbers indicate the proportion of strokes in a certain direction.

### 5.2.2.2. JNDs

Individual JNDs were entered into the ANOVA with the within participant variable Direction Shift from the texture orthogonal (0°, 45°, and 90°; depicted in Fig 5.3). The main effect of Direction Shift was significant,  $F(2,30) = 5.513$ ,  $p = .009$ . The linear contrast analysis revealed a significant linear increase in the JNDs with larger Direction Shift,  $F(1,15) = 8.758$ ,  $p = .005$ . As expected, JNDs were higher with larger Direction Shifts from the texture orthogonal. In addition, our directional a-priori hypothesis allowed for a secondary analysis through one-sided  $t$ -tests between individual conditions (Bonferroni-corrected alpha levels at 0.017). The JNDs were significantly higher for the 90° condition than for the 0° condition,  $t(15) = 2.959$ ,  $p = .005$ . The JNDs in the 45° condition were not significantly higher than the JNDs in the 0° condition,  $t(15) = -.690$ ,  $p = .256$ . They were also not significantly lower than the 90° condition,  $t(15) = 2.219$ ,  $p = .021$ , but showed a trend. We conducted a sensitivity analyses with G\*Power 3 (Faul, Erdfelder, Lang, & Buchner, 2007). The power of finding an effect of 0.15 mm (8.5 % Weber fraction difference) or more was at least 96% for the Bonferroni-corrected one-sided  $t$ -tests (standard deviation assessed as 0.143 mm by the average standard deviation of the differences between all conditions). However, 0.15 mm is a rather large effect, comparable to difference for moving and stationary roughness discrimination in fine textures (Hollins & Risner, 2000). It is reasonable to expect such large effect sizes for the comparison between the extreme conditions of directional shift 0° (maximal temporal cues) and 90° (no temporal cues). The middle condition should vary by less, which is why the associated  $t$ -tests might not have had sufficient power to detect an effect.



**Figure 5.3.** Average JNDs for the 3 conditions of movement direction shift from the texture orthogonal. Error bars are indicating within-participant standard errors (Loftus & Masson, 1994).

### 5.2.3. Discussion Experiment 1

In overall analysis participants were better in discriminating the spatial period of the texture as they moved more orthogonal to the texture. Although not all individual comparisons were able to confirm the effect, moving orthogonally or obliquely to the texture was or tended to be better than moving in line with the texture. The results are consistent with the prediction of a systematic monotonic increase in perceptual precision with movement directions closer to texture orthogonal, which we had made from the systematic increase of the temporal frequency of signals. A higher temporal frequency of signals likely allows for a better differentiation of textures based on temporal cues. Thus, our results support the idea that movement direction can

influence perceptual precision, and that different movement directions come along with differently useful sensory signals for texture period.

In Experiment 1, we were interested in the effect of movement direction relatively to the texture orientation. However, one might wonder whether the absolute direction of the movement might also have affected texture perception. Such effects of the absolute movement direction were previously described for other tasks, such as shape perception (Drewing, 2012). In order to test whether the absolute movement direction might have additionally influenced the spatial period judgments, we reanalyzed the staircase data by fitting psychometric functions for all trials with absolute movement direction (i.e. the same exploration tunnel). Neither the points of subjective equality (PSEs),  $F(2,30) = 1.447$ ,  $p = .251$ , nor the just noticeable differences (JNDs),  $F(2,30) = .891$ ,  $p = .421$ , were significantly affected by the absolute direction of the movement. That is, in contrast to the results for relative movement direction we did not find evidence that also absolute movement direction considerably influenced perceptual precision nor did the different motion angles introduce a noteworthy bias in the perceived spatial period.

In optimal exploration, the systematic relationship between the movement direction relative to texture orientation and precision of perception should be exploited (Najemnik & Geisler, 2005; Klatzky & Lederman, 1999; Kaim & Drewing, 2011). Some studies demonstrated that exploration movements are adjusted based on previously accumulated sensory signals - for different movement parameters during a haptic localization task (Saig et al., 2012), and for finger force during softness perception of differently compliant objects (Lezkan & Drewing, 2015). In order to test for similar mechanisms in texture perception we designed Experiment 2, in which we measure the freely chosen movement direction for texture exploration. We expect to find

results complementary to Experiment 1, that is, that sensory signals for texture orientation influence movement direction.

### 5.3. Experiment 2

In Experiment 2, we investigate movement direction in different strokes of the exploration process. We expect that movement directions are adjusted over time when doing so can improve perceptual performance, but not when there is hardly an effect of movement direction on perception. In order to test this assumption, we created two kinds of stimuli, again using 3D printing. The first type of stimuli, standard gratings, was composed of a groove pattern following the sine-wave function along one dimension, like the stimuli of Experiment 1 (periods 1.27 and 1.44 mm; Fig. 5.4). The texture pattern of the second type of stimuli, comparison gratings, was composed of the intersections of two orthogonal sine-wave function patterns (periods: 1.02 to 1.69 mm). Thus, standards have one clear orientation, and a systematic relationship between movement direction and temporal frequency of stimulation exists: We state that for the standards, finger movements in the direction of the texture orientation generate no temporal cues to the texture period. In contrast, orthogonal movements generate optimal temporal cues by maximizing the temporal frequency of cues and, therefore, also maximizing the differences in temporal cues from different textures. For comparisons, in contrast to standards, there is not a single direction which maximizes the temporal frequency of stimulation. Movements in two orthogonal directions ( $0^\circ$  and  $90^\circ$ ) over comparisons provide similar temporal cues to spatial period. Participants explored one standard and one comparison stimulus grating in a trial and reported which of the two had a higher spatial-frequency. We manipulated the orientation of the stimuli in each trial, and measured movement direction for individual strokes.



Participants were free to use as many strokes as they wanted. We predicted that, movements over the standard will be preferentially directed orthogonally to the texture orientation after sufficient sensory signals for orientation have been gathered. In contrast, we did not expect corresponding adjustments for the comparisons. The basic methods and a work-in-progress analysis of the raw data from the current Experiment 2 were presented in a conference paper (Lezkan & Drewing, 2016). For the sake of readability, we repeat the experimental methods in the present study. Importantly, however, the presented results are novel because raw movement data were entirely reanalyzed using improved algorithms (as described for Experiment 1).

### **5.3.1. Methods and Materials**

#### **5.3.1.1. Participants**

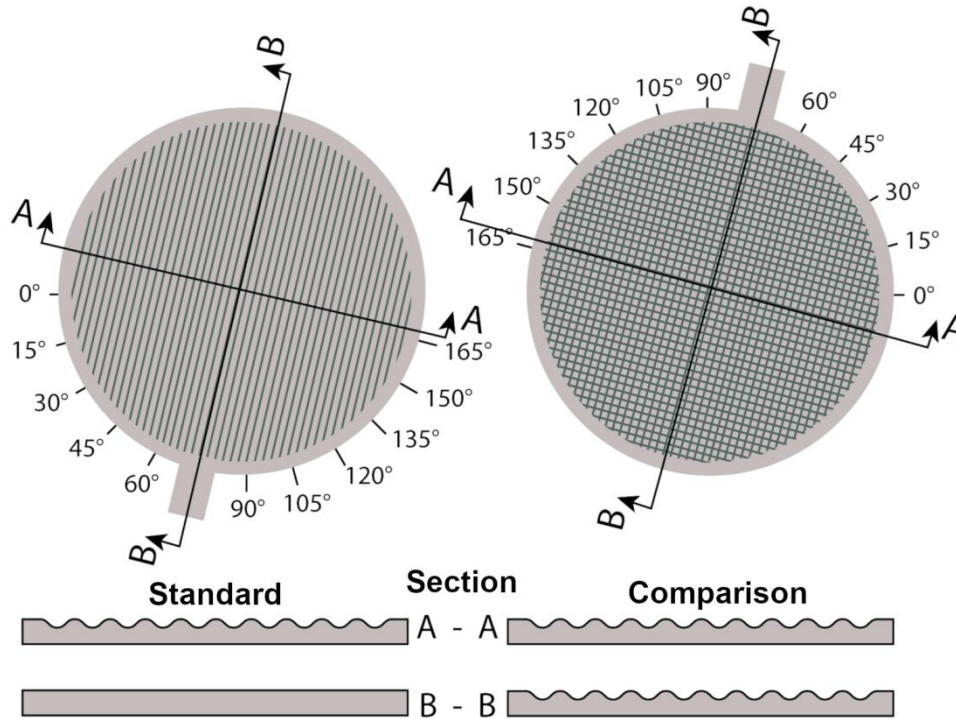
Thirteen right-handed healthy participants (age range: 19 – 32 years; 7 females; two-point discrimination threshold 3 mm or lower) were paid for participating. Participants were naïve to the purpose of the experiment and had not participated in Experiment 1.

