Predictive mechanisms in passive and active touch

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"Je ne sais pas si ce monde a un sens qui le dépasse. Mais je sais que je ne connais pas ce sens et qu'il m'est impossible pour le moment de le connaître. Que signifie pour moi une signification hors de ma condition? Je ne puis comprendre qu'en termes humains. Ce que je touche, ce qui me résiste, voilà ce que je comprends." (Camus, 1942, p.18)

„Ich weiß nicht, ob diese Welt einen Sinn hat, der über mich hinausgeht. Aber ich weiß, daß ich diesen Sinn nicht kenne und daß ich ihn zunächst unmöglich erkennen kann. Was bedeutet mir ein Sinn, der außerhalb meiner Situation liegt? Ich kann nur innerhalb menschlicher Grenzen etwas begreifen. Was ich berühre, was mir Widerstand leistet - das begreife ich.“ (Camus, 1942/1996, p. 47)

Hong (1999), "String Mirror_WB_hands_02” (shared in agreement with the artist)

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Abstract

Perception is an active process which is shaped by prior sensory experiences and expectations about the objects and situational demands that an agent is confronted with. The first part of this work focuses on neural adaptation processes in passive tactile perception, while the second part will examine the role of prior visual information and different context factors for optimization of active haptic explorations.

In the first study we exploited tactile adaptation aftereffects to reveal previously unknown communalities in the somatosensory processing of spatially structured tactile features. Two-point distance, macro-scale roughness, and curvature have been extensively studied in isolation in the past and are deemed critical for shape and material perception. Their potential overlap in sensory processing however had remained unexplored. Across four experiments, we here demonstrate that adaptation to one property can produce aftereffects in the perception of the other properties: For roughness and tactile distance specifically, cross-property aftereffects were bidirectional, specific to orientation and skin region, weaker than the respective within-property aftereffects, and did not result from peripheral receptor fatigue. Together, the results suggest a common neural substrate for processing spatially structured tactile features at early cortical levels, providing a window into how low-level spatial features may be organized to support coherent object perception. A second study compliments the first one: here, we investigated whether there is a relationship between biophysical skin properties with basic tactile abilities and the tactile distance aftereffect. While previous studies clearly demonstrated that peripheral factors are not the origin and cause of tactile aftereffects, it had remained unclear whether they could have an additional impact on aftereffect expression, possibly explaining interindividual differences in e.g. the aftereffect strength. Results revealed that higher hydration and elasticity were related to increased tactile sensitivity and spatial acuity. The magnitude of distance aftereffects, however, was independent from both skin properties and tactile abilities; suggesting that the underlying cortical processes are rather robust and stable. Interindividual variability in the aftereffect magnitude might instead stem from e.g. cortical idiosyncrasies causing differences in the susceptibility to neural adaptation.

For active touch, we examined in the third study if and how prior visual information can be exploited for texture exploration. Participants had to discriminate grating textures by spatial frequency while receiving prior visual cues of varying quality about texture orientation. These priors influenced exploratory movement direction similarly to adjustments known to emerge during exploration and to enhance perception, but notably, they did so already at initial contact. The degree of adjustment scaled with the quality, i.e. informational value of the priors, consistent with established motor control models. The findings show that humans can flexibly learn to use abstract visual priors to optimize haptic explorations, with the learning process and direct usage substantially depending on the priors' quality. In the fourth study, we corroborated and extended findings from study 3 with an investigation in a more naturalistic VR-setting, assessing haptic exploration of real-life materials (sand, sponge, sandpaper), and how naturalistic prior visual information affects the initial movement selection beyond single movement parameter adjustment but with regard to holistic movement selection. Results showed that with adequate prior visual information, participants explored materials in a more efficient way: they used specialized exploratory procedures earlier, with higher probability, and explored materials for a shorter time.

In the fifth study, we assessed factors that humans might take into account for termination of exploratory behavior. (Expected) task demands are known to influence, e.g., force tuning in softness exploration. Exploration extension generally improves discrimination performance up to a saturation point. We therefore hypothesized that humans adjust exploration durations according to current task demands and assessed this in a haptically rendered grating discrimination task. However, exploration extension increases motor costs, which humans typically seek to minimize; to examine the role of motor costs for haptic explorations, we artificially manipulated motor effort by implementing counteracting forces in a force-feedback device. Results showed that increased task demands were compensated by exploration extension, but the extent of this compensation depended on the motor costs the agent was confronted with. This likely reflects the agent's dynamically updated cost-benefit expectations.

Altogether, this dissertation provides new behavioral evidence on how efficiency of touch perception is supported by robust early cortical mechanisms jointly encoding different tactile features, as well as higher-level prediction processes that enable exploratory movement adjustments for optimized sensory data gathering.

Contents

List of Abbreviations

2AFC: two-alternative forced-choice

2IFC: two-interval forced-choice

JND: just noticeable difference

PSE: point of subjective equality

VR: virtual reality

HMD: Head-mounted display

RF: receptive field

SA: slowly adapting

RA: rapidly adapting

SI: primary somatosensory cortex

SII: secondary somatosensory cortex

EP: exploratory procedure

ANOVA: Analysis of Variance

log: logarithm

1. Introduction

This work will investigate predictive mechanisms within two branches of somatosensation: 1) tactile perception, i.e. the sensations derived from passive stimulations of the skin (exteroception), and 2) haptic perception, i.e. the active sensorimotor exploration of objects and materials which involves the dynamic interplay of exteroception and motor control.

The predictive nature of perception and action is widely and long acknowledged. Fittingly, object perception has even been described to be akin to the generation of scientific hypotheses (Gregory 1980). Predictions arise from various processing stages and can be based on many different signals and information sources. They enable humans to make sense of ambiguous, noisy, or unreliable sensory input by exploiting statistical regularities and recurring patterns; to make decisions despite uncertainty, to control their body, and to act efficiently and proactively (for an overview, see e.g. De Lange et al., 2018; Denham & Winkler 2020; Enns & Lleras, 2008; Hayhoe et al. 2020). This work treats low-level neural adaptation processes that shape tactile perception, as well as anticipatory mechanisms shaping exploratory movement selection and -execution in active touch, i.e. the reciprocal relationship between action and perception. “Predictive mechanisms” here serves as an umbrella term under which a multitude of functionalities can fall (see e.g., Vishwanath, 2019). Neural adaptation (e.g., Benda, 2021), predictive coding (e.g., Rao & Ballard, 1999), motor prediction (e.g., Wolpert & Flanagan, 2001), and higher-level anticipatory mechanisms (e.g., Pezzulo, 2008) are distinct, but conceptually related constructs. On a single-cell level, adaptation for example might act as a basic element for predictive coding (Benda, 2021). In this work, I will not challenge conceptual separations, neither will I reassess (dis)similarities between functionalities (for this, see e.g., Feuerriegel, 2024; Kunde et al., 2007; Symonds et al. 2017). I will focus on the two subtopics individually while the role of prior experiences and (dynamic) expectations for tactile and haptic perception serves as an overarching, recurrent theme.

The first section of this chapter provides a general overview on touch perception starting from the peripheral level (skin and receptors) and the somatosensory processing pathway. Further, the phenomenon of tactile adaptation aftereffects will be introduced. The second section deals with active touch, where I review a selection of empirical findings on exploratory movement optimization. The last section serves as an outline for the research questions and studies included in this dissertation.

1.1 Somatosensory processing

Tactile perception involves the intake of sensory information via cutaneous receptors at peripheral level, the transmission via neuronal afferents, and the central processing and computation of the percept. Haptic perception can be understood as active tactile perception: motor action leverages the intake of sensory information at peripheral level. The cutaneous receptors are mostly located in the dermis of the skin and include mechanoreceptors (touch, pressure, vibration) (Fig. 1A), thermoreceptors (temperature), and nociceptors (pain, itch). Kinesthetic afferents from the muscle spindles and Golgi tendon organs additionally provide proprioceptive information about limb position, muscle strain and related applied forces (Loeb & Mileusnic, 2015). Noxious stimuli are signaled exclusively by free nerve endings. Cutaneous mechanoreceptors sense stimuli via physical deformation of their plasma membranes: These contain mechanically gated ion channels which open or close in reaction to pressure, vibration, and stretching (e.g., Johansson & Vallbo, 1983). Four functionally different tactile units (and corresponding mechanoreceptors) have been identified, displaying different response types and receptive field characteristics (see Fig. 1B). When stimulated, mechanoreceptors increase their firing rate proportionally to the stimulus intensity but adapt over time: phasic receptors adapt quickly, reducing firing rapidly, while tonic receptors maintain elevated activity longer (Catton, 1970). Meissner and Pacinian corpuscles are rapidly adapting receptors, sensitive to dynamic changing deformations (Meissner; RAI fibers) and high-frequency vibration (Pacinian; PC/RAII). Merkel cells and Ruffini endings are slowly-adapting receptors, sensitive to low-frequency vibrations, static touch and spatial distortions (Merkel; SAI), as well as skin stretch and sustained pressure (Ruffini, SAII) (Johnson, 2000). Further, the size of the respective receptive fields differs between those afferent units (Johansson, 1978). A receptive field is defined as the spatial area within which a stimulus of sufficient intensity will influence the firing of a sensory neuron. While Pacinian and Ruffini endings have comparably large receptive fields, Merkel cells and Meissner corpuscles allow for discrete sensation with small receptive fields with little overlap. Logically, these are most prominent in the fingertips, while Pacinian corpuscles are widely distributed across the hand, particularly supporting actions like sustained grip force control or monitoring slip (Zangrandi et al., 2021). For Ruffini corpuscles, it remains unclear as to whether these endings are found in human skin (e.g., Paré et al., 2003).

After excitation of these receptors, the input travels via primary afferent fibers to the cortex (Fig 1B). Specifically, signals travel via heavily myelinated Aβ fibers (mechanoreceptors) (Li et al., 2011), moderately myelinated Aδ fibers (thermoreceptors, nociceptors) (ibid.), unmyelinated C fibers (nociception, temperature, pleasant touch) (Ackerley & Watkins, 2018), and group I/II fibers (proprioception) (Matthews, 1981). These fibers enter the central nervous system through the dorsal horn of the spinal cord or, for the head, the trigeminal nucleus in the brainstem. Within the spinal cord, the signals are segregated into two main pathways: One is the dorsal column-medial lemniscus (DCML) pathway, which carries fine touch, vibration, and proprioceptive signals (from Aβ and Group I/II fibers) (Willis et al., 1978), and the other one is the anterolateral system (spinothalamic tract), which carries pain, temperature, and crude touch signals (from Aδ and C fibers) (Al-Chalabi et al., 2023). A key feature of these pathways is that their axons cross to the opposite side of the nervous system (decussation; ipsilateral to contralateral) on their way to the brainstem. From the brainstem, axons then project to the thalamus, a major relay center that integrates and begins modulating sensory information. From there, signals are sent to cortical areas; predominantly the primary somatosensory cortex (SI) (see George & Das, 2019).

In SI, inputs from different body parts are organized spatially in a somatotopic map (sensory homunculus) (Penfield & Rasmussen, 1950). The higher the sensitivity of a body area (mostly due to smaller receptive field size and/or higher density of peripheral receptors), the higher the cortical magnification; i.e. the larger are stimuli perceived on the respective body area (e.g., Roux et al., 2018). Similar to the primary visual cortex (VI), where neurons are selective for oriented bars or gratings (e.g., Goris et al., 2015), SI neurons display direction selectivity or edge orientation selectivity (Hsiao et al., 2002; Warren et al., 1986). SI is further divided into several subregions named Brodmann area 3a/3b, 1, and 2 (anterior to posterior), which form a functional gradient (e.g., Schellekens et al., 2021). The secondary somatosensory cortex (SII), divided primarily into area S2 and the parietal ventral (PV) area (e.g., Krubitzer et al., 1995), receives input from SI and the thalamus. Neurons in SII have large, sometimes bilateral receptive fields (Petit et al., 1990) and are involved in integrating information from both sides of the body to process complex features like object identity (Disbrow et al., 2001). SII further projects to, inter alia, higher-order regions responsible for visuospatial attention, action planning, and social aspects of touch (Ishida et al., 2024; Suvilehto et al., 2021). In sum, ascending the somatosensory hierarchy, neurons become selectively responsive to increasingly complex and abstract features while displaying greater invariance to the specific spatial details of the stimulus (see also, e.g., Glassman, 1994; Saadon-Grosman et al., 2020).

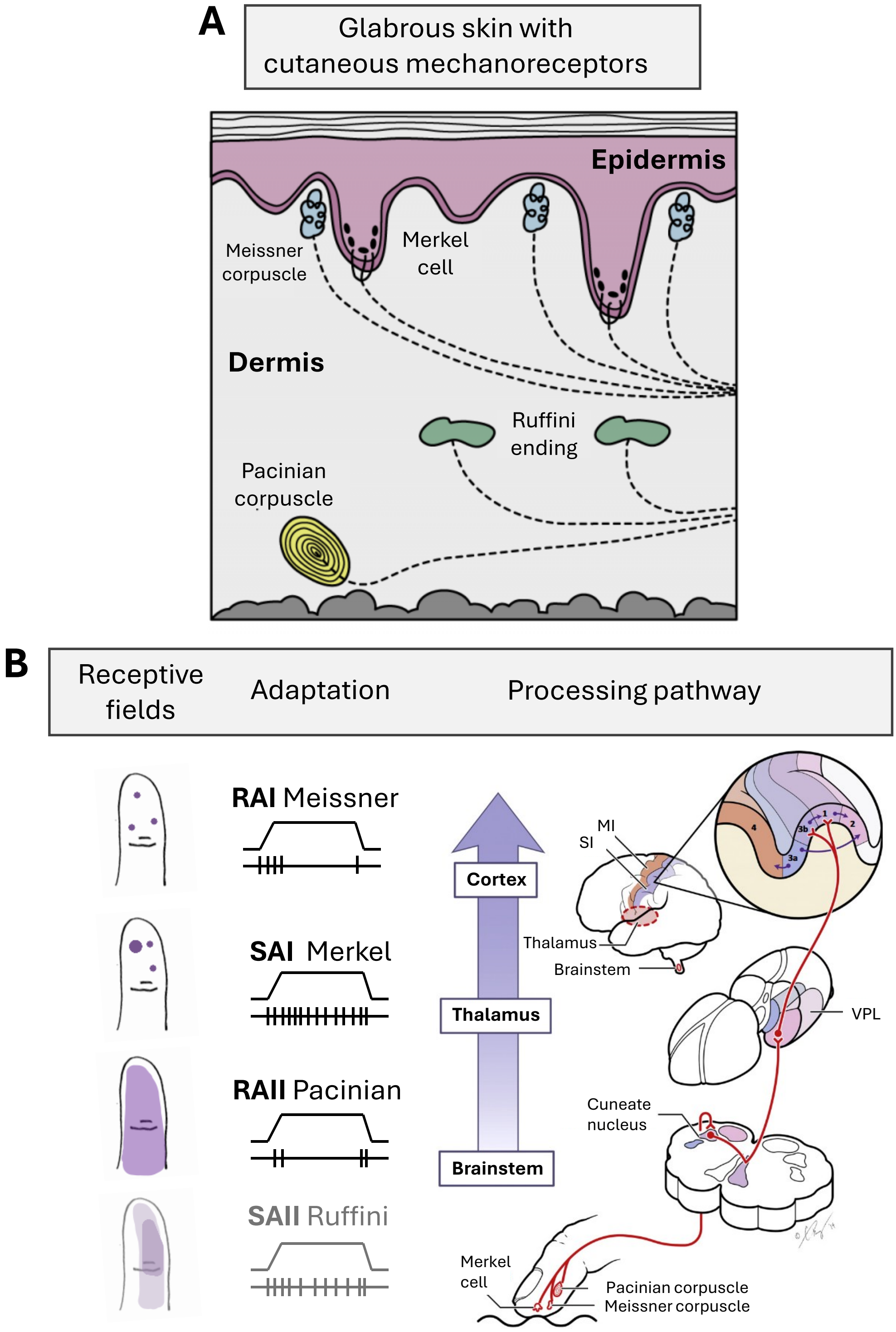

Figure 1. (A) Schematic cross-section through smooth glabrous skin containing mechanoreceptors. (B) From left to right: Visualization of receptive field size for the different mechanoreceptors (Ruffini is greyed out given their questionable status in human skin). Classification of afferent units based on their response to a ramp and hold stimulus applied on the skin surface. Processing pathway from periphery to cortex (VPL: ventral posterolateral nucleus). Adapted from Henley (2021), Johansson & Vallbo (1983), and Saal & Bensmaia (2014).