#### **5.3.1.2. Apparatus and Stimuli**

The setup was identical to that used in Experiment 1, and stimuli had the same size and grip. Standard gratings were constructed exactly as for Experiment 1 (Fig. 5.4), using two standard stimuli with the periods (P) of 1.27 mm and 1.44 mm (1 D sine-wave). In this experiment, however, we defined comparison stimuli in a way that they would not have a single clear orientation while still having spatial periods comparable to the standards. This was achieved by computing the texture height of the comparison stimuli from two overlaid sine-wave functions that were oriented perpendicular to each other. The intersection of both textures defined the comparison. A cut through two orthogonal axes of comparison stimuli would result

in identical images (Fig. 5.4), and the texture height  $z$  was at each point the minimum of the two sine-wave functions (2 D sine-wave; peak amplitude  $A = 0.3$  mm):

$$z = \min\left(\frac{1}{2}A \sin \frac{2\pi x}{P} + \frac{1}{2}A, \frac{1}{2}A \sin \frac{2\pi y}{P} + \frac{1}{2}A\right) \quad (2)$$



**Figure 5.4.** Sketch of a stimulus pair. The standard stimulus on the left is an oriented grating defined by the sine-wave function on one of the axis. The comparison stimulus on the right is a grating with no clear orientation defined by the union of two sine-wave functions on two axes. The two stimuli are depicted in the texture orientation of 75°.

We created 5 comparison gratings with periods  $P$  of 1.02, 1.19, 1.35, 1.52, and 1.69 mm. For each of the two standards, we used three comparisons. Two comparisons were defined by  $\pm 20\%$  of the standard's period, because 20% corresponds to the Weber fraction in active touch (Nefs, Kappers, & Koenderink, 2001; Experiment 1). The third comparison was the same stimulus for both standards (1.35 mm); it has 6% lower period than the standard of 1.44 mm and 6% higher period than the standard of 1.27 mm. Based on the stimulus construction, we defined texture orientation in standard gratings as the orientation of the parallel grooves. By definition,

comparison gratings had two equal groove orientations. In the following, we will refer to one of them as the texture orientation ( $75^\circ$  in Fig. 5.4). It is important to note that the comparison grating had the same temporal frequency of stimulation for two movement directions, along ( $0^\circ$ ) or against ( $90^\circ$ ) its orientation. All other movement directions lowered the frequency of stimulation only moderately ( $< 30\%$ ). The highest deviation in temporal frequency of stimulation is produced by a movement direction of  $45^\circ$  to the texture orientation, which corresponds to a multiplication with  $\sin(45^\circ)$  ( $\approx 0.7 = -30\%$ ). Therefore, there is hardly an effect of texture orientation on the frequency of stimulation for comparisons, in contrast to standards.

### **5.3.1.3. Design and Procedure**

In each trial, a standard and a comparison stimulus were explored and participants had to judge which of the two had a higher spatial-frequency—regardless of other differences between the textures. We manipulated the orientation of the stimulus pair on the force sensor ( $15^\circ$ ,  $45^\circ$ ,  $75^\circ$ ,  $105^\circ$ ,  $135^\circ$ , and  $165^\circ$ ; Fig. 5.4). We measured the movement directions over the standard and comparison gratings. Hereby, we focused on the first, middle and last stroke per stimulus, as they represent movement adjustments at different segments within the exploration process.

We used two standard stimuli paired with one of three comparisons (standard 1.27 mm with comparisons 1.02, 1.35, and 1.52 mm; standard 1.44 mm with 1.19, 1.35, and 1.69 mm). The standard was either presented at the left or the right side in order to control for potential effects of the hemispace. Both gratings of one stimulus pair were placed in the same orientation.

The focus of this experiment was on the adjustments of movements based on sensory signals gathered over the exploration process. Hence, it was essential to design this experiment in a way that encourages participants to perform a higher number of strokes over each texture. We chose a difficult perceptual task (small differences in the periods of standards and comparisons)

in order to ensure that several strokes would be required to gather sufficient information for a correct response. Further, in free exploration, it is possible that participants avoid additional movement due to the associated additional movement costs. Movement costs, however, can be counterbalanced by rewarding the performed movement (Todorov & Jordan, 2002). Therefore, we introduced the experiment as a game and included rewards for correct responses. By giving a correct response participants could earn 10 or 100 points, which was equally distributed among all trials. Overall, the experiment consisted of 2 [standards] x 3 [comparisons] x 6 [orientations] x 2 [standard left or right] x 2 [10 or 100 points] = 144 trials. The order of the trials was randomized. Trials were presented in 3 successive blocks of 48 trials. Between two blocks, participants were instructed to take a break of at least two minutes. In total, the experiment lasted 2-3 hours. Prior to the experiment participants performed a flexible training with up to 8 trials to ensure that they understood the task.

Before each trial, the number of points corresponding to a correct response (10 or 100) was displayed on screen. When the first stimulus was displayed, a dot indicated the start position. Exploration started randomly either with the left or the right stimulus on a random position at the stimulus border ( $20^{\circ}$ - $350^{\circ}$ , in steps of  $30^{\circ}$ ). Participants were free to perform as many strokes and to switch as often between stimuli as they wanted. Participants received 16€ plus an additional euro for every accumulation of 500 points. Winning of this additional euro was indicated by a visual and auditory signal, which was displayed randomly 1-3 trials after the points had been accumulated. The total payment was not lower than 23€ (guessing) and not higher than 31€ (perfect performance).

#### 5.3.1.4. Data Analyses

Exploration movements on each stimulus were segmented into individual strokes. For the exploration of each stimulus we analyzed 3 strokes (first, middle, last). If the total number of strokes was even, the middle stroke was defined as the later one of the two possible. Strokes were segregated from the movement data as in Experiment 1 (and thus raw data was reanalyzed by improved algorithms as compared to Lezkan & Drewing, 2016). The analysis was based only on those trials in which participants performed at least two strokes on each stimulus. When participants performed exactly two strokes, the second stroke was coded as the middle and last stroke. We aligned all stimulus orientations with an orientation of  $0^\circ$  in order to collapse data over trials. To do so, we rotated stroke directions by their corresponding texture orientation in opposite direction. We weighted individual strokes with their duration, as strokes had considerable differences in their duration. Based on the weighted data we calculated individual histograms of movement directions (bin size:  $15^\circ$ ) separately for each combination of grating type and stroke (first, middle, or last). Each histogram displays which proportion of exploration time one participant moved in a specific direction. For an overall analysis, we computed an average histogram for each combination of grating type and stroke based on the individual participant analyses. For each combination of stroke (first, middle, last) and grating type (standard, comparison) circular statistics on the averaged binned data were conducted using the Matlab Circular Statistics Toolbox (Berens, 2009). We performed a *V*-test, a variant of the Rayleigh test, which tests the hypothesis that the population is not distributed uniformly around the circle but has a specified mean direction (see Mardia & Jupp, 2000), which was  $90^\circ$  in our case. We applied Bonferroni-corrected alpha levels at 0.0083 ( $\alpha=.05/6$ ). This statistical analysis outputs *V*-values, which are higher the bigger the deviation of the empirical distribution from a

uniform distribution is and the more consistent the empirical mean direction is with the predicted one. Therefore, non-significant results could either be due to a uniform distribution, or a distribution with a mean that deviates from the predicted direction of  $90^\circ$ . We predict that movement directions will get increasingly distributed non-uniformly over the course of the exploration of the standard stimulus. That is to say, we expect significant results for the last stroke over the standard.

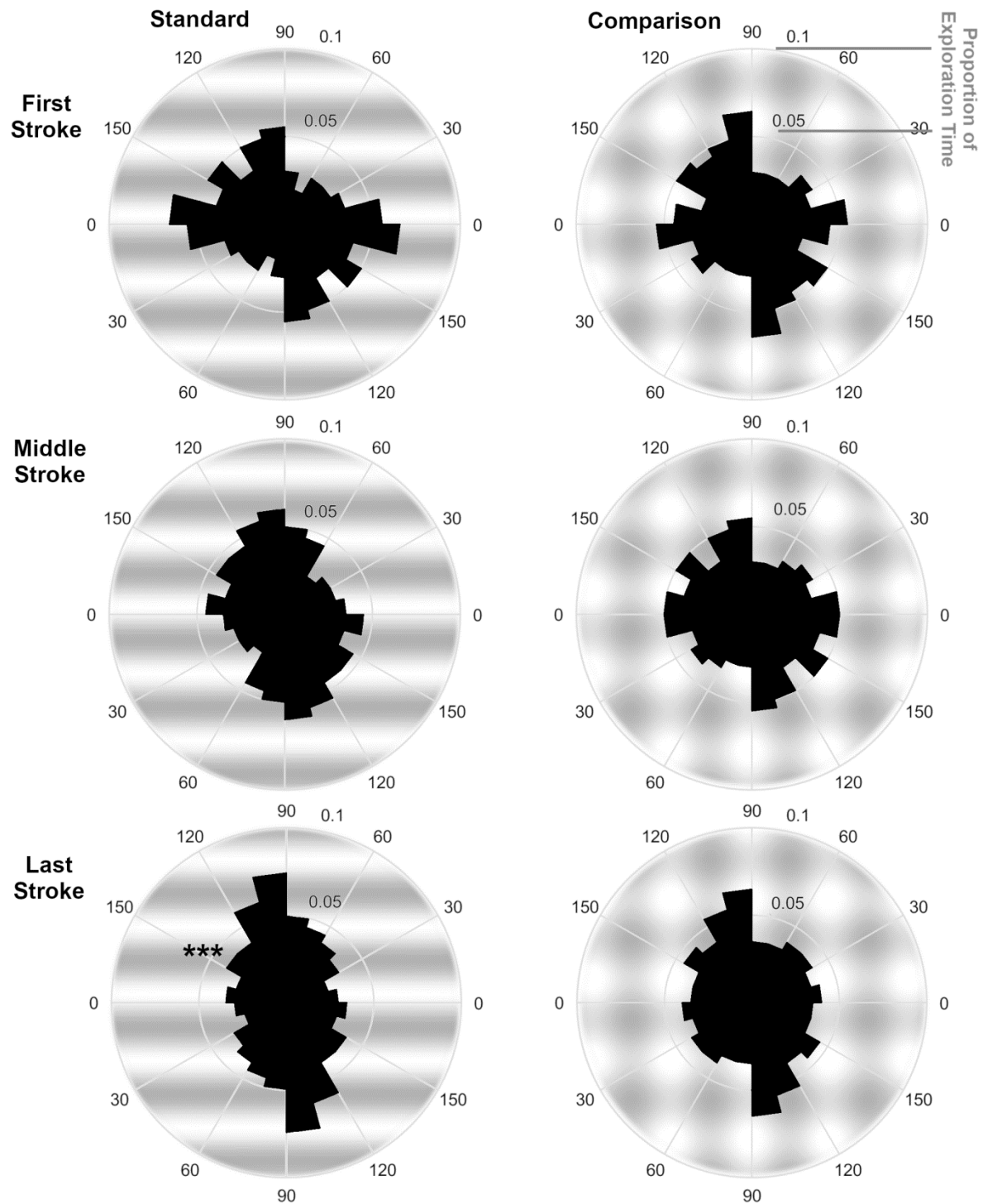
### **5.3.2. Results**

#### **5.3.2.1. Exploration and Task Performance**

On average, participants spent 7.55 seconds ( $SD = 2.75$ ) on the standard and performed 4.29 strokes ( $SD = 1.93$ ), and they spent 7.45 seconds ( $SD = 2.52$ ) on the comparison with 4.02 strokes ( $SD = 1.84$ ). They switched twice between the stimuli ( $M = 2.05$ ,  $SD = .82$ ): once from first to the second stimulus and then once back to the first stimulus. The time spent on the stimulus did not significantly differ for the two gratings,  $t(12) = .688$ ,  $p = .505$ , but participants used more strokes for the standard gratings,  $t(12) = 2.585$ ,  $p = .024$ . Participants gave 59.2% correct responses on average ( $SD = 8\%$ ), which is significantly higher than guessing (50%),  $t(12) = 3.956$ ,  $p = .002$  ( $t$ -test against 50% after rationalized arcsine transformation). There was no significant difference in the arcsine-transformed percentages of correct responses between the trials with different spatial periods of the standard stimulus,  $t(12) = .024$ ,  $p = .814$ . Similarly, the texture orientation did not produce a significantly non-uniform distribution of the number of correct answer, when being tested in a Rayleigh test,  $R = 0.12$ ,  $p = .889$  (means of percentage correct answers ranged between 55.1 % and 64.7 %).

### 5.3.2.2. Movement Directions

For the first, middle, and last stroke over the standard or the comparison grating we plotted the angular distributions of movement directions in Fig 5. We performed *V*-tests on each distribution testing whether it is not uniform but rather has a specified mean direction of  $90^\circ$  (Bonferroni-corrected alpha levels at 0.0083). In the first stroke, the *V*-tests were not significant for both gratings (standard:  $V = -8.622$ ,  $p = .892$ ; comparison:  $V = .167$ ,  $p = .491$ ). Similarly, in the middle stroke both tests did not reveal significant results, although there is a trend for the standard stimulus (standard:  $V = 10.492$ ,  $p = .069$ ; comparison:  $V = -2.922$ ,  $p = .659$ ). As predicted, participants showed a significant non-uniformity in their movement directions and moved orthogonally ( $90^\circ$ ) to the grating orientation in the last stroke over the standard,  $V = 19.425$ ,  $p = .003$ . In the last stroke over the comparison, non-uniformity did not reach significance,  $V = 7.275$ ,  $p = .152$ . The overall results of the *V*-tests are well reflected in the individual participant analyses when applying (Bonferroni-corrected) *V*-tests to the individual data. As expected, no participant showed more significant adjustments to the comparison than to the standard. The data of three participants had the same pattern as the average data, with an adjustment in the last stroke over the standard only. One participant adjusted in the last and middle stroke over the standard while showing no adjustment for the comparison. Four participants adjusted their middle and last stroke significantly to the standard, and the last stroke to the comparison. Five participants showed no significant adjustments to standard or comparison. For non-uniform individual distributions, the precision of the mean estimation ranged between  $\pm 5.94^\circ$  and  $\pm 24.23^\circ$  (95% confidence interval).



**Figure 5.5.** Movement direction histograms for each stroke and texture type separately including all participant data. Textures were aligned to a 0° orientation. Note, possible movement directions varied only between 0-180° and were mirrored on the lower part of each figure.



Additionally, in order to examine the changes in movement directions which occurred over the exploration process, we calculated the proportion of movements directed orthogonally to the texture (directions of  $90^\circ \pm 15^\circ$ ) for the first and the last stroke. As it can be seen in Figure 5.5, 25% of the last strokes over standard gratings were adjusted to move approximately orthogonally to the texture orientation (directions of  $90^\circ \pm 15^\circ$ ). In contrast, only 17% of the first movements approximated this direction. When calculated for all individual participants, the difference in percentage of movements following the  $90^\circ (\pm 15^\circ)$  direction between the first and the last stroke over the standard is significant,  $t(12) = 4.123$   $p = .001$ . This is to say participants changed their movement direction significantly, from the first to the last stroke.

### 5.3.3. Discussion Experiment 2

Experiment 2 demonstrated that participants adjust their movement direction over the course of exploration. In the first stroke, movement directions were not dependent on texture type or orientation, but rather were uniformly distributed. However, in the last stroke participants moved along the texture orthogonal for uniquely oriented textures. Movements in the last stroke were not only directed in  $90^\circ$  to the texture orientation, but they also were significantly adjusted from the first stroke. These results suggest that motor adjustments are based on available sensory signals for texture orientation.

One might wonder why participants' task performance was only at about 59 %. It is important to note in this regard that we purposely chose a difficult task in order to ensure that participants would perform multiple exploration movements. The difference in spatial period between the two stimuli of stimulus pair ranged from 20% ( $\sim 1$  Weber fraction) to 6%. Thus, performances below 70% are reasonable. Additionally, structural differences between textures

(1D sine-wave vs. 2D sine-wave), can explain further performance problems. Note though, as participants were significantly better than chance, they were actually performing the task, and not guessing. We also tested whether fatigue might have decreased participants' performance. However, a comparison of performance in the first vs. in the second half of trials, did not indicate any systematic fatigue effect (paired  $t$ -test after rationalized arcsine transformation for percent correct responses,  $t(12) = .636, p = .573$ ).

In Experiment 3, we further test the hypothesis that motor adjustments are based on sensory signals by investigating whether sensory signals that underlie the perception of texture orientation are also used in the adjustment of movement direction. We compare the precision of the direct perception of texture orientation with that of movement adjustments to texture orientation. We use a method similar to the 'oculometric' functions that have been invented to compare eye movement precision to perceptual precision in vision (e.g., Watamaniuk & Heinen, 1999; Stone & Krauzlis, 2003; Gegenfurtner et al., 2003). Oculometric functions mimic the construction of (perceptual) psychophysical functions by recoding eye movements into binary "motor decisions" (e.g., movement to left vs. right half of visual field). Here, we define corresponding 'movometric' functions for exploratory movement direction. We manipulate the spatial period of the gratings, because perceptual discrimination of gratings is known to be better for gratings with larger grooves (Johnson & Phillips, 1981), and expect that spatial period will affect perceptual and movement precision in a similar way.

## 5.4. Experiment 3

Experiment 3 consisted of two parts: In each trial of the perceptual part, participants explored one oriented texture with two strokes within a limited exploration tunnel and judged the

texture orientation relative to their movement direction. In the equivalent trial of the motor part, participants again performed two strokes on the same oriented texture within the limited exploration tunnel and then performed one stroke in a freely chosen direction. Here, we assessed the rotation of the freely chosen direction relative to the previous movement directions. Half of the participants started with the perceptual part and the other half with the motor part. In both experimental parts, we varied the texture orientation relatively to the exploration tunnel in the same way. Additionally, we manipulated the spatial period of the texture. The data from the perceptual part served to estimate psychometric functions on the perceived texture orientation relative to the movement direction. The data from the motor part was used to define ‘movometric’ functions on the movement adjustments made during the free stroke. In the ‘movometric’ function, the rotation of the movement direction (clockwise vs. counterclockwise) corresponds to the binary response in the psychometric function. Therefore, cumulative Gaussian functions estimating the JNDs can be fitted to the perceptual and motor response. In this way, we are able to directly compare perceptual and movement data. Because they both follow the same sensory signals, we expect that the JNDs of both the haptic orientation perception and the movement direction increase for smaller spatial period.