1.2 Tactile adaptation aftereffects

"Having steadily looked for a few seconds at a particular part of the cascade, admiring the confluence and decussation of the currents forming the liquid drapery of waters, to observe the vertical face of the sombre age-worn rocks immediately contiguous to the waterfall, I saw the rocky surface as if in motion upwards (...)" (Addams, 1834, p. 373)

The prolonged exposure to a stimulus can provoke neural adaptation which then can result in a perceptual aftereffect, i.e., the change in the perception of subsequently presented stimuli (e.g., Bharmauria et al. 2022; Thompson and Burr, 2009; Weber et al., 2019; Webster, 2011). Reports of perceptual adaptation aftereffects can be traced back up until the time of Aristotles (circa 330 BC; translated by Beare, 1908). He reported the motion aftereffect, which was later popularised by Robert Addams (1834) as the "waterfall illusion". Aftereffects are a universal phenomenon in perception, as evidence has been found for all modalities, most abundantly in vision and touch (Webster, 2011). In the tactile and haptic domain, various perceptual properties have been shown to be susceptible to aftereffects, including size (Köhler & Dinnerstein, 1947), softness (Metzger & Drewing, 2016), curvature (Vogels et al., 1996; Vogels et al., 2001), and roughness (Kahrimanovic et al., 2009). To illustrate: for curvature perception, experiments showed that a flat surface is judged concave if the preceding touched stimulus was convex and vice versa (Vogels et al., 1996; Vogels et al., 2001). For surface roughness, it was found that after adapting to a rough texture, perceived roughness of a test stimulus was decreased in comparison to the roughness perceived with the non-adapted finger and, importantly, adaptation to a smooth surface produced the opposite effect (Kahrimanovic et al., 2009).

Based on the current state of knowledge, the underlying functioning of adaptation aftereffects can be described as follows (see e.g., Thompson & Burr, 2009; Webster, 2011): Many perceptual dimensions such as orientation are decoded by populations of neurons (or neural channels) that are narrowly tuned but slightly overlap in their sensitivity to specific values along that dimension, such as different angles. These neurons respond most strongly to stimuli matching their preferred value and to a lesser degree to nearby values, e.g. slightly different orientations (e.g., Ghisovan, 2008). From the activity pattern across these channels the brain then infers the value of a stimulus, ultimately creating the percept. Crucially, when neurons are exposed to their preferred stimulus for an extended period, their sensitivity decreases; i.e., neural adaptation leads to repetition suppression (for an in-depth review on different mechanistic accounts see, e.g., Feuerriegel, 2024). As a result, neurons tuned to the adapted value respond less than those tuned to nearby values, which shifts the overall activity pattern away from the adaptation stimulus (Dragoi et al., 2001). This shift can lead to a repulsive aftereffect: When a new, different test stimulus is presented, it is perceived as being further away from the adapted value (e.g., Jin et al., 2005; Suzuki & Cavanagh, 1998). Notably, if the test stimulus is identical to the adaptor, no bias occurs in the perceptual readout. For cases with a very limited number of broadly tuned neuronal channels (norm-based coding), adaptation (to any other stimulus than the average/neutral point) leads to renormalization and has more global effects, i.e. the read-out of every test stimulus value will be biased in consequence (as in Rhodes & Jeffery, 2006; Webster, 2007). For some stimuli, both repulsion *and* normalization can occur (Storrs & Arnold, 2012).

The psychophysical results derived from aftereffect experiments not only provide insights into the existence and organization of tuned neuron populations but also allow to make inferences about the cortical level at which they are likely located, based on the varying degrees of specialization/tuning complexity and receptive field size across cortical areas (as mentioned in section 1.1). Low-level aftereffects that result from earlier cortical processing, such as the tactile distance aftereffect (Calzolari et al., 2017), show strong selectivity for stimulus characteristics like orientation or location. Higher-level aftereffects resulting from later cortical processing on the other hand can generalize across orientation, location, and stimulus size (e.g., Arnold et al., 2015; van der Horst et al., 2008). Further, evidence was found for cross-modal transfer from, e.g., vision to touch (Konkle et al., 2009) or touch to vision (Wang & Alais, 2024). Because of their potential to elucidate on neuronal sensory processing albeit being a completely noninvasive method, aftereffects have aptly been termed before as the "Psychologists microelectrode" (Frisby, 1980).

Researchers have agreed on several functional roles of the neural adaptation underlying the observed aftereffects, considering it a crucial part of sensory processing (e.g., Barlow & Földiák, 1989; Wark et al., 2007). One such function is gain control. Neurons have a limited dynamic range, yet natural signals vary greatly in their means and variance; by centering neural responses around the current average input, adaptation prevents response saturation and improves coding efficiency (Clifford et al., 2007; Stocker & Simoncelli, 2005) Further, adaptation contributes to the formation of a predictive code, in which only deviations (i.e., prediction errors) are explicitly signaled, while the mean expected stimulus is represented implicitly. This conserves energy, i.e. increases metabolic efficiency, and enhances the detection of novelty as predictable stimuli are effectively “subtracted”, allowing the sensory system to allocate full resources to processing unexpected input (Boehnke et al., 2011; Clifford et al., 2007; Ranganath & Rainer, 2003). Recalibration is suggested to be one further key role of adaptation (Webster, 2011). This is essential for perceptual constancy, such as in color constancy, where the visual system maintains stable color perception despite changes in lighting conditions (e.g., Foster, 2011).

While neural adaptation often serves beneficial functions, aftereffects provide a striking example of how it can also lead to misperception. These perceptual distortions, which arise from shifts in neural responsiveness, illustrate that the same mechanisms that typically enhance sensory processing can also produce misleading outcomes. Fittingly, the discrepancy between the perception under standard, unadapted conditions versus the perception after adaptation has previously been termed as the “coding catastrophe” (e.g., Schwartz 2007). In everyday life however, such pronounced distortions are rare (Haak & Mesik, 2016); adaptation more often supports subtle recalibration processes (such as color constancy) that are essential for maintaining stable perception in a dynamic environment. In sum, perceptual aftereffects can be indicative of neural strategies for optimizing sensory read-out. They pose a behavioral probe into the mechanisms underlying perception; which can reveal crucial insights into somatosensory processing. For these reasons, we extensively exploited aftereffect-paradigms within study 1 and 2.

1.3 Haptic perception and action

“Perception is not something that happens to us, or in us. It is something we do." (Noë, 2004, p. 1)

While all sensory modalities exhibit enactive components, touch exemplifies the reciprocity of action and perception most directly. We constantly modulate our touch perception with our hands. The dynamic nature of haptic perception becomes evident when reflecting on different situations and comparing how we act during those; e.g., how the movements involved in exploring the smoothness of a wooden surface differ from those used when palpating a belly to inspect an infected appendix. The standard definition of active touch encompasses both exteroception and proprioception/kinesthesia and refers to movements aimed at generating sensation (Gibson, 1962): Active touch is therefore often used synonymously with exploratory movements and generally excludes manipulatory movements such as pressing a button or carrying an object. One of the first mentions of active touch and first attempts to establish active-passive-dichotomies can be traced back to the early 19th century. In 1811, J.G. Steinbuch described touch as a volitional act, laying the foundation for later conceptual distinctions (Steinbuch, 1811). Further elaborations followed: Wilhelm Wundt laid more groundwork (Wundt, 1862), and his student Theodor Heller introduced the distinction between analytic (successive) and synthetic (simultaneous) touch, based on his research on blind individuals (Heller, 1895). Even E.H. Weber, one of the most influential figures in psychophysics, acknowledged the advantages of active touch, albeit focusing almost exclusively on passive touch for his own studies (Hughes & Jansson, 1994; Weber, 1834/1948). Several additional efforts to establish a consistent nomenclature followed (e.g., Bürklen, 1917/1932; Révész, 1938/2013), although these contributions have since faded from mainstream recognition (for an overview, see Wagner, 2016). One of the most prominent figures in haptics nowadays might be David Katz, also standing close to Gestalt theorists (MacLeod, 1954), who successfully challenged the view that touch was a purely receptive mechanical sense and instead explored its dynamic nature (Katz, 1925). Eventually, J.J. Gibson, echoing many of Katz's major points, explicitly demonstrated the superiority of active touch over passive touch due to its capacity to optimize the intake of the most relevant stimulus information (Gibson, 1962).

Finally, S.J. Lederman and R.L. Klatzky famously established the concept of so-called exploratory procedures (EPs) in modern literature on haptic perception. EPs refer to specific types of movements that humans employ to efficiently gather information from objects they are interacting with. Those movements are tailored to the object's properties and the information intended to be retrieved (e.g., Lederman & Klatzky, 1987) (Fig. 2). For texture for example, spatial and temporal cues are gathered with lateral motions such stroking and swiping, enhancing the responses of SA1 (Johnson & Lamb, 1981) and PC afferents (Weber et al., 2013*)*. Even within specific object property categories such as softness (which can be narrowly defined as compliance, i.e. the inverse of stiffness (e.g., Di Luca, 2014)), movements have been shown to be tuned according to the respective dimensions of that property: Different dimensions of softness (e.g. deformability, viscosity, furriness, granularity) were shown to be associated with distinct hand and finger movements during active exploration (Cavdan et al., 2019, Dövencioğlu et al., 2022). Importantly, haptic perception is bidirectionally related to exploratory movements; which means that exploration influences perception, and perception influences exploration (e.g., Cooke et al., 2010, Di Luca, 2011).

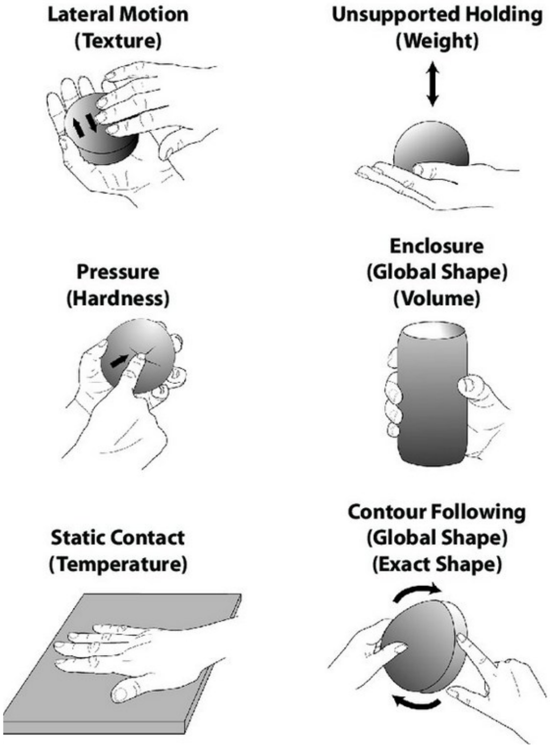

Figure 2. Exploratory procedures and their associated properties. Reproduced from Lederman & Klatzky (1987).

Typically, haptic explorations span a timeframe of multiple seconds during which sensory signals from various sources are integrated over the course of the time (Klatzky & Lederman, 1999). Integration of *simultaneous* redundant signals within and across perceptual modalities often follow the principle of Maximum-Likelihood-Estimation (MLE) (e.g., Alais & Burr, 2019; Ernst & Bülthoff, 2004; but e.g., Domini, 2023; Meijer et al., 2019). In MLE, different estimates are weighted by their reliability (the inverse of their variance) and averaged (Ernst & Banks, 2002, Knill & Saunders, 2003). For the integration of *sequential* signals however, and for extended haptic or visual explorations in particular, simple MLE models were found to be insufficient (e.g., Drugowitsch et al., 2012; Lezkan & Drewing, 2018b; Metzger et al., 2018; Toscani et al., 2016). Instead, recursive Bayesian models (Wu & Klatzky, 2018) and modified Kalman models (Metzger et al., 2018) were shown to better model serial information processing over longer timescales. The modified Kalman filter (Kalman, 1960) can capture changes in the underlying stimulus estimate by combining continuously applied Bayesian inference (earlier signals would constitute as a Bayesian prior) and the option of unstable estimates over time due to, for instance, memory decay (Metzger et al., 2018). Most relevant for the present work is that, irrespective of the specific framework and application, there is broad consensus that the reliability of sensory input is a primary determinant of the weight attributed to it by the sensory system. Further, basic variations in exploration behavior itself can modulate the reliability of perceptual estimates: performing more exploratory movements generates more sensory signals and thereby increases the reliability of the perceptual estimate (up to a saturation point), as evidenced by multiple studies (e.g., Gescheider et al., 1999; Giachritsis et al., 2009; Lezkan and Drewing, 2018b; Louw et al., 2005). During comparison of stimuli, switching between them has been demonstrated to further improve performance by reducing memory demands (Metzger & Drewing, 2020), while perceptual masking impaired performance (Drewing & Lezkan, 2021).

Exploratory procedures, albeit following stereotypical patterns to a certain extent, are not executed rigidly across the whole timespan or across different situations. There remains a large range of possible hand shapes and kinematics during these movements. In texture exploration for example, movement parameters such as contact force, speed and derivates, or trajectory direction can be dynamically fine-tuned. Section 1.4 will provide concrete examples for such movement adaptations. Closed-loop processes based on sensory signals gathered over the course of the exploration enable this motor adaptation (feedback processes) (e.g., Saig et al., 2012). Herein, sensory information from cutaneous and kinesthetic afferents is not only gathered for creating the percept, but is used for online movement adjustment, which in turn can facilitate sensory intake (e.g., Weiss & Flanders, 2011). Open-loop processes, i.e. an agent's experience, expectations, and usage of prior information, also play a significant role for movement adaptation (feedforward processes) (e.g., Zoeller et al., 2019). Haptic perception is characterized by an interplay of those processes (Aktas et al., 2025; Lezkan et al., 2018; Tampers & Flanders, 2013): When prior expectations are continuously updated through sensory processing, they can impact movement control over the entire exploration course (Tampers & Flanders, 2013) (cf. Fig. 3). Vice versa, prior influences such as motivational factors can affect the extent to which sensory signals are being exploited for movement optimization (Metzger & Drewing, 2018). For open-loop processes, signals can come from many different categories, that is prior information about object properties from, e.g., visual access or prior haptic experience, information about one's own abilities, information about situational constraints (e.g., limited available amount of exploration time), or information about the benefits of an exploration (cf. Gilbert & Sigman, 2007). By making use of pre-contact information and expectations derived from previous interactions, exploration efficiency can be increased without having to wait for sensory feedback. Trivially, just as the sensory signals gathered during exploration, prior information about object properties can also be directly integrated in the percept (e.g., Metzger & Drewing, 2019). Here, I treat prior information in the context of the behavioral link, i.e., how the information is exploited for exploratory movement adaptation during information gathering.

Most mechanisms involved in exploratory movement tuning can be subsumed under the umbrella term “predictive mechanisms”, hence the title of this work. For clarity: *Motor prediction* also falls into this capacious category and is widely acknowledged as a core element of motor control. Although antecedents of the concept can be found in much earlier writings (for an overview: Grüsser, 1986), it was Hermann von Helmholtz who most famously popularized the idea that the brain estimates its, e.g., eye position not by sensing it directly, but by using a copy of the motor command (an efference copy). This would allow the brain to localize visual objects by combining retinal input with the predicted gaze direction. Helmholtz demonstrated this with a self-experiment showing that passive eye movement causes visual instability, as the prediction is not updated (1866/1986). The notion that the brain predicts the somatosensory outcome of a movement (“forward model”) and is continuously comparing it with the actual sensory input produced by the movement was validated by many others and has become a central theory of sensorimotor control (see e.g., Fiehler et al., 2019; Johansson & Cole, 1992; Shadmehr & Krakauer, 2008; Wolpert & Flanagan, 2001). Motor prediction has further been studied in the context of self-touch (predictive attenuation, e.g., Bays et al., 2008; Blakemore et al., 2000) and in the context of tactile suppression to explain decreased sensitivity to (task-irrelevant) external stimuli before and during goal-directed body movement (Fraser & Fiehler, 2018; Juravle et al., 2017; Voudouris & Fiehler; 2022; see also: tactile gating, e.g., Colino et al., 2014; Kilteni & Ehrsson, 2022). All this though is not in the focus of this thesis; instead, prediction will be treated in the context of optimizing information gathering during active touch. Hartmann (2009) formulated a distinction which might be useful to clarify on the scope: Based on their lab’s works on the rodent whisker system, the author proposes that exploratory behavior involves two levels of prediction: 1) at the cognitive level, the animal forms a hypothesis about an object and chooses an action to test it and reduce uncertainty; 2) at the motor-control level, the animal carries out the required movement, which itself involves predictive control (for reviews on whisking behavior, e.g., Diamond et al., 2008; Saraf-Sinik et al., 2015). In the current thesis, the presented projects (Study 3,4, and 5) focus on what

Hartmann's framework refers to as the cognitive level (see also Kunde et al., 2007), with only occasional parallels drawn to underlying principles of the motor-control level. For the last part of this section, I will summarize literature on exploratory movement adaptation in humans with a special focus on the type of signals used and in which sense certain behavioral changes can be understood as movement *optimization*.