#### **5.4.1. Methods and Materials**

##### **5.4.1.1. Participants**

Twelve right-handed healthy participants (age 20 - 33 years, 8 females; two-point discrimination threshold of 3 mm or lower) entered the sample of this experiment. Participants were naïve to the purpose of the experiment and had not participated in the other two experiments.

#### **5.4.1.2. Apparatus and Stimuli**

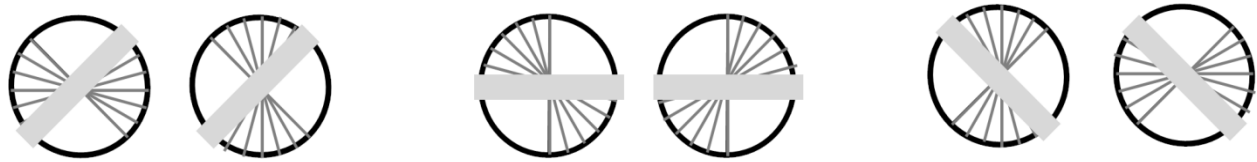
The apparatus was identical to that used in Experiment 1. Stimuli were defined as in Experiment 1. We used two different spatial periods  $P$  for the standard stimulus (1.44 and 1.86 mm). For the motor part, we additionally used 3 stimuli as the comparison stimulus ( $P=1.27$ , 1.61, and 2.03 mm).

#### **5.4.1.3. Procedure and Design**

This experiment consisted of two parts: a perceptual part and a motor part. Half of the participants started with the perceptual part and the other half with the motor part. In the perceptual part, we aimed to estimate individual psychometric functions, and in the motor part individual ‘movometric’ functions. Both parts were equivalent in the experimental design and were each preceded by 6 trials of training.

In the perceptual part, the task of the participant in each trial was to report the texture orientation of the standard stimulus relative to the exploration tunnel. We visualized two response options in order to get intuitive orientation judgments (Zangaladze, Epstein, Grafton, & Sathian, 1999) on the upper third of the screen (Fig. 5.6, actual size of each response option ~ 45.5 x 45.5 mm). Each of the response options stood for a class of texture orientations relative to the exploration tunnel. Response options were represented with single lines. On the left we presented the class of texture orientations, in which the texture orthogonal was rotated counterclockwise from the exploration tunnel. On the right we presented the class of texture orientations, in which the texture orthogonal was rotated clockwise from the exploration tunnel. The participant could choose one of the classes of the texture orientation by pressing virtual buttons rendered with the PHANToM. We presented texture orientation because this is intuitive for the participants to report. For our analyses, however, we recoded orientation to the

corresponding texture orthogonal. As the dependent variable we measured the proportion of trials in which participants reported that the texture orthogonal was rotated counterclockwise to the exploration tunnel.



**Figure 5.6.** Visually displayed response options in the perceptual part of Experiment 3. Options are plotted individually for the 3 exploration tunnels (from left to right:  $45^\circ$ ,  $0^\circ$ ,  $135^\circ$ ). The light grey bar depicts the exploration tunnel and the dark grey lines represent each for sample texture orientations. The left button always visualized the class of texture orientations rotated clockwise from the exploration tunnel, and thus texture orthogonals were rotated counterclockwise. The right button visualized the class, defined by counterclockwise rotation of orientation, and thus the texture orthogonal rotated clockwise from the exploration tunnel.

In the motor part, participants performed a two-interval forced choice (2-IFC) task judging spatial period. At the beginning of each trial, one of the comparison gratings was placed in their hands. For the haptic exploration of the comparison there were no restrictions; textures could be rotated and explored with both hands. Afterwards participants explored the standard grating. The standard grating had the same spatial period and relative orientation (of the textures orthogonal to the exploration tunnel) as in the equivalent trial of the perceptual part. However, now - after the two strokes within the exploration tunnel - the subjects were free to perform one additional stroke in any direction they wanted. We measured the movement direction in the free stroke as the dependent variable. More specifically, we looked for the proportion of trials, in which the movement direction was achieved by counterclockwise rotation from the exploration tunnel.

In each experimental part, participants explored a standard stimulus with two strokes within one of three predefined exploration tunnels ( $0^\circ$ ,  $45^\circ$ , or  $135^\circ$ ). We manipulated the spatial

period of the stimulus ( $P = 1.44$  mm,  $P = 1.86$  mm) and the rotation of the texture orthogonal relative to the exploration tunnel in 9 steps ( $-60^\circ$ ,  $-45^\circ$ ,  $-30^\circ$ ,  $-15^\circ$ ,  $0^\circ$ ,  $15^\circ$ ,  $30^\circ$ ,  $45^\circ$ ,  $60^\circ$ ;  $0^\circ$  indicates the exploration direction orthogonal to the texture) following the method of constant stimuli. Additionally, the starting point within the exploration tunnel could be at either end of the tunnel which was determined randomly. In each experimental part, every combination of spatial period and relative orientation was presented 10 times, resulting in a total of 540 trials per participant (2 [spatial periods] x 9 [relative orientations] x 3 [exploration tunnels] x 10 [repetitions]). Each experimental part was subdivided into 5 blocks with 2 repetitions each and the resulting 108 trials per block were randomly ordered. Each experimental part resulted in one session of about 3 hours.

#### **5.4.1.4. Data Analyses**

For the perceptual part, we calculated the proportion of trials in which the participant responded that the texture orthogonal was rotated counterclockwise from the exploration tunnel as a function of the actual relative rotation of the texture orthogonal. Cumulative Gaussian functions were fit to the individual psychometric functions for each standard (see Fig. 5.7a for example data). For this purpose, the `psignifit4` toolbox for Matlab that implements maximum-likelihood estimation procedures was used (Schütt, Harmeling, Macke, & Wichmann, 2016). Points of subjective equality (PSEs) were estimated by the Gaussian parameter  $\mu$  and just noticeable differences (JNDs) by  $\sigma$  (84% discrimination thresholds). In Figure 5.7 the JND is indicated as the difference between the rotation values of the texture orthogonal that are associated with 50% and 84% proportions of “counterclockwise” responses.

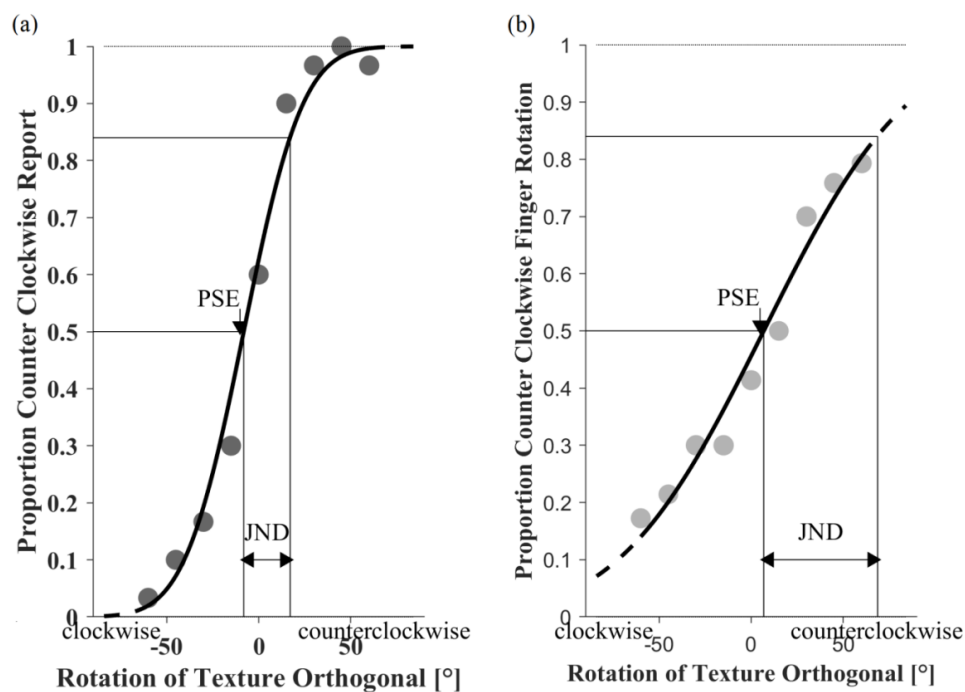
For the motor part, the movement directions in the free stroke were analyzed as described in Experiment 1. Thereafter, we recoded movement directions into the dichotomous variable

rotation from exploration tunnel (clockwise vs. counterclockwise). If a participant moves only a few degrees different from the previous stroke direction, the categorization into clockwise vs. counterclockwise rotation is straightforward. However, if a participant moves almost orthogonally to the previous stroke (around  $90^\circ$  /  $-90^\circ$  rotation) the proper categorization of the underlying rotation is less clear. Therefore, trials were included only if the relative movement direction of the last stroke was rotated between  $-85^\circ$  and  $+85^\circ$  from the exploration tunnel, and we were able to segregate 3 strokes (90% of trials). That is, we included data from trials with a relatively clear interpretation, which thus improved measurement precision. The total number of presented trials (270 per condition) was chosen in advance to be well above the number required for stable fitting of psychometric curves (Schütt et al., 2016), so that the exclusion of some trials would not be problematic. We determined whether the executed movement direction was achieved by clockwise or counterclockwise rotation from the exploration tunnel. Rotations between  $0^\circ$  -  $85^\circ$  were defined as counterclockwise rotations, whereas rotations between  $-85^\circ$  -  $0^\circ$  were defined as clockwise rotations.