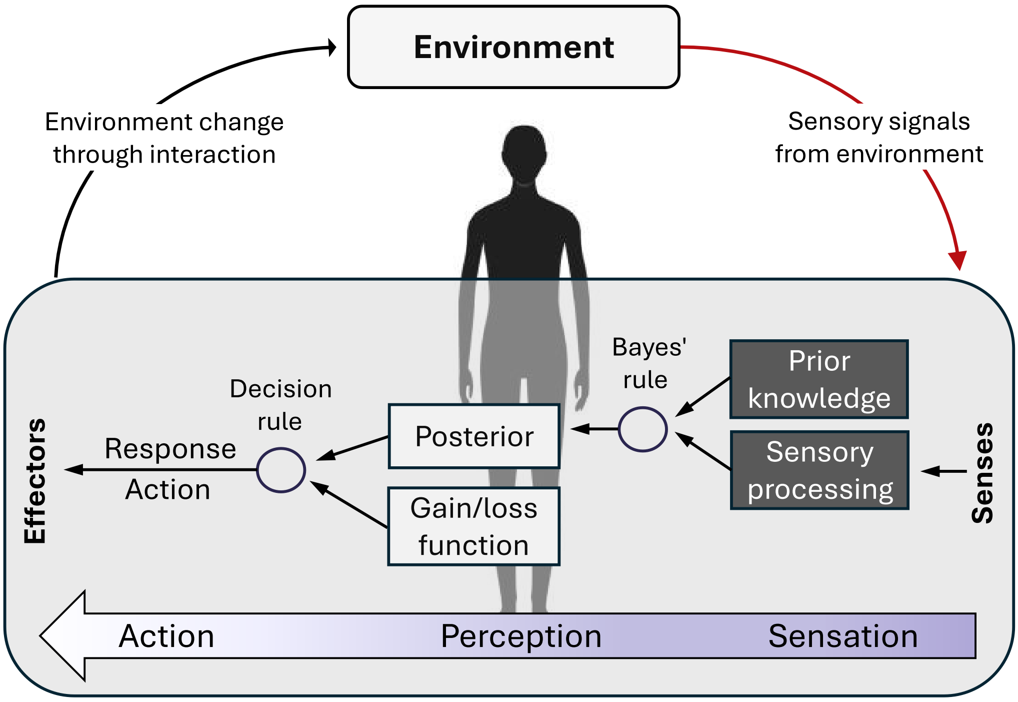

Figure 3. Sensation-Perception-Action Loop including Bayesian inference. Adapted from Ernst & Bülthoff, 2004.

1.4 Behavioral optimization of haptic explorations

Empirical evidence demonstrated that participants adjust different parameters of a variety of exploratory movements when explorations were "spontaneous", i.e., not experimentally constrained (e.g., Callier et al., 2014; Katircilar & Drewing, 2023; Nefs et al., 2002; Smith et al., 2002; Tanaka et al., 2014; Weiss & Flanders, 2011). In a tactile target search task for example, participants were observed to execute higher normal forces and decrease their scanning movement speed when searching for recessed in comparison to raised targets, likely in attempt to maximize the amount of skin penetrating the recessed squares to improve the probability of target detection (Smith et al., 2002). For grating explorations, a study found that velocities of lateral stroking movement and applied force differed between grating stimuli of varying frequencies. Force adaptation was assumed to vary to increase the amplitude of indentation of the skin when it has not reached the bottom of the grooves between the ridges yet (Nefs et al., 2002). In these examples, movement adaptation relied on the sensory information gathered over the course of the exploration. In a similar setup, movement parameters were further adapted to the goal of the task, as evidenced by higher scanning velocities and shorter break times between stimuli in the discrimination task than in the identification task (Tanaka et al., 2014). Another study extended this to a variety of stimuli of differing roughness, hardness, and slipperiness, demonstrating that movement kinematics such as scanning speed and trajectory shape depend both on the perceptual task and the texture itself (Callier et al. 2014). Both of these studies highlight the role of open-loop processes, i.e., agents do not only fine-tune their exploratory movements according to the surface characteristics itself but also according to the type of information they aim to retrieve. Similar was shown for the exploratory procedure “wielding” during inspection of metal rods (Riley et al., 2002): Analyses of the recurrent spatial patterns of the hand motions revealed differences in wielding execution across different perceptual intentions; i.e. depending on whether participants aimed to inspect length, width, or grasp position. Overall, those studies show that both the objects' properties and the agents’ intentions can shape the (initial) execution of an exploration.

Later, the general notion that humans dynamically adjust their exploratory movements was underpinned with controlled experiments that demonstrated the benefit of certain movement characteristics, allowing the conclusion that the changes observed in the respective studies or earlier work are beneficial and thus likely reflect optimization behavior. Gamzu and Ahissar (2001) for example again studied movement velocity in haptic grating discrimination and observed that for spontaneous explorations, some participants reduced their scanning velocity during the initial trials. In a consecutive experiment, the reduced velocity was found to allow for better discrimination performance than the initial higher velocity. This suggests that humans actively alter movement characteristics to improve sensory signal accumulation. Similarly, Lezkan and Drewing (2018a) demonstrated that participants optimize texture perception by adjusting their exploratory movement direction in way that maximizes temporal cue intake, which they found to increase task performance. In both studies, adjustments are performed on the basis of successively gathered sensory signals. In a study involving shape discrimination tasks (Drewing, 2012), participants displayed clear strategic preferences for exploratory directions that were previously shown to yield optimal performance (Drewing & Kaim, 2009); particularly when they were rewarded for "good perceptual performance". This suggests that exploration optimization can further be fostered by prior influences such as reward expectations. Effects of prior experience and information have been further assessed for softness exploration: one study found that participants adjust the peak indentation forces of their pressing movements to the expected stimulus' softness in order to improve perception (Kaim & Drewing, 2011). Extending that study, Lezkan and colleagues (2018) replicated the finding that participants systematically apply lower forces when softer objects (as compared to harder objects) are indicated by implicit prior information (blocked presentation, i.e. predictable sequences; see also: Katircilar & Drewing, 2024) and further demonstrated that the usage of prior information yielded stronger movement adaptations than the usage of sensory signals (Lezkan et al., 2018). Additionally, results showed that the usage of sensory information for movement adaptation can be fostered by high motivation, manipulated by introducing rewards for good performance. This underlines the interdependence of open- and closed-loop process and reemphasizes the importance of motivational factors. Another study building onto Kaim and Drewing (2011) investigated the influence of different types of prior knowledge on initial peak forces (Zoeller et al., 2019). Implicit prior information (blocked presentation) was used for force adaptation, whereas explicit (verbal or visual) interfered with movement adaptation. It remained unclear whether the exploitation of prior knowledge only is possible when implicit prior knowledge is induced, but not with explicit knowledge; or whether available knowledge must be of somatosensory nature in order to be “usable”. To elucidate on that, we conducted study 3 and 4. Zoeller and Drewing (2020) further demonstrated that when the number of allowed indentations was limited, participants applied higher initial forces, likely compensating for the reduced sensory input. This suggests that exploratory strategies can be adjusted in anticipation of situational constraints.

In sum, it becomes evident that humans fine-tune their exploratory movements in response to a variety of signals to enhance perceptual outcomes, with the degree of adaptation and the affected movement parameters varying across signal classes and - types.

1.5 Outline and Experimental Approaches

This work investigates adaptation and optimization processes in passive and active touch, i.e. changes in sensory processing or exploratory movement control that arise from previous experiences, expectations, and the usage of prior information. Overall, the projects are designed to assess adaptation across fundamentally different dimensions, ranging from low-level cortical sensory adaptation to higher-level anticipatory processes shaping movement selection and -execution in active touch.

In the first study, we employed a rather novel approach: we investigated cross-property tactile adaptation aftereffects to gather insights about potential shared somatosensory processing pathways between different tactile properties. Notably, we leveraged adaptation aftereffects as a tool to reveal processes encoding perceptual attributes, rather than investigating the nature of neural adaptation itself. Tactile two-point distance, macro-scale roughness, and curvature are critical for shape and material perception. While these dimensions have been extensively studied in isolation, their potential overlap in sensory processing has remained unexplored. Our study addresses this gap by providing the first behavioral evidence that all three are jointly encoded by a shared early-stage somatosensory mechanism. Across four psychophysical experiments, we demonstrate that adaptation to one property can elicit aftereffects in another, revealing cross-property interactions. For roughness and tactile distance specifically, the interactions exhibited hallmark signatures of early cortical processing, showing strict location- and orientation specificity, ruling out peripheral desensitization and higher-order decisional factors. Quantitatively, cross-property aftereffects were significant but weaker than within-property aftereffects, demonstrating that the computation of these features arises from a common primitive preprocessing that precedes feature-specific analysis. The second study complements the first one: Although we knew from the previous study (and other work, Calzolari et al., 2017; Kahrimanovic et al., 2009) that tactile distance and roughness aftereffects are not due to mere peripheral desensitization but rather arise from early cortical processing, we could not exclude the possibility that interindividual differences in the expression (here: magnitude) might be moderated by peripheral factors such as skin disposition. This is especially plausible as certain biophysical skin proprieties are known to be related to other perceptual parameters such as tactile sensitivity. To deepen our understanding of the somatosensory processing underlying tactile aftereffects, we hence conducted a systematic assessment of the relationship between skin properties, basic tactile abilities, and adaptation aftereffect magnitude. While results showed skin hydration and elasticity to be correlated with basic tactile sensitivity and spatial acuity, replicating and extending previous work, they were however not associated with increased or decreased aftereffect magnitude. The neural adaptation process underlying the tactile distance aftereffect hence seems to be a rather stable process and interindividual variance might rather be due to cortical idiosyncrasies.

With the third study, we enter the topic of active touch, focusing on the usage of visual prior information as this information type has only been sparsely covered in the past and yielded inconclusive results. We assessed this for texture exploration, which is usually characterized by easy-to-investigate stereotypical movements, i.e. stroking over surfaces (e.g., Ledermann and Klatzky 1987). Participants explored grating textures and discriminated them by their spatial frequency in a two-alternative forced-choice task, receiving abstract visual priors about texture orientation that varied in visual quality. We found that visual priors on grating orientation evoked similar adjustments of movement direction as those that were previously shown to develop over the course of an exploration and to increase perceptual performance (Lezkan & Drewing, 2018a) but, importantly, already at initial contact. Moreover, the extent of adjustments on trial basis was positively related to the visual quality (i.e., informational value) of the priors, aligning with established information processing models and previous findings on general motor control (see section 1.3.; Berniker & Koerding, 2011; Koerding & Wolpert, 2004). Also, the gradual establishment of adjustment behavior in the first place was shown to depend on the average priors' quality and, possibly, the task demands at hand. Together, results demonstrate that humans autonomously learn to use visual priors to optimize their haptic exploration, i.e., facilitating the intake of sensory information. The flexible nature of that process is conspicuously illustrated by the effects of the priors' informational value on their usage and the establishment of adjustment behavior. With the fourth study we extend the previous one, not only by applying a similar paradigm in a more naturalistic setting, but also by assessing the usage of visual information for holistic movement selection beyond the fine-tuning of singular movement parameters. Instead of using artificial stimuli such as 3D-printed (Study 1, 2, 3) or virtually rendered gratings (Study 5), we here included natural stimuli that humans typically are familiar with and for which they use characteristic exploratory procedures when interacting with them. We further used naturalistic prior information (presented via VR) instead of abstract visual cues and aimed to investigate how the availability of that information affects participants movement selection at initial contact with regard to EP type and exploration efficiency. Results showed that participants used specialized EPs earlier, with higher probability, and explored materials for a shorter time when they had access to valid prior visual information on the material. This demonstrates that humans use visual prior information to increase the efficiency of naturalistic haptic explorations by anticipatory planning of holistic movement schemes.

The last study focuses on a parameter that has not been systematically assessed so far in the context of spontaneous exploration optimization: the duration of an exploration process. Exploration duration can strongly differ across situations: an experienced kitchen chef might be quick when using the finger test to determine the doneness of a steak, though explorations might take longer when trying to estimate the scratchiness of an expensive wool sweater. As mentioned in section 1.3, additional sensory signals are generated with additional movements and longer exploration duration yields better performance up to a certain point. Humans, however, typically stop before reaching the point of maximal performance (Giachritsis et al., 2009; Louw et al., 2005; Metzger & Drewing, 2021). A plausible reason for this premature termination is that motor effort could play a role, as naturally, exploration extension is associated with additional movement costs and those were shown to play a critical role for general motor control (e.g., Rigoux & Guigon, 2012; Todorov, 2004). Further, (expected) task demands have been shown to affect optimization behavior (e.g., Kaim & Drewing, 2011). Hence, we aimed to investigate a potential interactive effect of task demands and motor effort on exploration duration. We conducted a 2AFC spatial frequency discrimination task under different conditions of task demands (by varying the discriminability of virtual grating stimuli) and motor effort (by implementing forces counteracting the participants' movements while switching between stimuli). Velocity and applied force were constrained via acoustic warning signals. Higher task demands were indeed associated with extended exploration duration, likely reflecting a compensatory mechanism that enables participants to attain a certain level of task performance, but this effect was reduced when task demands were increased. We concluded that exploration duration is a parameter which can be subject to optimization processes, likely being driven by dynamic cost-benefit expectations.

2. Shared early processing of distinct tactile features

A similar version of this manuscript has been submitted and is currently under revision: Jeschke, M., Azañón, E., & Knut Drewing, K. (under review). Shared early processing of distinct tactile features. iScience

The extent to which spatial tactile properties share neural pathways remains unclear, yet it is key to understanding how the brain constructs coherent object representations from distributed spatial inputs. One basic spatial property is the perceived tactile distance between two simultaneous touches on the skin. It exhibits adaptation aftereffects: When body areas are repeatedly touched at two points, subsequently presented smaller distances are perceived as smaller than on unadapted areas. We investigated whether tactile distance adaptation influences the perception of other spatial properties, macro-scale roughness and curvature, indicating shared neural mechanisms. In Experiment 1, adapting the skin to a fixed tactile distance reduced perceived roughness of subsequent gratings with smaller groove widths, as assessed through passive touch at the finger pad. This aftereffect likely originates from early cortical processing, as it is orientation-specific and independent of peripheral receptor desensitization. Experiment 2 demonstrated that curvature perception increases after adaptation to a two-point distance larger than the curve, suggesting overlap in processing pathways. Experiment 3 further supported early processing involvement, as the distance-to-roughness aftereffect did not transfer to adjacent skin regions of the same finger. Experiment 4 revealed bidirectional aftereffects: roughness adaptation also influenced distance perception. However, within-property aftereffects were stronger than cross-property effects. By revealing the existence of cross-property adaptation aftereffects with low-level characteristics, our findings provide evidence that tactile distance, roughness, and curvature share early somatosensory processing. This suggests that spatially defined properties undergo a common initial processing stage, sharing initial steps rather than existing in a hierarchical processing arrangement.

2.1 Introduction

Humans continuously extract tactile information to perceive objects and materials, whether through active exploration or via passive touch. Here, we investigate basic mechanisms underlying somatosensory processing during passive touch, focusing on how the brain combines spatial representations from tactile inputs. Specifically, we examine tactile distance, i.e., the perceived distance between two spatially separated points on the skin, and its relationship with surface roughness and curvature perception. While these properties are often studied in isolation, it remains unclear whether they rely on distinct or overlapping processing mechanisms. Addressing this question can reveal whether the brain generalizes spatial coding strategies across domains or maintains specialized processing streams for related but functionally distinct types of spatial information.

The perception of tactile distance has been found to be a basic somatosensory process (Calzolari et al., 2017) which is strongly modulated by low-level influences like receptor density, anisotropies in the shape of tactile receptive fields (RFs), and resulting differences in cortical magnification (Longo & Haggard, 2011; Longo et al., 2020). The computation of the distance between isolated points may be related to the encoding of critical properties in object discrimination, such as roughness and curvature: While tactile distance likely reflects fundamental spatial organization, both roughness and curvature perception also rely heavily on the integration of spatial cues (e.g., Conner & Johnson, 1992; Panday et al., 2024), making computational similarities between them plausible. In the current study, we examined whether certain mechanisms underlying the processing of spatial distance overlap with those involved in roughness and curvature, in order to infer the cortical level at which these interactions occur, and to determine whether one property serves as a foundational scaffold for processing the other properties. Understanding processing overlap and distinguishing between these two possibilities, i.e., common early processing versus sequential hierarchical integration, is essential for understanding how and when discrete tactile cues are combined to support object perception, as features like separation, surface variation, and curvature are central to recognizing material properties and object identity.

To address these questions, we leveraged tactile adaptation aftereffects as a means to examine cross-property interactions. Adaptation-aftereffects, i.e. the change in perception of stimuli after prolonged exposure to another stimulus, are a widely used psychophysical tool (see Thompson & Burr, 2009), as they allow researchers to infer how different stimulus dimensions are processed e.g. by populations of selective neurons (Solomon & Kohn, 2014). All properties in the scope of this study have been previously shown to be subject to aftereffects (Calzolari et al., 2017; Kahrimanovic et al., 2009; Vogels et al., 1996); Calzolari and colleagues demonstrated for instance that after adaptation to a tactile distance, participants perceive subsequent smaller distances as smaller than on unadapted skin areas (Calzolari et al., 2017). Note that in both Calzolari et al. and the present study, we focus on the computation of the abstract property of distance (e.g., 2 cm) between two points, independent of their specific location on the skin. This is achieved by repeatedly presenting two isolated, simultaneous points across different skin areas on the finger pad or hand. While localized receptive field-based processing is necessary for computing distance, our approach ensures that this computation is not tied to two particular receptive fields. Instead, it allows for a more generalized perception of distance that transcends specific spatial arrangements. To study the interplay between the different properties, we used a modified approach and investigated whether adaptation to one property can affect perception of the other, producing a corresponding aftereffect. Such cross-property aftereffects have been only rarely employed and predominantly in the context of visual aftereffects (Cooney et al., 2015; Cruickshank & Schofield, 2005; Georgeson et al., 2002; Palumbo et al., 2015). To our knowledge, only one study employed a similar approach for touch, demonstrating that adaptation to high frequency vibrations (> 100 Hz) impaired perception of fine textures but left perception of coarse textures mostly unaffected (Hollins et al., 2001).

We expected that adaptation to a specific tactile distance, coded through two isolated points on the skin, should influence the perception of macro-scale roughness: The Duplex theory of texture perception postulates that fine textures rely on a temporal-vibratory code, driven by the interaction between the finger and the surface, producing vibrations that are processed by fast and rapidly adapting mechanoreceptors. In contrast, the perception of coarse textures such as those used in this study depends on a spatial code, which is based on the variability in skin deformation (Hollins et al., 2001; Taylor & Lederman 1975; Yoshioka et al., 2001). Perceived roughness of coarse textures is mostly affected by changing inter-element spacing, element width and spatial frequency, with roughness perception increasing as the separation between elements becomes larger (Drewing, 2018; Lederman & Taylor, 1972; Sutu et al., 2013). Hence, we expect that adaptation to a certain tactile distance affects how subsequent groove-ridge gratings are perceived. Specifically, if gratings with substantially smaller groove widths than an adapted distance are perceived as less rough on the adapted finger, this would provide a striking causal demonstration that spatial coding is fundamental to roughness perception. We tested this in the first experiment of our study (Experiment 1).

Building on the possibility of shared mechanisms for complex object perception, we investigated in Experiment 2 whether adaptation to tactile distance also induces cross-property aftereffects in curvature perception (van der Horst & Kappers, 2008). To test this, we used convex curved strips (Fig. 5B) with constant contact lengths (Panday et al., 2014) but differing heights, resulting in varying curvature values. We hypothesized that adaptation to a distance that is notably larger than the length of the subsequently applied curve's indentation area would lead to an underestimation of the length of the indentation area. With the base-to peak-height staying constant, the gradient of the curve might consequently be perceived as steeper, i.e. perceived as more curved (Pont et al., 1997). Vice versa, when adapting to a notably smaller length, the opposite should happen, i.e., subsequently presented curves would be perceived as less curved. Contrasting effects of large versus small adaptation, i.e., a cross-property aftereffect from tactile distance to curvature, would highlight the importance of distance processing not only for roughness, but for the computation of properties that involve spatial processing in general.

We further aimed to infer the cortical level of processing where such interactions occur. Aftereffects are highly informative regarding the cortical functioning underlying the perception of properties: While low-level aftereffects stem from earlier cortical processing and thus show strong selectivity for stimulus characteristics such as orientation or location (Knapen et al., 2009; Knapen et al., 2010), higher-level aftereffects putatively arise from later cortical processing and can generalize across orientation, location, or stimulus size (Green & Oliva, 2010; Suzuki, 2001). The tactile distance aftereffect has been shown to exhibit typical low-level characteristics, namely orientation- and region-specificity (Calzolari et al., 2017); investigations on roughness and curvature aftereffects however so far provided either none or mixed behavioral evidence on their cortical origins (Hollins & Risner, 2000; Kahrimanovic et al., 2009; van der Horst et al., 2008; Vogels et al., 1996). Here, we assessed a potential orientation-specificity of the cross-property aftereffect from tactile distance to roughness perception in Experiment 1. Specifically, we tested whether the cross-property aftereffect only occurred when the application axes of adaptation stimuli and test gratings were aligned, i.e., when the two-point adaptor and test gratings both were applied along the length of the finger pad (Fig. 4B), and not when the two-point adaptor was rotated orthogonally to the test grating (Fig. 4B). Such orientation-specificity would suggest that the cross-property aftereffect arises at early stages of somatosensory processing, likely within primary somatosensory cortex (SI). Additionally, no transfer should occur when the adaptor consisted of a single tactile point instead of two (Fig. 4B), serving as a control for desensitization of peripheral mechanoreceptors and reemphasizing cortical involvement. We extended findings on the potential cortical processing level by assessing location-specificity with a third experiment (Experiment 3), testing whether the aftereffect spreads across adjacent skin regions of the same finger. Further, we applied both adaptor and test stimulus across the width (Fig. 4E) instead of along the length of the finger pad as we did in Exp.1, reinsuring that the aftereffect occurs independently of orientation as long as application axes are aligned.

Finally, to assess whether cross-property aftereffects reflect a common preprocessing stage or whether one property acts as an initial processing scaffold for the other, we compared them to their respective within-property aftereffects. Comparisons of aftereffects comprised distance adaptation to roughness perception; the reversed paradigm, i.e. roughness to distance; and the two congruent variants, i.e. roughness to roughness and distance to distance. If adapting to the same property produced for both properties a stronger aftereffect than cross-property adaptation, this would suggest early common non-hierarchical processing underlying the observed interactions: While congruent adaptation conveys all cues relevant for property computation, incongruent adaptation includes only part of them, thus resulting in weaker aftereffects. This would be the case for both roughness and distance. Alternatively, if one property were located upstream in the somatosensory pathway as a first step in the processing hierarchy, the difference between congruent and incongruent adaptation should be substantially smaller for that upstream property compared to the other. This is because whenever the downstream property is stimulated, the upstream property is also engaged as input and thus becomes strongly adapted regardless of congruent or incongruent conditions.

In summary, our results demonstrate cross-property adaptation aftereffects from tactile distance to roughness and curvature which are not due to peripheral desensitization, indicating that tactile distance shares common cortical processing with these properties. We investigated the character of these interactions in more detail for distance and roughness specifically and revealed that the aftereffects are bidirectional, exhibit low-level characteristics such as orientation- and location-specificity, and are weaker than the respective within-category aftereffects. Tactile distance and macro-scale roughness hence appear to undergo a similar early stage of somatosensory processing, reflecting shared early-stage mechanisms instead of a hierarchical processing arrangement.

2.2 Methods

2.2.1 Experiment 1

Participants

Due to the very large effect sizes reported for the tactile distance aftereffect (dz ≥ 1.59) (Calzolari et al., 2017), we expected a medium- to large effect for the current study (dz = 0.65). Based on that, we conducted an a priori sample size calculation for a power of 80% and an alpha of 5%. Projected sample size was 17 for the one sided one-sample t-test and 17 for a matched-pairs two sample t-test (G*Power; Erdfelder et al., 1996). To allow for complete Latin-square randomization of experimental conditions we collected data from 18 right-handed students from Justus-Liebig University Giessen (14 female, age 18-33 years, mean: 23.29 years). None of them reported cutaneous impairments or sensory deficits. We confirmed that by conducting a two-point discrimination test; all had two-point discrimination thresholds lower than 3 mm on their index fingers (Johnson & Phillips, 1981). All participants were naïve to the purpose of the experiment, provided written informed consent, and received financial compensation (8€/hour). The experiment was approved by the local ethics committee LEK FB06 and conducted in accordance with 2013 Declaration of Helsinki, except for preregistration.

Stimuli and Setup

Participants sat in front of the experimenter with their hands lying next to each other on a hand rest (height 10 cm, distance between finger pads of the index fingers approx. 25 cm), palms facing upwards, blindfolded, and wearing headphones with active noise-cancelling. A computer with MATLAB R2020b (MathWorks Inc. 2007) was used to guide the experimenter and collect responses. The experimental procedure was built using the Psychophysics Toolbox (Brainard et al., 1997). All haptic stimuli were 3D-printed (Fig. 4A; printer: Formlabs Form 3, XY-resolution of 25 microns, layer thickness of 25 - 300 microns). We used two different adaptation stimuli consisting of either one spike (single-point adaptation stimulus) or two spikes (two-point adaptation stimulus) separated by 4 mm (between their inner edges). Each spike had a radius of 1 mm at their tip and a height of 8 mm and were placed on top of a 25 mm × 20 mm × 20 mm cube. Test stimuli were gratings with a groove width of either 2-, 3- or 4-mm. Ridge width was 1 mm and amplitude was 3 mm for all gratings. The gratings were 3D-printed with a surface of 25 mm × 20 mm × 5 mm and a handle (height: 30 mm, diameter: 5

mm) at their bottom. We chose an amplitude size that prevented ground contact to maintain the linear relationship of element spacing and perceived roughness (Sutu et al., 2013).

Procedure

Each trial consisted of an adaptation phase and a test phase. During the adaptation phase, blindfolded participants were touched across the left index finger pad with either the two-point adaptor along the proximodistal axis, i.e., across the length of the finger pad (same orientation condition), along the mediolateral axis, i.e., across the width (orthogonal rotation condition) or with the one-point adaptor (single-point orientation condition), in three separate conditions (order counterbalanced across participants using a Latin square design). The application area was defined as depicted in Fig. 4A, and individual applications of the adaptation stimulus were evenly distributed across the area, with distinct space between consecutive applications, so that the stimulus was never applied systematically to the exact same points on the skin. The aim was to adapt to the abstract property of distance (i.e., the spatial relation between two tactile events), rather than to adapt two exact locations on the skin. The adaptation was conducted for 10 seconds before each trial except for the first trial after each break and at the start of each condition, for which we implemented an intensive 60 second adaptation phase. Adaptation durations were the same as those used by Calzolari and colleagues (2017). After the 10 (or 60) secs adaptation, two test stimuli were applied sequentially, one to each index finger pad. The test stimuli consisted of gratings of 2-, 3-, and 4-mm groove width presented in 5 possible combinations: right index finger/ left index finger (RF/LF): 2/4, 2/3, 3/3, 3/2, 2/4, forming the RF/LF ratios 0.5, 0.66, 1, 1.5 and 2. These ratios are equivalent to the ones used by Calzolari and colleagues (2017). Note that the right index finger is used here as a comparison area which should not be affected by adaptation to the left finger (2017). Test stimuli were applied with a continuous stroking movement in the proximodistal direction as depicted in Fig. 5C, with the ridges being oriented horizontally from the participants' perspective. To eliminate contrast enhancement due to simultaneous stimulation, discrimination performance was assessed in a sequential two-interval forced choice (2IFC) task. Application of test stimuli started randomly and equally often on the left and the right hand and participants had to judge if they perceived the first or the second stimulus to be rougher, responding verbally with no time restriction. The total trial number was 180 (5 pairs (ratios) x 3 conditions × 12 repetitions per pair). Adaptation as well as test trials were conducted using passive touch, eliminating motor and proprioceptive feedback and the possibility to actively alter scanning speed and pressure in order to gain additional information.

Importantly, the experimenter had undergone a training beforehand to replicate the pressure and timing between touches that experimenters used in the studies on tactile distance aftereffects by Calzolari and colleagues (2017). Nonetheless, we do not suspect pressure or timing of stimulation to be highly relevant in the context of producing these aftereffects. The experiment took ~1.5 hours, with 10 minutes breaks between the three main blocks that constituted the three adaptation conditions.

Analysis

For each participant, we computed the proportion of trials in which they judged the RF stimulus to be rougher; separately for each RF/LF ratio and each adaptation condition. For statistical analyses and fitting the data, we used common logarithms of the five RF/LF ratios to produce a symmetrical distribution from the point of actual equality ($x = 1$). For intuitive interpretation, we converted the mean of the logarithms back into ratios. For each of the three adaptation conditions separately, we fitted cumulative Gaussian distributions (two free parameters: μ [alpha] and σ [beta]) as functions of the logarithmic RF/LF ratios to the individual participants' data, using a Maximum Likelihood criterion. For that, we used the Palamedes Toolbox (Prins & Kingdom, 2018), implemented in MATLAB. The points of subjective equality (PSEs) were defined as the estimated RF/LF stimulus ratios at which participants were equally likely to judge either the LF or the RF stimulus as rougher. As an indicator of the perceptual bias, we use the difference between the PSE and the point of objective equality = 1. PSE values smaller than 1 indicate a tendency to perceive a texture applied to the adapted finger as less rough than without adaptation. PSE values larger than 1 indicate the opposite. Due to a violation of the assumption of normality ($p = <.001$ in a Shapiro-Wilk-test), we conducted a Friedman test on the individual log PSEs with the within-participant factor adaptation condition (same, orthogonal, single-point) in combination with Conover's post hoc tests for all adequate comparisons. Additionally, we conducted Wilcoxon rank-tests against log 1 (= zero) for the median log PSE values of each of the three adaptation conditions. Whenever we had a clear hypothesis on the expected direction of an effect, we employed one-sided t-tests or their non-parametric equivalents. This is explicitly stated throughout the results section for all experiments. Otherwise, two-sided tests were used, which is not explicitly stated. Further, all post-hoc tests were conventionally conducted as two-sided.

2.2.2 Experiment 2

Participants, Methods and Analyses

Based on the results of experiment 1, we expected large effects for a transfer of the tactile distance aftereffect to curvature perception and consequently collected data of 18 participants, following similar power-considerations (11 female, age 18-30; mean: 22.38). None of them had participated in the previous experiment.