Furthermore, we calculated the proportions of trials in which the participant rotated their finger movement counterclockwise from the exploration tunnel. To the individual ‘movometric’ functions for each standard period, we fit cumulative Gaussian functions (see Fig 7(B) for example data) using the `psignifit4` toolbox for Matlab [46]. While fitting ‘movometric’ functions, we allowed for positive and negative slopes of the cumulative Gaussian, and choose the better fitting of the two curves. We used the fitting parameter  $\eta$  as a measure of goodness-of-fit for the negative slope fit and the positive slope fit. As  $\eta$  accounts for overdispersion and varies between 0 (no overdispersion) and 1 (high overdispersion), the fit with the lower  $\eta$  was chosen (for details, see Schütt et al., 2016). For 18 of 24 data sets, the positive slope resulted in the better

fitting curve, while for 6 data sets the negative slope provided a better fit. Because also a negative slope indicates an adjustment to the texture orientation, we will consider all the data for further analyses. However, it is important to note that the predicted main effects of the ANOVA remained significant when participants with negative slopes were excluded.

The individual psychometric and ‘movometric’ PSEs and JNDs for each standard period were entered into repeated-measures ANOVAs with the factors Mode (perception vs. movement) and Standard Period ( $P=1.44$  vs.  $1.86$  mm).



**Figure 5.7.** Example data of participant 9 for one standard ( $P = 1.86$  mm). (a) Psychometric curve: the proportion of trials in which the participant perceived the texture orthogonal to be rotated counterclockwise from the exploration tunnel against the actual relative rotation of the texture orthogonal. (b) ‘Movometric’ curve: plotting the proportion of trials in which the participant rotated the finger counterclockwise from the exploration tunnel to perform the free stroke against the relative rotation of the texture orthogonal to the exploration tunnel.

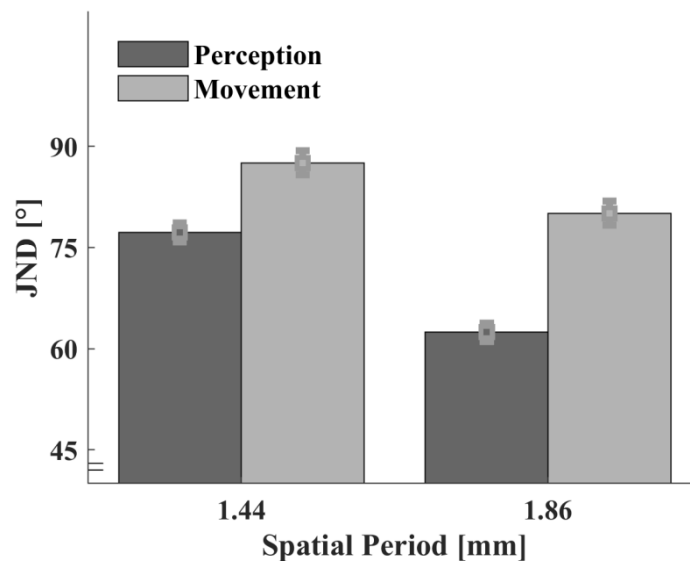
#### 5.4.2. Results



### 5.4.2.1. PSEs

As expected, none of the PSEs differed significantly in a single sample *t*-test against the relative Rotation of  $0^\circ$  ( $p \geq .222$ ;  $P = 1.44$  mm: perception  $-3.9^\circ$ , movement  $3.2^\circ$ ;  $P = 1.86$  mm: perception  $-1.7^\circ$ , movement  $2.4^\circ$ ). This result indicates that no constant biases are observed for the perceptual or the movement data. Additionally, neither any main effect nor the interaction,  $F(1,11) = .203$ ,  $p = .661$ , were significant in an ANOVA with the within-participant variables Mode (perception vs. movement),  $F(1,11) = 1.432$ ,  $p = .257$ , and Standard Period (1.44 vs. 1.86 mm),  $F(1,11) = .027$ ,  $p = .871$ .

### 5.4.2.2. JNDs



**Figure 5.8.** Average JNDs. JNDs from the psychometric (dark grey) and the ‘movometric’ curves (light grey) plotted with their within-participant standard errors (Loftus & Masson, 1994).

Individual JNDs (Fig. 5.8) entered an ANOVA with the within-participant variables Mode (perception vs. movement) and Standard Period (1.44 vs. 1.86 mm). As expected, JNDs were lower for higher Spatial Period,  $F(1,11) = 34.015$ ,  $p < .001$ . The JNDs were significantly lower in the perception Mode,  $F(1,11) = 5.369$ ,  $p = .041$ . The interaction between the two

variables did not reach significance,  $F(1,11) = 2.016$ ,  $p = .183$ . The estimated statistical power of our experimental design to find an effect of at least  $10^\circ$  in a one-sided test is more than 90% (standard deviation assessed as  $11^\circ$ ).

### 5.4.3. Discussion Experiment 3

Experiment 3 carefully examined the relationship between the perceived orientation of a haptic texture and a freely chosen movement direction over the texture. Our results show that both perception and movements were influenced by spatial frequency. Participants perceived the orientation of textures with low spatial frequencies more precisely. This expands previous findings about the role of spatial period for orientation discrimination (Van Boven & Johnson, 1994; Zhang et al., 2005) to active perception. Additionally, we show that movement adjustments were more pronounced in the condition of low spatial frequencies. This allows us to conclude that perception and movements are based on a similar mechanism in natural haptic exploration of surface texture.

Furthermore analyzing participants' 'movometric' and psychometric curves, we found that movements were less precise than perception. This result is in line with Gegenfurtner and Franz (2007), who showed that visual location perception was more precise than pointing movements to a seen location, and explained this finding by additional motor variance. Along these lines, studies on visual perception reported (at least for certain time windows) that perceptual precision was better than movement precision (e.g., Watamaniuk & Heinen, 1999; Ross, Goettker, Schütz, Braun, & Gegenfurtner, 2017). However, other studies on visual perception report similar perceptual and eye movement precision (e.g., Gegenfurtner et al., 2003; Stone & Krauzlis, 2003; Braun & Gegenfurtner, 2016). These different findings are likely due to

the complexity of the tasks, whereby less fine and more complex movements, such as the present hand movements, seem to come along with more motor variance (Vetter, Flash, & Wolpert, 2002; Ko, Poletti, & Rucci, 2010; Fitts, 1954). However, it is important to note that in the present experiment we measured movements and perception in different experimental parts with different tasks. Although the identical standard stimulus with the identical texture orientation was presented in each given trial for both experimental parts for a specific participant, differences in the precision of movements and perception may have arisen by the fact that both were not measured in exactly the same moment in time rather than by motor variance alone. In contrast to the studies on visual perception (Gegenfurtner et al., 2003; Stone & Krauzlis, 2003; Gegenfurtner & Franz, 2007) we, therefore, do not want to draw strong conclusion about the exact differences in the information processing. Nevertheless, given these possible differences in the measurement of movements and perception, the main effect of spatial period provides even stronger evidence for common mechanisms in orientation perception and movements in the exploration of spatial frequency.

## **5.5. General Discussion and Conclusion**

This study investigated the interdependence between perception and movement directions for oriented textures. On the one hand, our results indicate that perception depends on the exact movement parameters executed: When participants followed the texture orthogonal in their movement directions more closely, they perceived the texture's spatial period more precisely as compared to moving in line with the texture (Experiment 1, absolute movement orientation seem not to play a similar role). On the other hand, movement control depends on the sensation of texture orientation: Only after gathering sufficient sensory signals did participants adjust their

movement in the direction of the texture orthogonal in free exploration (Experiment 2). In addition, sensory signals that are used to perceive texture orientation are likely also used for movement adjustment, as shown by the finding that the precision of perception and movement adjustments were influenced in the same manner by the spatial period of the stimuli (Experiment 3). Taken together, our study speaks in favor of sensorimotor control mechanisms that improve haptic perception by choosing parameters of exploratory movement on the basis of sensations.

Our results extend previous research in several ways. First, as for the long standing debate about the role of temporal cues produced by movements in texture perception (e.g., Hollins & Risner, 2000; Weber et al., 2013), we provide an estimate for the advantage of movements, at least in the context of our spatial period discrimination task. We can estimate the advantage of temporal cues, when comparing JNDs measured in Experiment 1 for movement orthogonal to the texture (= optimal temporal cues) to the JNDs for movements in line with the texture (= no temporal cues). JNDs are composed of the variance for standard ( $\sigma_s^2$ ) and the variance for the comparison stimulus ( $\sigma_c^2$ ), which is assumed to be equal in our design ( $\sigma_c^2 = \sigma_s^2$ ). Under the assumption of independent percepts of comparison and standard, the JND can be directly related to the variance of the stimulus ( $\text{JND}_j^2 = 2 \sigma_s^2$  for the condition j). The empirical JNDs indicate that the variance doubles when temporal cues are removed. In this case, the Maximum Likelihood Estimation (MLE) model of optimal integration (e.g., Ernst & Bühlhoff, 2004) suggests that temporal cues are equally important and therefore should be weighted equally to spatial cues for the frequency estimation. However, it is important to note, that in contrast to other studies addressing the question on the role of temporal cues (e.g., Hollins & Risner, 2000; Lederman, 1974) we asked for a spatial frequency instead of a roughness judgment. Therefore, we cannot draw conclusions about roughness perception from our study.

Nevertheless, we would suspect that when measuring roughness discriminability and manipulating directional shift of movements from texture orthogonal, results could be comparable. The reason is that we chose stimuli in a range where spatial period manipulation and roughness perception are monotonically related (see Drewing, 2016). Additionally, it should be noted that previous research was also often measuring the magnitude of perceived roughness rather than its discriminability (e.g., Lederman, 1974 ). Second, we introduced a new method, the ‘movometric’ functions, which allowed a systematic comparison between movements and perception. Such functions are not limited to the context of our task. Natural movement adjustments for diverse exploration tasks can be used to assess the movement precision as in the present study. This only requires that movement data be converted to binary responses in order to fit ‘movometric’ functions. Future research could define such ‘movometric’ functions for movement adjustments within other exploratory procedures. For instance, indentation force is a key parameter in softness exploration (Lezkan & Drewing, 2015). Here one could fit ‘movometric’ functions to the probability that indentation force was reduced or increased as a function of stimulus softness, and then compare these to psychometric data on perceived softness.

Moreover, it is interesting to note, that not all participants moved in the way we expected. In Experiment 2, individual data for 4 out of 13 participants showed adjustments in the last stroke also over the comparison stimulus, and yet this stimulus did not have one clear orientation. While this adjustment does not seem to be very useful, it also does not harm perceptual performance. In Experiment 3, some participants adjusted their movements to the oriented textures in a way that deviated from our prediction. That is, some of the fitted psychometric curves had negative slopes. This indicates that the respective participant moved

along the texture orientation rather than orthogonal to it. Nevertheless, it is important to note that even reverse adjustments indicate that these participants used sensory information to adjust their movement direction. Based on the results from Experiment 1, we could argue that these participants moved in an inefficient way. However, one possible explanation for both observations might be that, in addition to our predicted bottom-up effects, movements are also influenced by top-down effects. Thus, in Experiment 2, the 90° direction of movement over the (not uniquely oriented) comparison was possibly chosen in order to match the movement over the standard grating of the same trial. Given that the task is to compare two stimuli, moving over each of them in the same way could be a reasonable strategy. Hence, even if there is no sensory information gain to maximize (bottom-up), the task itself might influence movement control (top-down). This is in line with a recent study which showed that movement kinematics depend on both the task and the texture characteristics (Callier, Saal, Davis-Berg, & Bensmaia, 2015).

The task requirements might explain the unnecessary (but not inefficient) adjustments we observed in Experiment 2, but how does the task relate to the inefficient movers in Experiment 3? On first sight, the task in Experiment 3 does not seem to induce movement in line with texture orientation. However, the instruction of having only one free movement might have provoked some participants to strategize more for this task compared to more natural exploration tasks (like Experiment 2). This was also indicated by the comments of 2 observers, who reported to have chosen movements orthogonal to the previous movement. In contrast to rather natural movement planning strategies, cognitive strategic decision making seems more prone to non-optimality (Trommershäuser, Maloney, & Landy, 2003; Tversky & Kahneman, 1974). Therefore, if some participants felt the need to choose a cognitive strategy, they might have chosen the wrong one. For instance, the strategy to move orthogonal to the previous movement

might seem like a good idea to collect information in the most diverse way. Taken together, some parts of the data might be due to task induced top-down influence on movement control. However, we suggest that these task effects act in addition to our proposed sensorimotor processes and are not an alternative to it. We base this assumption on the fact that these movement effects are represented in some individual participants, not the average data across participants. Hence, they also do not devalue our significant findings. Further studies might systematically investigate the importance of top-down influences for movement control in haptic exploration.

Overall, we presented evidence that perception and movement are highly interdependent for the exploration of oriented textures. Sensory information about texture orientation is used to adjust movement directions towards the texture orthogonal. As a consequence, optimal sensory information about the structure of the texture can be extracted and used for the perceptual task. Interestingly, this co-influence happens, although it was shown that textural orientation and structure information are not processed within the same pathway (Zhang et al., 2005; Sathian, 2016; Sathian, Zangaladze, Hoffman, & Grafton, 1997). By introducing a method, which allows for a direct comparison between perception and movement control, we were able to demonstrate that shared sensory information is supplied to both systems. Future studies can apply our method to study other perceptual dimensions, which will help to understand the interplay between sensory and motor processes in general.





## 6. Discussion

### 6.1. Summary – How Perception Evolves

In Study I and II, I investigated how sequentially gathered sensory signals are integrated. Study I focused on the perception of virtual textures, by contrast, Study II focused on softness perception of natural deformable objects. Nevertheless, results of both studies match each other well and allow me to suggest a common model for the optimal integration of sequential signals. This is to say, a model for how perception evolves during the exploration process.

Across the first two studies, the number of exploration movements (1-8 strokes in Study I; 2-5 indentations in Study II) was varied and the effects on discrimination thresholds were analyzed. Discrimination thresholds (i.e., perceptual variance) decreased with more exploration movements in both cases. This decrease was less steep than predicted from the MLE model of optimal integration ( $-1/2$  on a  $\log(\text{threshold}) - \log(\text{no. of movements})$  scale, see Quick, 1974; Ernst & Bühlhoff, 2004). This is to say, perception benefited from additional movements, but the benefit was smaller than predicted by a simple model of an optimal integrator which is usually applied to predict the integration of simultaneous signals. In order to better understand this finding, I tested the MLE model by its second criterion, the prediction of the empirical weights. The MLE model predicts that estimates derived from individual movements over the same object should be equally noisy and, therefore, contribute to the final percept with equal weights (e.g., Ernst & Bühlhoff, 2004). In order to estimate the empirical weights, I introduced a discrepancy between sensory signals from one ‘discrepant’ movement and sensory signals from the remaining movements. During the ‘discrepant’ movement, participants received a stimulation which differed from the stimulation in all other movements on this stimulus. The hereby

measured pattern of empirical weights differed depending on whether this ‘discrepant’ movement was within the exploration of the first or the second stimulus. While movements within the first stimulus contributed with equal weights, this was not the case for the second stimulus. Here, movements were systematically weighted higher the closer they were to the first stimulus. Taken together, neither MLE predictions on discrimination thresholds (i.e., perceptual variance) nor its predictions on weights were consistent with the empirical data in Study I and II.

In order to account for the temporal dynamics arising from sequentially gathered information, I developed an extended model of an optimal observer. More specifically, this model predicts the following: During the processing of the first stimulus, sensory signals are integrated into a final estimate with equal weights (i.e., consistent with the MLE model). However, this final estimate is, then, transferred to a kind of memory structure where it is stored. Because memory representations decay over time (see e.g., Murray, Ward & Hockley, 1975; Olkkonen, McCarthy & Allred, 2014), the memory representation of the first stimulus gets noisier during the exploration of the second stimulus. Based on neurological studies (e.g., Romo et al., 2002; Romo & Salinas, 2003; Hernandez et al., 2010), I additionally assumed that a comparison process between the memorized estimate of the first stimulus and the movement-specific current estimate of the second stimulus takes place during each movement over the second stimulus. As a consequence, each movement is processed differently within the exploration of the second stimulus. Taken together, the model predicts that the estimates from different strokes of the first stimulus are integrated with equal weights, whereas weights should systematically decrease for later movements over the second stimulus. In Study I (Experiment 3), this theoretical model was mathematically formalized in a Kalman filter approach (Kalman, 1962). Model predictions resulted to be consistent with empirical weights. In sum, Study I and II

suggest that in order to understand the integration of sequential signals (in contrast to simultaneous signals) more complicated mechanisms need to be considered. These mechanisms include factors as memory and the nature of the task (e.g., comparison). Nevertheless, the goal of the perceptual system in the extended model fits previous understanding of optimality, meaning that it aims for the least noisy final percept.

## **6.2. Summary – How Movements Evolve**

Study III and IV investigated online adjustments of key movement parameters during the exploration of softness (Study III) and texture (Study IV). Both studies compared first movements, which are based on the minimal sensory input, and last movements, which are based on the maximal sensory input to each other. These comparisons allowed describing how movement parameters evolve on the basis of sequentially gathered sensory signals.

When object properties are actively explored, different exploratory movement patterns (also known as exploratory procedures, EPs) serve perception differently well. The optimal way to explore softness is to apply a normal force to the surface with the fingers, i.e., to indent the object (Lederman & Klatzky, 1987). The movement parameter indentation force can be further optimized, by applying higher force especially for rather hard objects (Srinivasan & LaMotte, 1995; Kaim & Drewing, 2011). For texture perception, the optimal exploration pattern is to move the finger side-to-side (Lederman & Klatzky, 1987). In Study IV (Experiment 1), I demonstrated that for oriented textures (defined by periodically repeating grooves) movements can be further optimized when they are directed orthogonally to texture orientation.