To assess cross-property aftereffects, participants' left-hand palm was adapted before each trial either to a distance stimulus (1.5 cm) that is smaller than the indentation area of a subsequently presented curvature stimulus, to a larger stimulus (4.5 cm), or the control single-point stimulus. Afterwards, a 2IFC discrimination task followed, where they had to report which passively applied curvature stimulus was more curved (see Fig. 5A). All stimuli were 3D-printed curvature models (Fig. 5B, printer: Ultimaker S5, XY-resolution of 6.9 microns, layer thickness of 20 - 200 microns), constructed after thorough prototyping that allowed ergonomic application at the palm and adequate difficulty levels similar to Exp.1. We ensured that while indenting, the whole length of the curve was in contact with the skin, and not only (varying) parts of it. The final stimuli selected included three cylinder-segments with a constant width of 2 cm and length of 4 cm, placed on top of a 2 × 4 × 1 cm base (see Fig. 5B). Differences in curvature between the cylinder segments are therefore only reflected by height differences between the segments, with base-to-peak heights of 0.536, 0.376, and 0.271 cm. By keeping segment length constant, which would otherwise vary proportionally with curvature, we avoid confounds that could complicate later interpretations (Panday et al., 2014). The segments were part of cylinders with radii of 4 cm, 5.5 cm, and 7.5 cm and resulting curvature values (conventionally expressed as R^{-1}) of 0.25, 0.1818, 0.1333 cm^{-1}. The large-distance stimulus comprised a two-point distance of 4.5 cm and the small-distance stimulus comprised 1.5 cm (which is feasible as the two-point discrimination threshold at the palm is 0.75 cm (Sato et al., 1999)). The single-point stimulus again served as control. Following the same logic as the previous experiment, test stimuli were presented in 5 possible combinations: right hand/ left hand (RH/LH): 0.13/0.25, 0.13/0.18, 0.18/0.18, 0.18/0.13, 0.25/0.13, forming the RH/LH ratios 0.53, 0.73, 1, 1.36, 1.86. The total trial number was 210 (5 pairs (ratios) x 3 conditions × 14 repetitions per pair). Test procedure was similar as in Exp. 1 except that the application area here was at the palm, to allow for feasible discrimination performances and stimulus construction. Distance adaptation stimuli were always presented in proximodistal orientation (along the length of the hand) and test stimuli were statically pressed onto the skin for ca. 1 second (along the length of the hand). The experiment took ~1.75 hours, with 10 minutes breaks between each of the three main blocks and a two-minute break halfway through each main block. Preprocessing of data and calculation of PSE-values was similar to Exp. 1. We performed a repeated-measures ANOVA on log PSEs with the within-participant adaptation type (levels: small, large, single-point) and t-tests against log 1 (= zero) for the mean log PSE values of each of the three adaptation conditions.

2.2.3 Experiment 3

Participants, Methods and Analyses

We again based the power analysis on the expectation of a medium-to-large effect (d = 0.65) for an aftereffect on the middle phalanx, yielding the sample size of $N = 17$ with a power of 80% for one-sided one sample test and a one-sided matched pairs t-test (alpha 5%). Based on these power considerations, we collected data of 18 right-handed students from Justus-Liebig University Giessen (11 female, age 19-29 years, mean: 23.78 years). None of the participants had participated in the previous experiments.

On each trial, participants were first adapted to a distance stimulus across their left finger pad. Again, a 2IFC-discrimination task followed, where gratings were either applied across their finger pad, across the middle phalanx, or across the base of the finger (see depiction in Fig. 4E), and they had to report which one they perceived to be rougher. Same stimuli were used as in Exp. 1: gratings of 2, 3, 4 mm groove widths and a 4 mm distance stimulus as adaptation stimulus. Application axis of adaptor and test stimuli was always mediolateral (i.e., only one adaptation condition). Test trials were conducted in random order at three possible areas: finger pad (same as the adapted area), middle, base of the finger. Total trial number was 180 (5 pairs (ratios) x 3 test area conditions × 12 repetitions per pair). The experiment took ~1.5 hours, with 10 minutes breaks between each of the three main blocks and a two-minute break halfway through each main block. We performed a repeated-measures ANOVA on log PSEs with the within-participant factor “test area” and conducted one-sample t-tests against zero for the mean log PSE values of each of the three testing area conditions.

2.2.4 Experiment 4

Participants, Methods and Analyses

Based on the large effect size (d = ca. 1) for the cross-property effect on the finger pad in Exp. 1/3, we expected a medium-sized (d = 0.5) congruency effect (i.e., stronger PSE-shift for congruent adaptation than for incongruent) when the tested property is roughness. Under the assumption of an hierarchical processing model, we would not expect such a congruency effect when distance is the tested property, resulting in a medium sized (d=0.5) two-by-two interaction effect in a repeated measures ANOVA (power 0.8), yielding a required sample size of $N = 27$. We collected data from 26 participants (13 female, age 18-30 (mean 24.0). None of the participants had participated in the previous experiments.

On each trial, first participants underwent an adaptation phase at the finger pad to either roughness or distance, depending on the condition. Afterward, a test phase followed, either with distance stimuli or grating stimuli (see Procedure Fig. 6A). To ensure adequate discrimination performance, we used tactile distances of 5, 6, 7 mm and in compliance with that, gratings with groove widths of 5, 6, 7 mm, forming the RH/LH ratios 5/7 (0.714), 5/6 (0.83), 5/5 (1), 6/5 (1.2), and 7/5 (1.4). Distance and grating stimuli of 7 mm (distance or groove width, respectively) served as adaptation stimuli, depending on the condition. The experimental design comprised the two factors “congruency” (adaptation condition) and “test property”. Test property was either distance or roughness. In the “congruent” adaptation condition, the adapted property matched the property tested afterward. In the “incongruent” condition, a different property was adapted than the one subsequently tested. The experiment consisted of four blocks; throughout the first two blocks, either distance or roughness was adapted. Throughout the latter two blocks, the other property was adapted, respectively. Order of adapted property (distance first/roughness first) was counterbalanced between participants. Within each block, trial order was randomized and the test property hence could vary from one trial to another. Total trial number was 240 (12 repetitions per ratio (5) × adaptation condition (congruent/incongruent) × test condition (distance/roughness). Adaptation and test area were at the left index finger pads, and adaptation as well as test application axis was proximodistal. The experiment took ~2 hours, with 10 minutes breaks between each of the four main blocks and a two-minute break halfway through each main block. We performed a repeated-measures ANOVA on log PSEs with the within-participant factors “Congruency” and “Test property” and four one sample t-tests.

2.3 Results

2.3.1 Experiment 1

In the first experiment we investigated the existence of cross-property aftereffects from tactile distance to roughness perception to explore a potential processing overlap of the two properties. If adapting to one would affect the perception of the other, this would suggest communalities in the somatosensory processing of the two properties. On each trial, participants' left index finger pad was adapted to one of three stimuli: a 4 mm distance applied via two simultaneous touches oriented along the length of the finger (i.e., proximodistal; same orientation as the upcoming grating), a 4 mm distance oriented across the finger (mediolateral; orthogonal rotation), or a single-point stimulus serving as control for desensitization (see Procedure Fig. 4B). A two-interval forced choice (2IFC) discrimination task followed where gratings were applied on the participants adapted and unadapted homologous finger pad, moved along the length of the finger (Fig. 4A), with groove distances of 2-, 3- or 4-mm. Participants then had to judge whether the first or the second stimulus was rougher.

From the individual proportion of trials in which participants judged the right finger (RF) stimulus to be rougher, we determined the point of subjectively equal roughness (PSE) in the adapted as compared to the unadapted skin (Fig. 4C, D). We performed a Friedman test to assess the effect of adaptation mode (three levels: same orientation, orthogonal rotation, single-point) on individual average log PSEs. This non-parametric test, appropriate for comparing related conditions, was chosen because the data violated the assumption of normality (Shapiro-Wilk test: $p < .001$). Results showed that cross-property aftereffects varied depending on the adaptation mode, as indicated by a significant main effect of the within-participant factor adaptation mode on individual log PSEs (Friedman test: $\chi^2(2) = 19.51$, $p < .001$, $W = 0.54$). Specifically, adaptation to a two-point stimulus applied on the finger pad affected the perception of subsequently presented gratings, decreasing the judged roughness on the adapted finger pad when both adaptor and gratings had a matching orientation (Wilcoxon-rank tests; median = 0.942, *MAD* = 0.045; $Z = 3.0$, $p = <.001$ (one sided), r (rank biserial correlation) = 0.97, indicating significant deviations of log PSEs from zero). However, no aftereffects occurred when the adaptor was rotated orthogonal to the orientation of the test axis (median = 0.982, *MAD* = 0.025; $Z = 49.0$, $p = .12$, $r = 0.43$) or when the adaptor consisted of single indentations (median = 0.995, *MAD* = .018; $Z = 75.0$, $p = .66$, $r = 0.12$). Bonferroni-corrected Conover's post-hoc tests further confirmed significantly lower PSEs when the adaptor and test had the same orientation compared to an orthogonal orientation ($t(34)= 3.15$, $p = .010$), or to a single-point adaptor (*t*(34)= 4.26, *p* = <.001). No significant difference was found between the orthogonal and single-point conditions (*t*(34) = 1.11, *p* = 0.83). Note that a previous analysis of the data of Experiment 1 has been pre-published in a conference paper (Jeschke et al., 2023). These results provide causal evidence for the spatial coding postulate and suggests communalities between the processing of tactile distance and roughness. In addition, the absence of aftereffects when the adaptor was rotated orthogonal to the orientation of the test axis or when it consisted of only single indentations suggests that the observed interactions arise from early cortical processing.

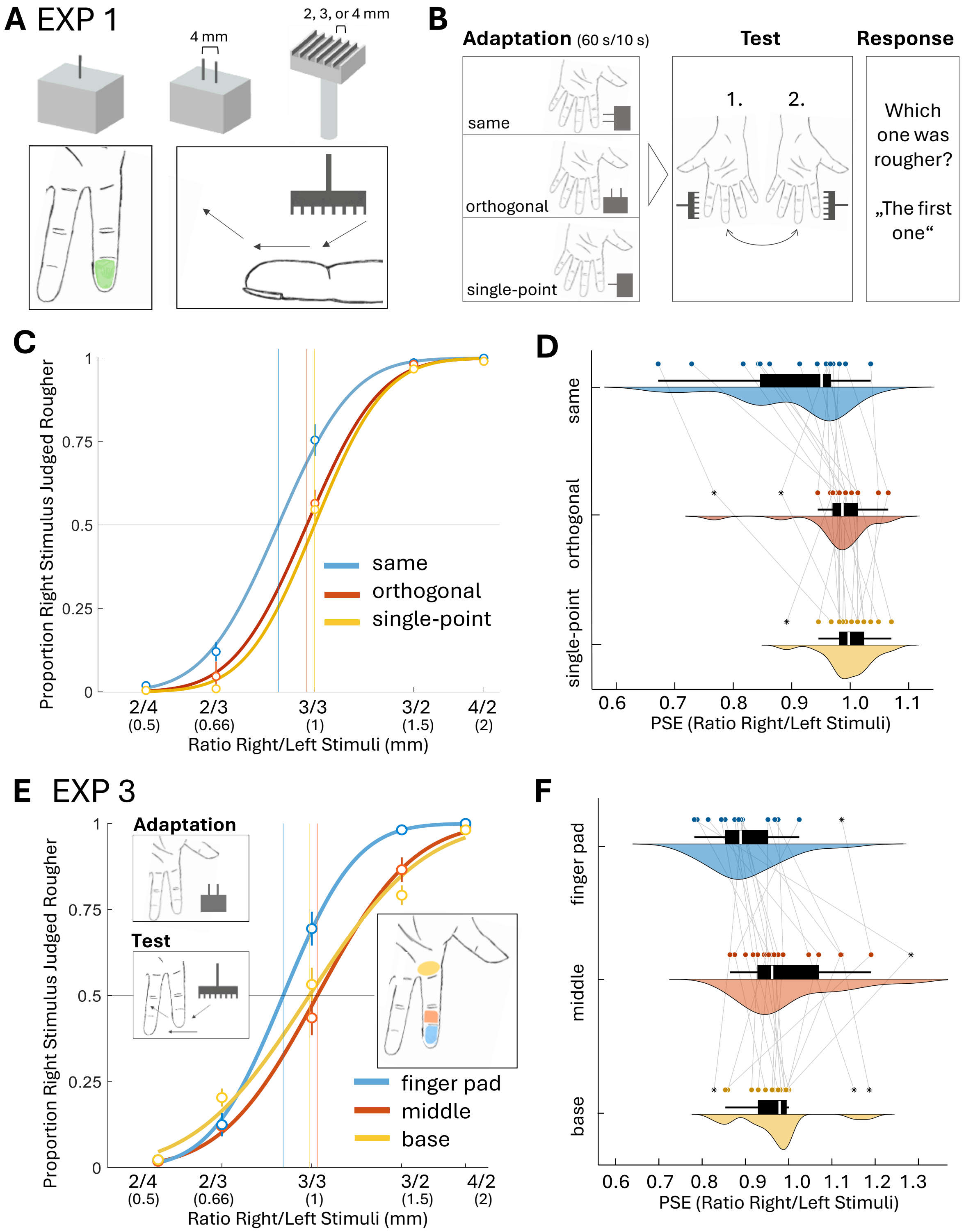

Figure 4. Procedure and results of Experiments 1 and 3. (A) Single-point adaptation stimulus, two-point adaptation stimulus, one example of the three test gratings (first row); application area of adaptation and test stimuli, application procedure of test grating (second row). (B) Experimental procedure. (C) Psychometric functions for the averaged proportions of the same orientation, orthogonal orientation and single-point adaptation conditions (*N*=18). Every data point shows the proportion of trials for which participants reported the test stimulus presented to the right index finger as rougher than the stimulus presented to the left (adapted) index finger

for each RF/LF stimulus ratio. Note however that participant's actual response was whether the first or the second applied stimuli was rougher. Psychometric functions are cumulative Gaussian functions. Error bars represent the SEM. Vertical lines represent mean PSEs of each condition. (D) Combined boxplot, density plot and scatterplot for same orientation, orthogonal orientation and single-point adaptation conditions. Connecting lines indicate data points belonging to the same participant. Boxplot: white line within black box displays median value. Black box spans from Q1 (25th percentile) to Q3 (75th percentile), representing the interquartile range (IQR), containing the middle 50% of the data. Whiskers extend from the box to the smallest and largest values within 1.5 × Interquartile range below Q1 and above Q3, respectively. Points outside this range are considered outliers. (E) Averaged psychometric functions for finger pad, middle phalanx and finger base test area conditions in Experiment 3 (N=18), where the effect of adaptation to distance on the left index finger pad was tested on three adjacent areas (finger pad, middle phalanx, and finger base. (F) Combined boxplot, density plot and scatterplot for finger pad, middle phalanx and finger base test area conditions.

2.3.2 Experiment 2

In a second experiment, we examined whether tactile distance adaptation induces a cross-property aftereffect on curvature, assessing whether the relationship observed between tactile distance and roughness in the first experiment also applies to curvature. Such a finding would further emphasize the role of distance processing in the broader computation of spatial tactile properties. To investigate this, we adapted participants' left-hand palm either to a two-point distance stimulus that was smaller than the indentation area of a subsequently presented curvature stimulus (1.5 cm), to a larger two-point stimulus (4.5 cm), or to a control single-point stimulus. Afterwards, a 2IFC discrimination task involving curvature stimuli followed, where participants had to report which stimulus they perceived to be curvier (see Procedure Fig. 5A). We conducted both adaptation and test phase at the palm instead of the finger for feasibility reasons (see methods section). We hypothesized that adaptation to a small distance at the palm of the hand is associated with subsequent decreased curvature perception on the adapted hand, while adaptation to a larger distance leads to increased curvature perception; both effects being produced by changes in perceived indentation length after adaptation to a two-point distance, thereby altering the perception of length/height curvature ratios. A control condition using a single-point adaptor should again produce no aftereffect. This pattern was largely reflected in the data: A one-way repeated measures ANOVA on individual log PSEs produced a significant main effect of adaptation mode (three levels: small, large, single-point) ($F(2, 34) = 16.26$, $p = <.001$ $\eta^2 = 0.49$). Bonferroni-corrected post-hoc tests between conditions revealed a significant difference between small and large adaptation ($t(17) = 5.46$, $p = <.001$, $d_z = 1.04$), with both conditions exhibiting significant deviations from a PSE of 1 (i.e., log PSE = 0) in opposite directions. Thus, adaptation to a small distance significantly reduced the perceived curvature of subsequently applied test stimuli (M = 0.90, SD = 0.18; one sample t-test (one-sided), t(17) = 2.55, p = .015, d = −0.60), whereas adaptation to a large distance increased perceived curvature (M = 1.10, SD = 0.172; t(17) = 1.98, p = .032 (one-sided), d = −0.47).

No conclusive evidence of an aftereffect was observed for the single-point adaptation (M = 0.95, SD = 0.18; t(17) = −1.53 p = .14, d = -0.36). Comparisons with the single-point condition revealed a significant difference between large and single-point adaptation (t(17) = 4.17 p = <.001, d_z = 0.80), but not between small and single-point adaptation (t(17) = 1.29, p = .62, d_z = 0.25). While the absence of a significant difference might suggest partially overlapping effects of small and single-point adaptation, this cannot be interpreted as evidence for equivalence, given the directional aftereffect was observed only for the small adaptor. In sum, tactile distance adaptation clearly affected subsequent curvature perception, as demonstrated by the contrasting effects of large versus small distance adaptation.

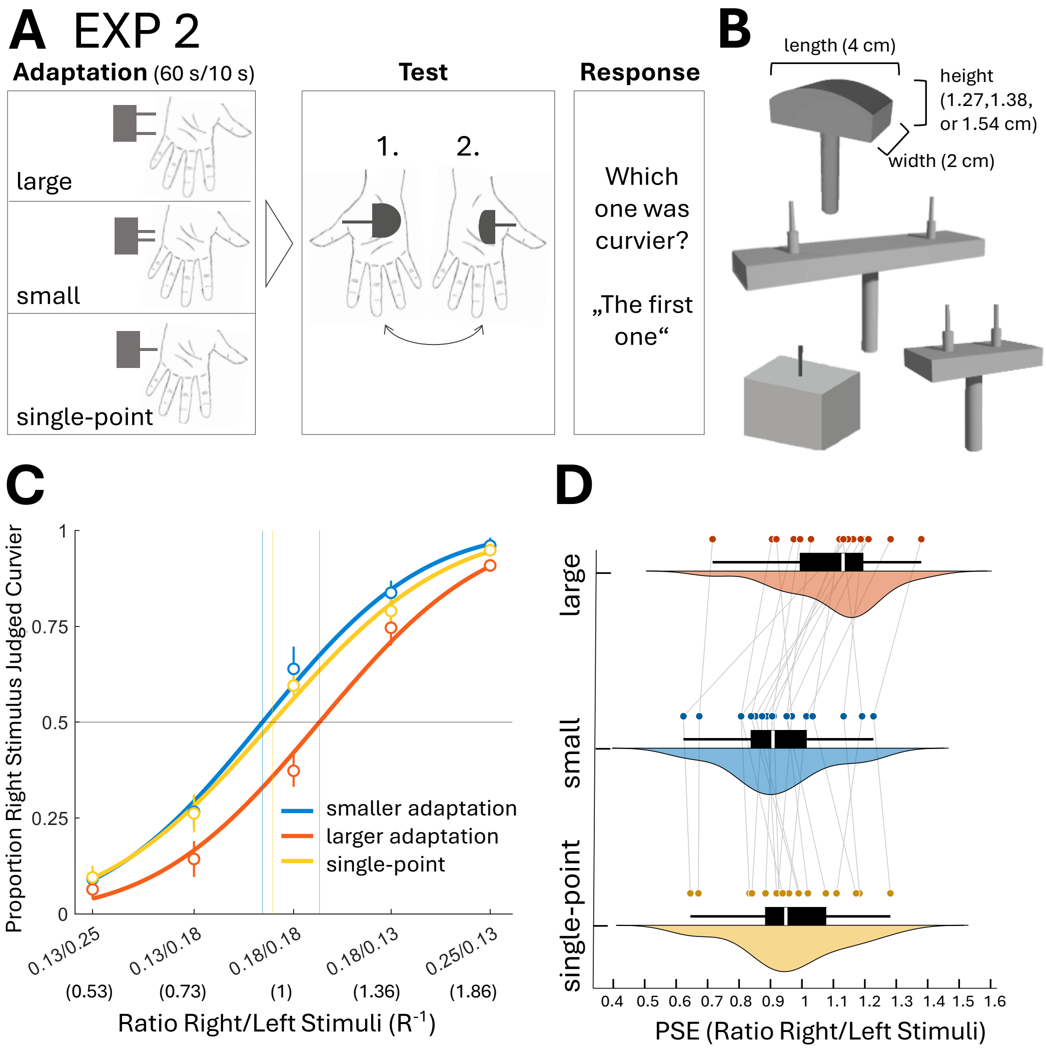

Figure 5. Procedure and results of Experiment 2. (A) Experimental procedure. (B) Haptic stimuli: one example of the three curvature test stimuli; large two-point distance adaptation stimulus (distance: 4.5 cm), single point adaptation stimulus, and small two-point distance adaptation stimulus (distance: 1.5 cm). (C) Psychometric functions for the averaged proportions of the small adaptation, large adaptation, and single-point adaptation conditions (*N*=18). Every data point shows the proportion of trials for which participants reported the test stimulus presented to the right hand palm as more curved than the stimulus presented to the left (adapted) hand palm for each RH/LH stimulus ratio. Note however that participant's actual response was whether the first or the second applied stimuli was more curved. Psychometric functions are cumulative Gaussian functions. Error bars represent the *SEM*. Vertical lines represent mean PSEs of each condition. (D) Combined boxplot, density plot and scatterplot for small adaptation, large adaptation, and single-point adaptation conditions.

2.3.3 Experiment 3

In Experiment 3, we aimed to further test our inference regarding the sensory processing level at which the observed interactions between tactile distance and roughness take place. In Experiment 1, we observed that the cross-adaptation aftereffect was orientation-specific. Here, we assessed the location-specificity of the cross-property aftereffect, testing whether distance adaptation of the finger pad also affects roughness perception on the middle phalanx and finger base (Fig. 4E). We expected an aftereffect transfer to the middle phalanx due to cortical spread within SI (Schweissfurth et al., 2011) but not as far as to the finger base. Further, contrary to Experiment 1, we applied both adaptor and test stimulus across the width instead of along the length of the finger pad (Fig. 4E), reinsuring that the aftereffect occurs independently of orientation as long as application axis are aligned. Results demonstrate that textures were again perceived as less rough on the finger pad of the adapted finger after adaptation to a two-point distance stimulus, but this aftereffect did not spread across adjacent skin regions of the same finger (Fig. 4E,F), suggesting that cross-property interactions stem from low-level sensory processing within the primary somatosensory cortex displaying distinct intra-digits separation (Sanchez-Panchuelo et al., 2012). A one-way repeated measures ANOVA revealed a significant main effect of the within-participant factor test area (3 levels: finger pad, middle phalanx, finger base) ($F(2, 34) = 5.86$, $p = .006$, $\eta^2 = 0.26$). Bonferroni-corrected post-hoc tests between conditions revealed a significant difference between finger pad and middle phalanx ($t(17) = 3.30$, $p = .007$, $d_z = 1.00$) and no difference between middle phalanx and finger base ($t(17) = 0.87$, $p = >1$, $d_z = 0.28$). However, the difference between finger pad and finger base did not reach significance ($t(17) = 2.43$, $p = .06$, $d_z = 0.78$), although the effect size suggests a substantial difference that may not have been detected due to limited power. In addition, one sample t-tests against 1 (i.e., log PSE = 0) reemphasized that the transfer of the aftereffect emerged only on the finger pad ($M = 0.89$, $SD = 0.13$, $t(17) = -3.78$, $p = <.001$ (one-sided), $d = -0.89$), but did not spread to the middle phalanx ($M = 1.04$, $SD = 0.17$; $t(17) = 0.77$, $p = .23$ (one-sided), $d = 0.18$), or finger base ($M = 1.10$, $SD = 0.136$; $t(17) = 0.38$, $p = .71$, $d = -0.09$).

2.3.4 Experiment 4

In Experiment 4, we aimed to infer whether a shared underlying mechanism drives the interactions between distance and roughness or whether the computation of one property might serve as initial upstream process, subsequently influencing perception of the other. To evaluate the potential (non-)hierarchical nature of the property-interactions, we tested and compared four aftereffect variants in the last experiment: two incongruent ones, i.e. the cross-property aftereffect from distance adaptation to roughness perception, and the reversed paradigm, i.e. roughness to distance; and the two congruent variants, i.e. roughness to roughness and distance to distance (Fig. 6A). We were mostly interested in how the aftereffects differ between the incongruent and congruent conditions. If the properties share common preprocessing, then incongruent adaptation should for both properties produce smaller aftereffects than congruent adaptation, as incongruent adaptation includes only part of the cues relevant for property computation. This would be reflected as a main effect of adaptation (in)congruency in an ANOVA. In contrast, under the assumption of a hierarchical organization, the aftereffect difference between incongruent versus congruent adapting would be smaller when testing the upstream property as compared to the downstream property. This asymmetry between the two properties would manifest as an interaction effect between adaptation (in)congruency and test property in the ANOVA. Results demonstrate that the cross-category aftereffect works bidirectional, i.e. from tactile distance to roughness and vice versa, but for both test properties a congruent adaptation produces stronger aftereffects than an incongruent one, suggesting early common shared processing of the properties instead of one property being an initial scaffold located upstream in the processing hierarchy.

A two-way repeated measures ANOVA with the factors congruency (congruent/incongruent) and test-property (distance/roughness) revealed a significant main effect of congruency ($F(1,25) = 22.94$, $p = <.001$, $\eta_p^2 = 0.48$), with congruent conditions being associated with lower PSEs than incongruent conditions. There was no main effect of test-property ($F(1,25) = 0.01$, $p = <.94$, $\eta_p^2 = 0.01$), and no interaction effect ($F(1,25) = 2.55$, $p = .12$, $\eta_p^2 = 0.09$). One sample t-tests (one-sided, as aftereffects are expected for all conditions) revealed significant aftereffects for all conditions: congruent adaptation on distance-test (distance to distance, $M = 0.91$, $SD = 0.09$, $t(25) = -5.00$, $p = <.001$, $d = -0.98$), and roughness-test (roughness to roughness, $M = 0.89$, $SD = 0.07$, $t(25) = -8.08$, $p = <.001$, $d = -1.59$), as well as incongruent adaptation on distance-test (roughness to distance, $M = 0.93$, $SD = 0.07$, $t(25) = -4.70$, $p = <.001$, $d = -0.92$) and roughness-test (distance to roughness, $M = 0.94$, $SD = 0.08$, $t(25) = -3.85$, $p = <.001$, $d = -0.76$).

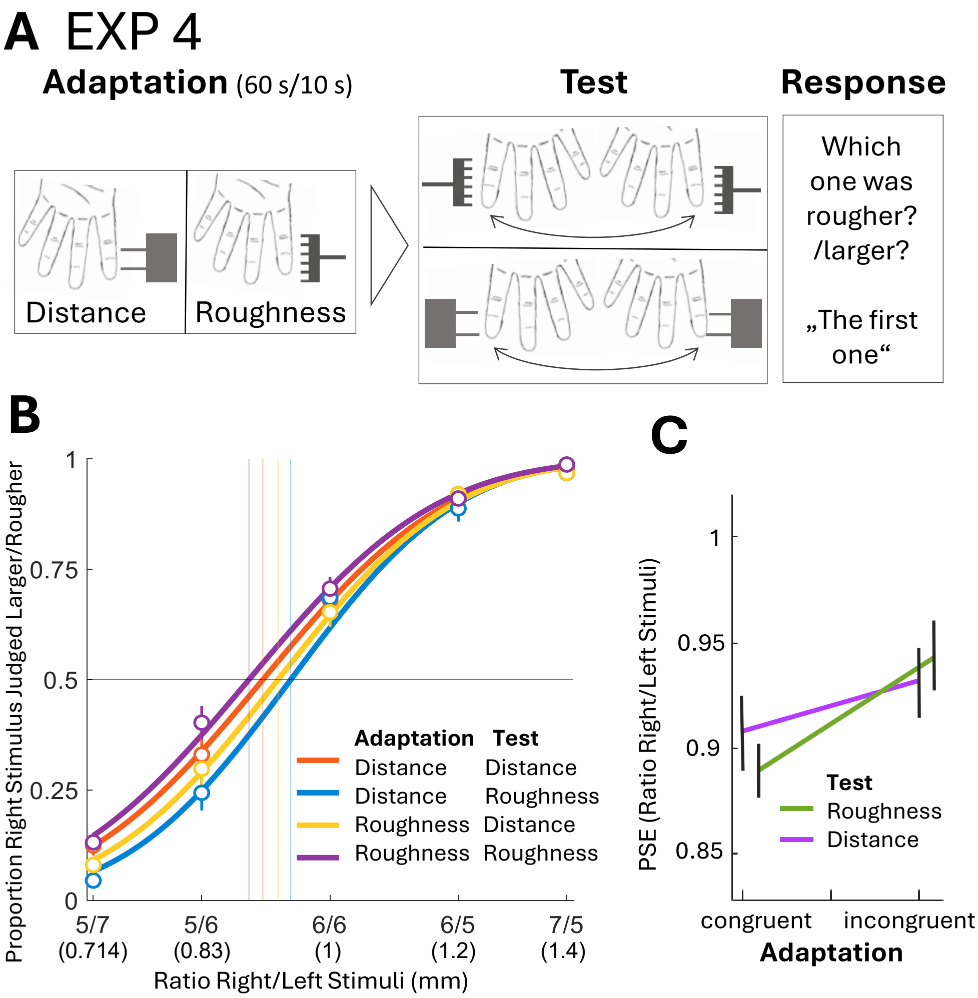

Figure 6. Procedure and results of Experiment 4. (A) Experimental procedure. (B) Psychometric functions for the averaged proportions of the conditions Distance-Adaptation/Distance-Test, Distance-Adaptation/Roughness-Test, Roughness-Adaptation/Distance-Test, and Roughness-Adaptation/Roughness-Test (*N*=26). Every data point shows the proportion of trials for which participants reported the test stimulus presented to the right index finger as rougher/larger than the stimulus presented to the left (adapted) index finger for each RF/LF stimulus ratio. Note however that participant's actual response was whether the first or the second applied stimuli was rougher/larger. Psychometric functions are cumulative Gaussian functions. Error bars represent the SEM. Vertical lines represent mean PSEs of each condition. (C) Line plot depicting the average values of Distance-Adaptation/Distance-Test, Distance-Adaptation/Roughness-Test, Roughness-Adaptation/Distance-Test, and Roughness-Adaptation/Roughness-Test. Error bars represent the SEM.

2.4 Discussion

In this study we provide evidence that tactile distance, roughness, and curvature share early somatosensory processing by investigating if and under which circumstances perceptual adaptation-aftereffects can transfer from one stimulus property to another. We observed cross-property adaptation-aftereffects where tactile distance adaptation influenced the subsequent perception of roughness. These effects arose from low-level cortical processing rather than from mere desensitization of peripheral receptors, as shown by the lack of adaptation aftereffects in control conditions using single-point stimuli. In addition, we demonstrated bidirectional cross-property aftereffects, characterized by low-level features such as orientation- and location specificity. Notably, bidirectional aftereffects between roughness and tactile distance were weaker than the respective within-property aftereffects, suggesting that these tactile properties share early somatosensory processing stages rather than standing in a hierarchical relationship with each other.

Importantly, adaptation to distance affected not only roughness perception but also curvature perception, as evidenced in Experiment 2 by contrasting aftereffects following adaptation to either a large or small two-point distance. This highlights the fundamental and generalizable nature of the observed effects: basic distance computation appears to follow similar initial processing as those mechanisms underlying the processing of spatial information from qualitatively distinct spatial inputs, which ultimately give rise to complex percepts such as curvature and roughness. In summary, our findings demonstrated that computations which underlie somatosensory processing of different spatially characterized properties share common early mechanisms.