I suggested that over the course of exploration, people can access or learn the connection between specific movements and its consequences in terms of noisiness of the sensory signals

(see Drewing, 2012) and actively adjust movements to optimal parameters. In other words, they adjust their movements to the parameters that lead to the most precise (i.e. least noisy) percept. Under these assumptions, exploration behavior can be described it as a multistep process within the sensorimotor control loop. Hereby, the very first movement generates sensory feedback, which is taken into account when the motor commands for the second movement are programmed. This second movement generates further sensory signals and the process continues in this way until a decision on the to-be-judged property is reached. Consequently, later in the exploration process, movement control is based on more sensory signals than earlier in the process. Assuming that the system is aiming for the least noisy final percept, I predicted that movements that are performed later in the exploration process (e.g., last movements) are closer to the optimal movement parameter value than first exploration movements.

In Study IV, I demonstrated that when exploring oriented textures, participants went from a random direction in the first movement to a tuned direction towards texture orthogonal in the last movement. In this study, additional evidence was presented for the fact that movement adjustments were based on sensory signals. That is, movements and perception were influenced by the same factor, the spatial period of the texture. A similar optimization of movement parameters based on sensory signals was also visible in Study III. Indentation forces were systematically adjusted from the first to the last movement towards higher forces for harder objects. However, this study showed that movement parameters are not only adjusted online. In fact, when a prediction, in form of implicit knowledge of the object softness, was possible, participants adjusted even more profoundly than based on sensory signals. Movement adjustments based on sensory signals (in contrast to movement adjustments based on predictions) depend on the amount of voluntary generated sensory signals, which is in a trade-off with the

needed effort. The more exploratory movements are performed, the more sensory signals are generated (see Study I & II). On the downside, however, additional movements are associated with additional movement costs (effort; see Study III). In Study III (Experiment 2), I demonstrated that motivation can foster the effect of sensory signals by evoking more voluntary movements. That is to say, when participants are motivated they trade in more effort for a better perceptual performance.

Overall, I propose that in the process of exploration, movements are executed with a dual goal. The first goal is to improve perception (see also Drewing, 2012; Lederman & Klatzky, 1987). In order to achieve this goal, movements are adjusted on the basis of sensory (and predictive) signals (see Study III & IV). Importantly, however, keeping movement costs low constitutes the second goal. Although this goal is known from motor control literature (e.g., Todorov & Jordan, 2002) and eye movement studies (e.g., Xu-Wilson, Zee, & Shadmehr, 2009), it was not considered in the haptic literature so far. In order to optimize for both goals, the motivation to achieve a high task performance determines where the balance between perceptual optimization - as a benefit - and effort - as a cost - of additional movements is found.

### **6.3. Limitations of a Specific Exploration Task**

In my thesis, I described how perception and movements evolve over the process of active haptic exploration. Overall, I suggested that the changes in both, movements and perception, are based on the sequentially gathered sensory signals. However, it is important to keep in mind, that the findings are reported in the specific context of a discrimination task between two alternatives. For measuring perception, we actually used a 2-IFC task, where one stimulus follows the other in a rigid order. Although this method is commonly used and

recommended (Blackwell, 1952), it implies a specific task (comparison) and a fixed order of exploration, both of which might influence perception. Similarly, discriminating between two alternatives might as well introduce task-specific influences on movements.

In general, the task could have a fundamental impact on movements in free exploration. For instance, free gaze was reported to be highly influenced by the observer's task (Ballard & Hayhoe, 2009; DeAngelus & Pelz, 2009). In the haptic literature task effects were not the focus of attention for a long time. For instance, in the study of Lederman and Klatzky (1987) the effect of the task cannot be completely disentangled from the effect of stimulation, because different stimulus sets were used for the assessment of different object properties (tasks). However, a recent study on texture perception systematically manipulated the task and the stimulus characteristics. There, movement parameters were found to depend as well on the task, namely rating hardness, roughness or slipperiness, as the surface characteristics (Callier, Saal, Davis-Berg, & Bensmaia, 2014).

In my investigations of haptic exploration movements (Study III & IV), some side-results can probably be attributed to the given task. For instance, in Study III, in which participants were asked to decide which of two stimuli felt softer, they touched disproportionately more often the stimulus, which they perceived as being softer with their last touch (Experiment 1: 75.74%; Experiment 2: 72.68%). Similar behaviors were previously reported for eye fixations (Krajbich Armel, & Rangel, 2010; Manohar & Husein, 2013) and for haptic preference (Mitsuda & Yoshioka, 2015). Future studies could examine whether this effect is indeed induced by the task by changing the task to 'harder' judgments (in contrast to the used 'softer' judgments).

Another example of probably task-driven exploration movements is reported in Experiment 2 of Study IV: Several participants (4 out of 13) did not direct their last movement

over the not clearly oriented comparison stimulus in a random direction, but, rather, systematically in the direction orthogonal to the standard orientation. It is likely that the reason for this is the comparison task: Participants might have tried to match movements over the comparison with movements over the standard grating in a given trial. Similarly, the perceptual data in Study I and II reflected comparison processes during the exploration of the second stimulus (see also Romo & Salinas, 2003). This is to say, my findings for movements and perception seemed to be influenced by the task to compare two objects.

Therefore, it would be interesting to investigate the natural exploration process with additional tasks in the future. To this end, methods might be applied, in which the stimulus property is compared to a reference that is not sequentially explored. For instance, the task could be to compare the orientation of a haptic texture to a visual bar that will be presented afterwards in an unpredictable orientation. After delays between the haptic texture and the visual comparison bar would be introduced, one could test whether discrimination performance reflects the decay of the representation of the first stimulus and whether it can be modeled with a Kalman-filter. In a simpler version of this task, the reference bar could have a fixed orientation. For such a setting, the response should be already prepared as soon as the haptic texture is explored. Therefore, memory decay should not play a role and sensory integration should follow a simple version of Kalman-filter, which predicts the same results as the MLE approach. Additionally, it would be interesting to investigate perception and movements in trials without a comparison task. For instance, exploration movement directions could be measured within one-stimulus trials in a magnitude-estimation task (Stevens, 1952). In this task, movements over not clearly oriented textures, like the comparisons in Experiment 2 of Study IV, should not be

influenced from movements on oriented textures, even if trials with both texture-types would be interleaved.

Taken together, in my studies I investigated the contribution of sensory signals gathered during the exploration process to the evolvment of natural movements and perception. Future research should expand these investigations to other perceptual tasks. Similarities in exploration movements as well as perception across various tasks will help finding general principles of natural active haptic perception.

#### **6.4. Memory Systems in the Process of Exploration**

I presented a model for the processing of sequential signals which describes that the comparison process, but not the integration, is affected by memory decay. According to this model, estimates from previous movements are stored without loss during sensory integration, as it is happening within the exploration of the first stimulus. This was evident from the fact that for the first stimulus, the information gathered from the first movement was entering in the final percept in the same way as information gathered in the last movement (see Studies I & II). In contrast to this, during the exploration of the second stimulus, the representation of the first stimulus is decaying (i.e., getting noisier) over time. While this is happening, the first stimulus is being compared to every movement-specific estimate of the second stimulus. In consequence, later movements over the second stimulus were contributing less to the final percept in the empirical data (see Studies I & II). This suggests that there are at least two memory systems involved. The first system retains sensory information for integration and is not affected by decay. The second memory system receives the final estimate of the first stimulus and is affected by memory decay.



The concept of haptic memory was far less investigated than visual memory. However, previous findings are consistent with the assumption of several subsystems in haptic memory (Gallace & Spence, 2009). The memory system, which retains sensory information for integration seems to coincide with the concept of sensory memory. Sensory memory is assumed to capture complete, modality-specific, sensory information for very short durations. Most of the knowledge on sensory memory is based in vision science, where it is also known as iconic memory (Sperling, 1960). In his seminal experiments, Sperling (1960) briefly flashed letter arrays and asked participants to report the letters. If participants were asked to report everything ('whole report') they only were able to report four to five letters. However, when immediately after the letter array a cue was presented, which indicated that only one specific row needed to be reported ('partial report'), participants reported any row almost perfectly. This implied that all letters were stored and still available at the time of the cue. A few studies addressed the question of a haptic equivalent to the iconic memory (Bliss, Crane, Mansfield, & Townsend, 1966; Gallace, Tan, Haggard, & Spence, 2008). Gallace et al. (2008) presented vibrotactile stimulation on multiple body parts in parallel. Participants were asked to either report the total number of stimulations ('whole report') or to judge whether a cued position had been previously stimulated ('partial report'). The authors found advantages of the 'partial report' in haptics and concluded that there is a haptic equivalent of the iconic memory. Based on our results we would assume that this memory system is also involved in the storage of movement-specific estimates for the integration process. However, it will be necessary to investigate the role of sensory memory in active haptic perception in the future. One possibility to pursue this, might be to use masking (e.g., Laskin & Spence, 1979), which (in contrast to non-stimulation

control) was reported to erase the content of sensory memory (Averbach & Sperling, 1961; Gegenfurtner & Sperling, 1993).