To evaluate the relationship between distance and roughness computation in detail, we compared cross-property aftereffects with their respective within-property aftereffects. The results suggest that, rather than one property serving as a foundational building block for the other, both properties may share a common early-stage preprocessing mechanism: For both properties, adapting to the same property (congruent adaptation) produced larger aftereffects than adapting to the other property (incongruent adaptation). If one property would be situated upstream in the somatosensory pathway as an initial step in the processing hierarchy of the other, then the difference between congruent and incongruent adaptation should be substantially smaller for that upstream-located property than for the other. As this was not the case, one can speculate about the underlying mechanism that might produce the observed cross property interactions instead:

Adaptation to large tactile distances may cause neurons specifically tuned to those distances to exhibit expanded receptive fields (RFs), reducing spatial resolution due to RF overlap (cf., Duncan & Boynton, 2003; Vierck & Jones, 1970). This would then lead to the perception of smaller distances (Longo & Haggard, 2011) or reduced roughness for subsequently presented smaller distances or finer gratings. Such RF modulation may arise from lateral inhibition and plasticity at the network level, involving shifts or expansions in RF boundaries (e.g., Ergenzinger et al., 1998). The transfer of aftereffects between tactile properties suggests that the adaptation to the spatial property of distance is not strictly receptor-type specific. Rather, it may involve RF changes in neurons receiving convergent input from multiple afferent classes (Saal & Bensmaia, 2014) contributing to all three properties due to their ability to encode both spatial details and sustained pressure (Connor & Johnson, 1992). The larger aftereffects observed for congruent compared to incongruent adaptation may then be explained by later differences during higher-level property-specific processing downstream.

There is evidence for correspondingly rapid RF-size modulation especially in the field of vision (Kastner et al., 2001; Womelsdorf et al., 2008) and also in touch (Alloway et al., 1989; Haggard et al., 2007). In the visual and the somatosensory system, lateral inhibition sharpens receptive fields by suppressing activity in neighboring neurons. For the tactile domain, pharmacological interventions have been shown to provoke a release from intracortical or thalamocortical inhibition, allowing excitatory regions of receptive fields to expand (Dykes et al., 1984), while attentional manipulations have been found to boost inhibition and consequently decreased RF size (Haggard et al., 2007). Similar mechanisms might account for the observed effects here, extending excitatory RF size through disinhibition in reaction to adaptation. This mechanism is particularly plausible for roughness perception, as supported by the spatial-variation model which proposes that roughness is determined via a computation of the variation of response patterns across sheets of RFs of SA1 afferents, with increased roughness perception for higher variation (Goodman & Bensmaia, 2017). If those RFs were to be enlarged, variation (and consequently the perceived roughness) across a certain area would decrease. A similar principle applies to curvature perception: As the receptive field enlarges, the perceived curved area decreases; leading to a higher perceived curvature.

The modulation of RF geometry as an underlying mechanism producing property interactions appears especially plausible given that the cross-property aftereffects observed in our experiments displayed low-level characteristics. Notably, the orientation specificity demonstrated in Experiment 1 aligns well with the concept of RF modulation: If we assume that the RFs are stretched along one particular axis due to adaptation, e.g., the proximodistal axis, this deformation would result in decrease spatial information along that axis, reducing distance perception specifically in that direction. Consequently, no aftereffect should occur if the test stimulus is oriented orthogonal to the adapted axis, as RF geometry remains unaltered along that axis (Calzolari et al., 2017).

Our findings provide robust evidence for the orientation specificity of the aftereffect from distance to roughness. Notably, prior studies have shown that stimuli are perceived as larger along the mediolateral axis of the finger than along the proximodistal axis, due to acuity anisotropies. This has been demonstrated in tasks involving grating orientation, two-point orientation, and gap discrimination tasks (Essock et al., 1997; Stevens & Patterson, 1995; Wheat & Goodwin, 2000) and the anisotropy is observed across different body parts (Longo et al., 2020; Longo & Golubova, 2017). Consequently, if we had conducted the adaptation along the proximodistal axis and then applied test stimuli along the mediolateral axis to assess orientation-specificity, any observed lack of aftereffect could be mistakenly attributed to these anisotropies rather than true orientation specificity. Specifically, test stimuli that are physically smaller than the adaptor may not be perceived as substantially smaller along the mediolateral axis due to higher acuity along that axis. This could obscure the expected aftereffect, which would normally cause the test stimuli to be perceived as smaller compared to stimuli applied on the non-adapted finger pad. To avoid this confound, we conducted adaptation along the mediolateral axis and tested along the orthogonal, proximodistal axis in Experiment 1. This design ensured that any absence of the aftereffect could be attributed to orientation-specific mechanisms rather than perceptual anisotropies. Furthermore, in Experiment 3 we applied both adaptor and test on the mediolateral axis, which produced the typical aftereffect again. This reaffirms that the lack of aftereffect in Experiment 1 was indeed due to rotation of the stimulus.

The orientation-specificity of the cross-property aftereffect between distance and roughness (Experiment 1) suggests that the aftereffect is mediated by orientation-selective neurons within the primary somatosensory cortex (SI), which are highly localized and finely tuned to specific orientations. Such neurons respond most robustly when stimuli are aligned with their preferred orientation, indicating that the neural mechanisms underlying the aftereffect are precise and spatially constrained. Given this premise, we did not expect the aftereffect to spread from the fingertip to the base of the finger. Although some propagation across adjacent skin regions within the same digit was anticipated due to cortical spread within SI (Schweissfurth et al., 2011), the absence of an effect on the middle phalanx in Experiment 3 is consistent with previous findings demonstrating precise intra-digit maps within area 3b of SI, both in humans and macaques (Iwamura et al., 1983; Sanchez-Panchuelo et al., 2012). Importantly, if the sensory mechanisms underlying the cross-property aftereffect involves geometry modulation of local receptive fields at early cortical processing stages, it is particularly plausible that the aftereffect would remain confined to the stimulated area without spreading to neighboring skin regions.

Previous studies have shown that coarse texture perception relies on spatial patterns of activation across mechanoreceptors, primarily slowly adapting SA1 afferents, and that spatial parameters such as inter-element spacing and groove width significantly influence perceived roughness (Drewing, 2018; Lederman & Taylor, 1972; Sutu et al., 2013). However, most of these studies inferred spatial coding either from stimulus-response mappings, where changes in tactile stimuli (like spacing or texture) are linked to perceptual outcomes without directly manipulating the underlying neural code (Hollins & Risner, 2000; Taylor & Lederman, 1975), or from neurophysiological recordings, revealing correlations between neural firing patterns and specific spatial features (Weber et al., 2013). These methods suggest associations between spatial coding and perception but fall short of proving that directly altering the spatial representation itself, i.e., specifically, the metric of inter-point distance on the skin, leads to changes in tactile perception. Our study provides this causal evidence: Modifying the spatial code through adaptation to a tactile distance systematically altered the perception of both roughness and curvature. Tactile distance adaptation primarily conveys spatial information by activating slowly adapting afferents (Merkel and Ruffini), while leaving rapidly adapting receptors (Meissner and Pacinian) mostly unaffected (Johnson et al., 2000). Although our roughness test phases involved both spatial and temporal-vibratory information, since gratings were passively moved along the finger pad (Hollins & Risner, 2000), the adaptation to two isolated points forming a specific distance still significantly influenced perception during the test phase. This highlights the critical role of slowly adapting afferents in computing macroscale roughness (Weber et al., 2013; Yoshioka et al., 2001) and demonstrates that spatial coding is not merely correlated with but is essential for the perception of coarse textures. It strengthens the Duplex theory by offering behavioral evidence that the spatial dimension of tactile input is a determining factor in roughness perception at the macro scale.

Experiment 2 demonstrated that adaptation to distance not only influenced roughness perception but also affected curvature perception. While both texture and distance share discrete spatial intervals as a common feature, curvature perception in passive touch is fundamentally different, as it arises from continuous deformation patterns on the skin when pressed against a surface. This difference makes the observed cross-property aftereffects between distance and curvature more surprising and intriguing. Notably, we found clear cross-property aftereffects between two-point distance and curvature for the large two-point stimulus. However, we did not observe differences between the two-point small distance adaptation and the single-point control, as both caused subsequently presented curvature stimuli to be perceived as less curved. One possible explanation for this result is that the single-point stimulus may have induced curvature adaptation on its own, potentially due to its perception as highly curved. Technically, each indentation of the distance stimulus produces a skin deformation similar to that caused by a small round stimulus, potentially resulting in a curvature percept to some extent (Pont et al., 1997). Under this premise, it is also possible that small distance adaptation had a similar impact as the single-point adaptation: Although 1.5 cm is not below the average two-dot discrimination threshold (Sato et al., 1999), it might be the case that the small distance adaptor was not consistently perceived as an actual distance, but rather as a single point. Previous studies on the tactile distance aftereffect also provided unclear results for small distance adaptation (2 cm), showing no substantial effects when a large distance was subsequently presented (Calzolari et al., 2017; Hidaka et al., 2020). This consistent lack of effects for small distance adaptation on the perception of larger distances makes it plausible that curvature adaptation might be responsible for the small distance adaptation on curvature perception observed here: If small distance adaptation does not influence large distance perception, it is plausible that it would also fail to affect the perception of larger length-areas. Nevertheless, the contrasting effect of the adaptation to a distance larger than the curvature stimulus provides strong evidence that tactile distance and curvature do share sensory processing. The large distance adaptor did elicit the expected effect, increasing perceived curvature of subsequently presented stimuli.

In sum, our findings clearly demonstrate that the computation of different spatially defined tactile properties relies on a common initial processing step, with modulation of receptive field geometry emerging as a plausible candidate mechanism underlying the observed interactions. The observation that percepts derived from qualitatively different stimulus properties undergo the same primitive preprocessing is highly significant and provides a foundation for investigating broader principles in future works. Cross-property aftereffects effectively revealed shared somatosensory processing between properties within the current study and employing such paradigms might hence be a useful tool in future studies to disentangle somatosensory computations and uncover previously unknown relationships.

3. The Relationship Between Biophysical Skin Properties, Tactile Ability, and the Distance Adaptation-Aftereffect

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Interindividual differences in biophysical properties such as skin hydration and elasticity have been demonstrated to play a critical role in influencing various aspects of tactile perception. Here, we assess their role for interindividual variation of basic tactile abilities and the tactile distance adaptation aftereffect in a young adult sample. Tactile abilities were defined by tactile sensitivity in a monofilament detection task and spatial acuity in a grating orientation task. In the distance aftereffect, when a body area is repeatedly touched at two points separated by a given distance, subsequently presented smaller distances are perceived as smaller than on unadapted areas. Aftereffect magnitude describes the perceptual shift in a distance discrimination task following adaptation. We examine whether differences in skin hydration and elasticity at the finger pad are related to tactile abilities which in turn affect the magnitude of distance aftereffects. Results revealed that higher hydration and elasticity were related to increased tactile sensitivity and spatial acuity, but the magnitude of distance aftereffects was independent from both skin properties and tactile abilities. While these results reemphasize the importance of healthy skin for tactile perception, they suggest individual differences in the magnitude of the distance aftereffect to be independent from peripheral skin properties.

3.1 Introduction

Humans can collect tactile information through passive and active touch to assess the attributes of objects and materials. In this context, biophysical properties such as skin hydration and elasticity have been suggested to play a critical role in influencing various aspects of tactile perception performance (Lévêque et al., 2000; Sakaguchi et al., 2024; Samain-Aupic et al., 2023; Verrilo et al., 1998). Hydration is defined as the water content of the stratum corneum, the first layer of the epidermis, and elasticity generally describes the skin's ability to recover its initial position after deformation. Performance parameters that are discussed to be affected by those properties are for example tactile sensitivity, which typically describes the ability to detect light pressure (Sakaguchi et al., 2024; Samain-Aupic et al., 2023), and spatial acuity, i.e.

the spatial resolution of the tactile perception (Lévêque et al., 2000; Sakaguchi et al., 2024). Here, we aimed to strengthen the evidence for that relationship, with a particular focus on interindividual differences in the biophysical properties of hydration and elasticity of an otherwise homogenous young sample, and to assess how these differences affect more complex tactile perception by studying the tactile distance adaptation-aftereffect.

Regarding hydration, experimental manipulations such as moisturizer application were found to benefit perception: By softening the stratum corneum and thus increasing the contact area between object and skin, hydrating interventions were shown for instance to improve roughness perception (Verrilo et al., 1998) and spatial acuity, assessed in a gap detection task (Lévêque et al., 2000). Similarly, higher water content of the stratum corneum due to single-time cream application was found to enhance tactile sensitivity, assessed in a suction pressure discrimination task (Sakaguchi et al., 2024). Although one study found no substantial effects of single-time cream usage neither for sensitivity nor for spatial acuity (Dione et al., 2023), prolonged application of cosmetic oil with added aromatic compounds however increased elastic fiber length at the respective skin site, and in turn enhanced both spatial acuity, assessed in a grating orientation task, and tactile sensitivity, assessed in a monofilament detection task (Samain-Aupic et al., 2023). In line with these findings, interindividual differences in biophysical and related mechanical properties of the skin have been suggested to be tied to perceptual performance: Lower skin stiffness, measured as the compliance of the finger pad during a rigid body compression test, was found to be associated with better discrimination of compliant surfaces, as softer skin generated greater rates of change in contact area (Li & Gerling, 2023). Similarly, skin conformance, i.e. a measure of how much the skin invades gaps in grating stimuli, was shown to partly account for differences in tactile spatial acuity in young subjects, again measured with a grating orientation task (Vega-Bermudez & Johnson, 2004). The decline in spatial acuity with aging however was suggested to be primarily caused by reduced afferent density rather than changes in skin properties (Vega-Bermudez & Johnson, 2004). This was highlighted by another more recent study, demonstrating that skin elasticity and hydration contribute to a lesser extent to the age-related changes in spatial acuity than afferent density (Deflorio et al., 2023). Overall, it becomes evident that there is a relationship between skin properties and basic tactile perception, most commonly assessed in the context of aging and moisturizing manipulations. By conducting a systematic assessment of interindividual naturally occurring differences in skin hydration and elasticity and their relation to basic perceptual parameters in young adults we aim to extend the existing literature.

We further aimed to investigate whether interindividual differences in these skin properties have implications for other tactile phenomena. Specifically, we investigate whether the expression of tactile aftereffects is affected by interindividual differences in skin properties. Adaptation-aftereffects describe the change in perception after prolonged exposure to the same stimulus. They exist in every sensory domain, with the largest reported variety of features in vision (see Favreau & Corballis, 1976). Numerous haptic aftereffects such as the tactile movement aftereffect or the softness aftereffect have been reported (Hollins & Favorov, 1994; Metzger & Drewing, 2016). Calzolari and colleagues showed that after adaptation to a tactile distance, participants perceive subsequent smaller distances as being smaller than on unadapted skin areas (Calzolari et al., 2017). Distance as a basic somatosensory property is defined as the distance between two distal points simultaneously applied onto the skin. This distance aftereffect exhibits characteristics typical for low-level cortical adaptation aftereffects, namely orientation- and region-specificity, i.e. the aftereffect does not occur when application axis or area are not congruent between the adaptation and test phase. This supports the assumption that tactile distance perception mainly arises at early stages of somatosensory processing (Longo et al., 2020; Longo & Haggard, 2011). As for every psychophysical measurement, there is interindividual variance for the strength of that aftereffect, i.e. individuals differ in the extent to which their subsequent perception is affected by the adaptation. While nearly all participants exhibit some degree of perceptual aftereffect, the extent of this effect varies considerably, with some individuals experiencing pronounced perceptual distortions, even for stimuli that would typically be easily distinguishable under no-adaptation conditions (Calzolari et al., 2017; Jeschke et al., 2023). In this study we examined whether interindividual differences in the magnitude of the tactile distance aftereffect can be explained by differences in skin properties and resulting differences in basic tactile perception. Distance perception here refers to very small stimuli at the finger pads in the order of millimeters (Jeschke et al., 2023).