A second memory system was described as the haptic working memory, which is longer lasting than sensory memory but limited in capacity (Gallace & Spence, 2009). Pasternak and Greenlee (2005) reported that working memory in sensory systems is usually investigated by a delayed discrimination task, in which the information from the first stimulus has to be hold in memory. With a similar method Sinclair and Burton (1996) found that during the delayed discrimination of vibratory stimuli the discrimination performance decreased rapidly during the first 5 seconds. The rate of such a memory related decrease is usually described by a power function of the time  $t$  with a negative exponent (Wixted & Ebbesen, 1991, 1997). Murray, Ward, and Hockley (1975) reported the power functions for two-point thresholds. In their study, participants discriminated whether they were stimulated on the same location with the first and a delayed second stimulus. While varying the duration of the delay, thresholds were measured at the different body locations. Interestingly, I incorporated the decrease function that Murray et al. (1975) reported for stimulations on the thumb in the Kalman filter model (Study I) and model predictions resulted to be consistent with our empirical data. Besides psychophysical studies, neurophysiologic studies reported evidence for a haptic working memory. Romo and colleagues (Romo & Salinas, 2003; Hernandez et al., 2010) described that the information from the first stimulus in a 2-IFC task is still visible in SII and other cortical areas (PFC, VPC, MPC, DPC), which seem to be related to the haptic working memory, up to 3 seconds after stimulation. In contrast to the sensory memory, working memory is assumed to be processed more centrally as implicated by common capacity limits for multimodal stimulation (Saults & Cowan, 2007). Nevertheless, the role of working memory in active haptic perception should be further

investigated in the future. Based on the literature, it is to expect that the rate of decay of the first stimulus estimate will depend on its noisiness (Wixted et al., 1975; Deco et al., 2010). Therefore, future research could manipulate the noisiness of the first stimulus estimate (by varying exploration extension or by adding noise; see Metzger & Drewing, 2017) and insert systematic delays between the first and the second stimulus, while measuring the rate of decay.

Taken together, I proposed a model for the integration of sequential signals which implicates the existence of at least two memory systems in haptic perception. This implication is in high agreement with previous literature on haptic memory. However, further research is needed to be able to describe the memory systems involved in the exploration process more specifically. Additionally, the role of memory for exploration movements needs to be further investigated. Previously, it has been suggested that sensory experiences are stored in memory by an internal model, which relates dynamics of the motor systems to resulting sensory signals. The internal model is then updated after comparing sensory signals generated with later movements and the expectations about them based on the internal model (Nowak, Glasauer & Hermsdörfer, 2004). This process was described to continue until the desired or even an imagined sensory feedback is achieved (Presyna, Pundi & Flanders, 2011). Future investigations could use a Kalman filter approach to model exploration behaviour, based on memory models. However, in order to do so movement parameters and perception need to be measured simultaneously in a comparable way after every movement within the exploration process. A first step in this direction might be to apply the method of ‘movometric’ functions, which we developed in Study IV as the motor equivalent to psychometric functions.

## **6.5. Future Perspectives for Science and Application**

In this thesis, I investigated several questions regarding the natural process of active haptic perception. Some of the findings lead to new possible research questions, which directly build on the presented work. As I described above, it would consolidate our understanding of haptic sensorimotor control if the role of the task and different memory systems will be further investigated in the future. Beyond this, continuing this line of research might lead to more far-reaching research questions and applications in the long run.

One promising topic for research and application would be to investigate the linkage between natural exploration movements and perception. Within Study IV, I showed that the same factor can systematically influence movements and perception. Namely, for textures with smaller spatial periods the perceived texture orientation and the movement direction over the texture were both noisier (as compared to bigger spatial periods). Future research could broaden our understanding of such systematic links between movements and perception. One possibility to approach this in the future might be to revisit the idea of ‘necessary’ exploration movements that was originally introduced by Lederman and Klatzky (1987). They referred to exploration procedures as ‘necessary’ whenever they were the only ones producing over chance performance. In cases when participants perform such a ‘necessary’ exploration movement, the probability is high that the corresponding perceptual dimension is being judged. Therefore, it would be feasible to extract these ‘necessary’ movement segments from natural exploration in order to predict the examined object property in the future. Predicting perception from observed hand movements might be a major topic for research and application in the future. Previously, scientists have suggested ways to decode perception from brain activity (e.g., Kay, Naselaris, Prenger, & Gallant, 2008). Some research focused on eye movements and, for instance, predicted

the observer's task from eye movement patterns (e.g., Boisvert & Bruce, 2016). More recently, these ideas are also evolving in the research field of haptics. Yokosaka, Kuroki, Watanabe, and Nishida (2017, 2018) described links between exploratory movements and subjective haptic ratings. The authors reported correlations between tactile ratings and hand and eye movements even for exploration with no specific task. Additionally, they showed that different observers highly agree with each other when rating the percept of another person after seeing videos of his or her exploration movements. Therefore, their results suggest that there might be a possibility of decoding haptic perception from the performed exploration movements. If in the future the explored haptic dimension or even the parametric value within this dimension could be predicted, several applications would emerge. For example, one could imagine that video-based software will assist sales personal in the clothing business to lead the customer to the desired material by analyzing their exploration movements on previous pieces of clothing.

Another fruitful direction of future research would be to broaden the understanding of the biological basis for sensorimotor control in natural explorations. This research might lead to improvements in at least two applied areas: the medical treatment of malfunctioning systems and the robotic sensing. In Study III of my thesis, motor adjustments based on sensory feedback were found to be moderated by motivation. More specifically, our participants gathered more sensory signals and adjusted their indentation forces more to the object softness when they were higher motivated. This finding could be taken as an indication for the involvement of the dopaminergic (reward) system in a functioning motor control during natural haptic exploration. In line with this speculation, Shadmehr, de Xivry, Xu-Wilson, and Shih (2010) showed that diseases of the reward system, such as Parkinson's disease or schizophrenia are connected to dysfunctions of movement control. Interestingly, patients with other disorders, like autism, were also reported to

have impaired sensorimotor control including feedforward and feedback processes (Mosconi, Mohanty, Greene, Cook, Vaillancourt, & Sweeney, 2015). Better understanding the biological mechanisms behind a functioning sensorimotor control will advance medical treatments in the area of neuroprosthetics and treatments for patients with lesions (for opinion papers on this topic, see Flanders, 2011; Shadmehr & Krakauer, 2008). Additionally, robotic applications might improve by better imitating the neural functions of a biological sensorimotor control system (for a review, see Pfeifer, Lungarella, & Iida, 2007). One possibility to reach this goal is to implement computational models that seem to reflect human movements and perception well in the area of robotic sensing. For instance, Bayesian approaches were successfully implemented for movement guidance during robotic perception of object identity (Lepora, Martinez-Hernandez, & Prescott, 2013) and texture perception with a biologically inspired tactile sensor (Fishel & Loeb, 2012).

## **6.6. Conclusions**

The present thesis investigated fundamental questions about the mainly sequentially working haptic sense. The results of Study I and II indicated that perception changes within the exploration process, as sequential sensory signals are continuously integrated. This integration differs from an optimal integrator model (MLE), which is usually applied to the integration of simultaneously presented signals. In order to account for the higher complexity of sequentially gathered signals, I presented a Kalman filter model. This model described a perceptual process which focuses on online comparisons and incorporates memory decay while maintaining its goal to minimize the variance of the final percept. Further, in Study III and IV, I presented evidence for the impact of sequentially gathered sensory signals on executed movements. The influence of sensory signals on movement control seemed to be moderated by motivation, which is probably

due to the motor costs for active gathering of sensory signals. Therefore, a central goal of movement control seems to be optimizing haptic perception while minimizing motor costs. Overall, the results suggest that in natural haptic exploration, the sequential gathering of sensory signals continuously impacts perception and movements. As they both rely on this common basis, perception and movements are highly interdependent.

In 1925, Katz wrote „*Farbschöpfend sind [] Augenbewegungen nicht wie die Bewegungen der Finger tastschöpfend sind*“ (Katz, 1925; in translation: “*Eye movements do not create color the way finger movements create touch.*”). Today, based on the presented literature and findings, it seems reasonable to expand his idea to say that “finger movements and touch (sensations) form each other mutually”.





## 7. References

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## Publikationsliste

### Zeitschriftenartikel:

- Lezkan, A., & Drewing, K.** (2018). Processing of haptic texture information over sequential exploration movements. *Attention, Perception, & Psychophysics*, 80(1), 177-192.
- Lezkan, A., Manuel, S.G., Colgate, J.E., Klatzky, R.L., Peshkin, M.A., & Drewing, K.** (2016). Multiple Fingers – One Gestalt. *IEEE Transactions on Haptics*, 9(2), 255-266.
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### Konferenzartikel:

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### Manuskripte:

- Lezkan, A., & Drewing, K.** (under review). Interdependences between finger movement direction and haptic perception of oriented textures. *PLOS ONE*.
- Lezkan, A., Metzger, A., & Drewing, K.** (under review). Active haptic exploration of softness: indentation force is systematically related to prediction, sensation and motivation. *Frontiers in Integrative Neuroscience*.



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