Perceptual intensity of adaptation and test stimuli has been suggested to affect the magnitude of visual aftereffects. Multiple studies found for example that the visual motion aftereffect is influenced by both the physical stimulus strength as well as the subjective perceptual strength (Georgiades & Harris, 2000; Ishihara, 1999; Roumani & Moutoussis, 2020). For instance, aftereffect magnitude was observed to increase with increasing adapting contrast and with decreasing test contrast (Ishihara, 1999). Similarly, the magnitude of the high-level facial expression adaptation aftereffect was found to increase monotonically as a function of the intensity of adapting facial expressions (Hong & Yoon, 2018). Transferring this to the tactile domain, we suspected that tactile aftereffect magnitude might vary under conditions of differing sensory response intensity; such as those linked to specific skin characteristics shown in previous studies (Lévêque et al., 2000; Sakaguchi et al., 2024; Samain-Aupic et al., 2023; Vega-Bermudez & Johnson, 2004; Verrilo et al., 1998). In this analogy, enhanced contrast in visual adaptation stimuli would be the equivalent of heightened tactile acuity. While previous studies demonstrated that peripheral factors are not the origin and cause of tactile aftereffects, it is yet unclear whether they can have an additional impact on their expression, possibly explaining natural interindividual differences in e.g. the aftereffect magnitude. By employing this novel exploratory approach we aim to deepen our understanding of tactile aftereffect mechanisms.

We included both hydration and elasticity as parameters of skin properties as well as both tactile sensitivity and spatial acuity (subsumed under "tactile ability" in the following as in Skedung et al., 2018). We investigated whether skin hydration and elasticity of the finger pad are related to the magnitude of a tactile distance adaptation aftereffect; mediated by resulting differences in tactile ability as assessed by tactile sensitivity to pressure and tactile spatial acuity. We expected higher sensitivity and acuity for more hydrated and more elastic skin. For the relationship between skin properties and aftereffect magnitude, we expected that more hydrated and elastic skin are associated with an increase of the sensory response to the adaptation and consequentially an increase of the resulting aftereffect.

3.2 Methods

Participants

Due to the very large effect sizes reported for the tactile distance aftereffect (Calzolari et al., 2017) and instances where certain skin properties have shown large effects on tactile precision (Vega-Bermudez & Johnson, 2004), we expected medium-to-large effects for the relationship between skin properties and aftereffect magnitude. Based on that, we conducted an a priori sample size calculation for a power of 80%, an alpha of 5%, and an effect size f^2 of 0.25 (medium-to-large). Projected sample size was $N = 34$ for a linear regression (G*Power; Erdfelder et al., 1996). We accordingly collected data from 34 right-handed students from Justus-Liebig University Giessen (19 female, age 18-30 years, mean: 23.38 years). None of them reported cutaneous impairments or sensory deficits. All participants were naïve to the purpose of the experiment, provided written informed consent, and received financial compensation (8€/hour). The experiment was approved by the local ethics committee LEK FB06 and conducted in accordance with the 2013 Declaration of Helsinki, except for preregistration.

Setup and Stimuli

For assessing tactile sensitivity, we used a calibrated set of 13 thin, polycarbonate rods with different diameters (Von Frey Filaments; Bioseb, USA). Application of a monofilament onto the surface of the skin with increasing pressure causes the rod to buckle and the monofilament bows out sidewards (buckling load). The ability of participants to detect the buckling of increasingly finer monofilaments (pressure threshold) was measured. The monofilament set comprised the buckling loads of 78, 59, 39, 20, 14, 10, 6, 4, 1.6, 0.7, 0.4, 0.2, 0.08 millinewton (mN). Intensity levels were chosen based on previous literature (Dione et al., 2023) and comprised values from a logarithmic scale of actual force and a linear scale of perceived intensity.

For assessing tactile acuity with a grating orientation task, we 3D-printed a set of 28 circular grating stimuli (printer: Stratasys Objet 30 Pro, resolution: 600 × 600 × 1600 dpi). These were constructed following the same principle as the well-established JVP domes, which have been widely used for assessing sensory capacity in grating orientation discrimination to qualify the tactile threshold for the spatial resolution (Johnson & Phillips, 1981). For our purpose, we implemented smaller steps sizes between stimulus intensities. Each grating stimulus consists of a circular, convex grating surface (2 cm diameter, curvature: 0.29 cm-1), mounted on top of a cylindrical handle (height: 3 cm). The set comprises 28 stimuli with equidistant groove and bar widths equal to 0.3 mm-3 mm (step size: 0.1 mm).

For the tactile distance aftereffect-paradigm, we 3D-printed a set of four stimuli (printer: Formlabs Form 3, XY-resolution of 25 microns, layer thickness of 25 - 300 microns). All stimuli consisted of 25 mm × 20 mm × 20 mm cubes. The test stimuli had two spikes on top (diameter: 1mm at their tip, height: 8 mm) with 5/6/7 mm distance to each other (between their inner edges), with the larger, 7 mm one also serving as the distance adaptation stimulus. The single-point adaptation stimulus had only one spike of the same diameter on top. A pilot experiment ensured adequate difficulty levels that allowed for proper psychometric fitting.

Procedure

Testing of participants involved first measuring skin hydration and elasticity, followed by psychophysical testing of tactile sensitivity, spatial acuity, and the distance aftereffect (in this specific order). All testing was carried out at the index finger pad of the left hand and participants were blindfolded and wore noise-cancelling headphones throughout the testing (as in Jeschke et al., 2023). We selected the index finger due to its highest sensitivity as demonstrated in two-point discrimination tasks (Johnson & Phillips, 1981). The hand was chosen arbitrarily, as both homologous fingers exhibit equivalent sensitivity (Spasojević & Obradović, 2013). Total duration of one session was ca. 1.5 hours, comprising ca. 5 minutes for skin measurements, 20 minutes for assessing tactile ability, and 60 minutes for the adaptation aftereffect paradigm.

Skin properties were assessed with different probes from Courage & Khazaka Electronic GmbH (Cologne, Germany). Finger hydration was measured with a Corneometer CM 825 in arbitrary units (a.u.), based on bioelectric impedance to provide measurements of the skin conductance (reciprocal of resistance). Each individual moisture value is an average of five repeated measurements (as in Deflorio et al., 2023; Skedung et al., 2018) across the left index finger pad. Location of measurement was the center of the finger pad, as well as the point 5 mm above, below, left and right to the center, identified by measuring the whole distal phalanx with a caliper (Burg Wächter Precise PS 7215). Finger elasticity was measured at the same locations with a Cutometer MPA 580 by measuring the vertical deformation of the skin when pulled into a 2 mm diameter probe with an optical sensor. Each of the five measurements consisted of a suction cycle of 2 s using a constant negative pressure of 450 mbar, followed by a 2 s period when the pressure was switched off (relaxation phase), allowing the skin to return to its original shape. We used the elastic recovery parameter (R5, also called net elasticity) computed by the Software MPA CTplus (Version 1.1.5.0) to represent finger elasticity in the current study (as in e.g., Skedung et al., 2018). This value contrasts the elastic part of the suction phase against the immediate recovery during relaxation phase; higher values here indicate higher elastic properties. As for hydration, each individual elasticity value is again an average of five repeated measurements.

To assess tactile sensitivity, we ran an adaptive staircase procedure similar to the one used in (Bell-Krotoski, 1993; Dione et al., 2023). After a familiarization phase with the monofilament of the highest force level (78 mN), testing began with the 39 mN monofilament, which the experimenter applied three times at different sites of the finger pad and the participant verbally responded “yes” as soon as they felt a stimulation. If they gave three correct responses, the monofilament level decreased by two levels (i.e., to 14 mN). If all stimulations were felt again, the monofilament level increased by one level to the adjacent higher force level (20 mN). The procedure continued in this step-wise order (descending two levels, ascending one level) until an incorrect detection within one series was given (miss). If the participant missed one detection during the series of the three applications, the adjacent higher force level was tested. The procedure was terminated when two errors within one series were made and the monofilament above was noted as the tactile detection threshold. Exact time of stimulation within one series was unknown. We ran this staircase twice, gathering two threshold values that were averaged afterwards, to achieve a more reliable estimate.

To assess spatial acuity, we conducted a modified staircase procedure adapted from a protocol by Wang and colleagues (Wang et al., 2023). Before the test session, participants received a familiarization phase during which the 3 mm stimulus was visually presented to them, and instructions were given verbally in combination with three example trials. Participants had to report whether the grating was oriented horizontally or vertically and received verbal feedback. A short practice session followed: In 20 practice trials, using again the 3 mm grating, participants had to achieve an accuracy of 75% in order to not be excluded from further testing (as participants with thresholds of >3 mm would not be able to properly perform the adaptation aftereffect-task). No participant was excluded. Afterwards, the test session started, and the staircase began with the 3 mm grating. On each trial, grating orientation was randomized and had to be verbally reported by the participant. If the participant gave two consecutive correct answers, the next lower grating width would be used; if the participant gave one incorrect answer, the next greater grating width would be used. The session was completed when twelve transition points were identified. A transition point is defined as the stimulation changing from decreasing widths to increasing widths and vice versa. The average of the grating widths at the last eight transition points was used to determine the threshold, corresponding to the intensity producing approximately 71% correct responses (Vega-Bermudez &. Johnson; Wetherill & Levitt).

The adaptation-aftereffect experiment included a 10-minute break between the two main blocks that constituted the two conditions (distance adaptation and control), and a 5-minute break within each block. The order of conditions was randomized and counterbalanced between participants. Each trial consisted of an adaptation and a test phase. During adaptation, participants were touched multiple times across the finger pad of the left index finger with either the two-point (7 mm distance) or the single-point stimulus (control), in separate conditions (Fig. 7). Single applications of the adaptation stimulus were evenly distributed across the area with distinct space between consecutive applications as the aim was to adapt to the abstract property of distance (i.e., the spatial relation between two tactile events) rather than adapting exact locations on the skin. The adaptation per trial was conducted for 10 seconds in a typical trial. However, in the first trial of each condition block and after each break, we implemented an intensive 60 second adaptation phase. The adaptation durations were the same as in (Calzolari et al., 2017; Hidaka et al., 2020; Hidaka et al., 2024). After the 10 (or 60) secs adaptation, two test stimuli were applied sequentially, one to each index finger pad with a one second interstimulus interval. Application of test stimuli started randomly and equally often on the left and the right hand. Participants had to judge if they perceived the first or the second stimulus to be larger and give their answer verbally without time restriction. The test stimuli of 5, 6, 7 mm were presented in 5 possible combinations: right index finger/ left index finger (RF/LF): 5/7, 5/6, 6/6, 6/5, 7/5, forming the RF/LF ratios 0.714, 0.833, 1, 1.2 and 1.4. The total trial number was 120 (5 pairs × 2 conditions × 12 repetitions per pair).

Analysis

Raw data are available at https://doi.org/10.5281/zenodo.14615922. Regarding the adaptation-aftereffect paradigm, we first computed for each participant the proportion of trials in which they judged the RF stimulus to be larger (note however, that the actual task of the participant was to indicate whether the first or second stimulus felt larger); separately for each RF/LF ratio and both adaptation conditions. For statistical analyses and fitting the data, we used common logarithms of the five RF/LF ratios to produce a symmetrical distribution from the point of actual equality ($x = 1$). For intuitive interpretation, we converted the mean of the logarithms back into ratios to report means. For each of the three adaptation conditions separately, we fitted cumulative Gaussian distributions (two free parameters: μ [alpha] and σ [beta]) as functions of the logarithmic RF/LF ratios to the individual participants' data, using a Maximum Likelihood criterion. For that, we used the Palamedes Toolbox (Prins & Kingdom, 2018). The points of subjective equality (PSEs) were defined as the estimated RF/LF stimulus ratios at which subjects were equally likely to judge either the LF or the RF stimulus as larger. As an indicator of the perceptual bias, we use the difference between the PSE and the point of objective equality = 1. PSE values smaller than 1 indicate a tendency to perceive a distance applied to the adapted finger as smaller than it objectively is. PSE values larger than 1 indicate the opposite. To derive a value representing the “pure” aftereffect magnitude, we subtract for each participant the average PSE of the control condition, serving as a baseline, from the average PSE of the distance condition. Thus, the diffPSE is free from any systematic bias due to mere stimulation or hand preferences. For inferential statistics, a one-way repeated measures Analysis of Variance (ANOVA) on log PSEs was conducted to check for main effect of the “adaptation condition” (two levels: distance adaptation and control). Additionally, two one-sample t-tests against log 1 (= zero) were conducted to further assess the PSE-shift. Eight simple linear regressions were used to assess the relationship between skin properties, tactile abilities and aftereffect magnitude. We test whether there is a relationship between hydration and tactile sensitivity, expecting higher sensitivity for higher levels of hydration. Likewise, we test whether higher elasticity is related to higher sensitivity. We further test whether higher hydration and elasticity are also related to higher spatial acuity. Regarding the aftereffect magnitude, we check whether there is a relationship with hydration and elasticity, expecting higher aftereffects magnitudes for higher hydration and elasticity. We further test whether higher sensitivity and/or spatial acuity is related to higher aftereffect magnitude. Given that we test a set of predefined well-justified hypotheses, alpha-levels will not be adjusted (Rothman, 1990; Streiner & Norman; 2011).

3.3 Results

Results showed that distance adaptation produced a substantial aftereffect in the expected direction, decreasing perceived size of the distance on the adapted finger when being adapted to the 7 mm distance, but not when receiving the single-point control. A one-way repeated measures ANOVA on log PSEs revealed a significant main effect of the within-participant factor “adaptation condition” (two levels: distance and control), $F(1,33) = 57.32$, $p = <.001$, $\eta^2 = 0.64$. One sample t-tests confirmed that the aftereffect appeared only in the distance adaptation condition ($M = 0.92$, $SD = 0.06$, range: 0.78-1.04; $t(33) = -9.03$, $p = <.001$ (one-sided), $d = -1.55$), but did not occur in the control condition ($M = 0.98$, $SD = 0.06$, range: 0.79-1.11; $t(33) = -1.63$, $p = .113$ (two-sided), $d = -0.28$).

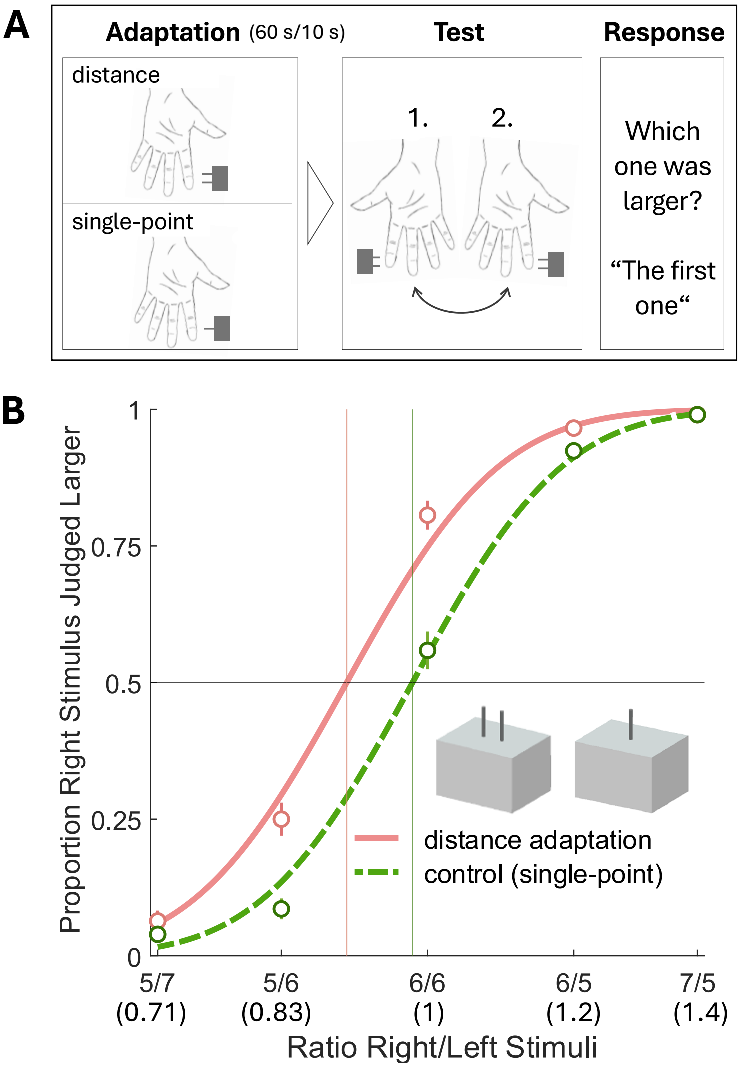

Figure. 7. (A) Experimental procedure. (B) Averaged psychometric functions for distance adaptation and control condition (N = 34). Every data point shows the fraction of times participants judged the stimulus presented to the right index finger as larger than the stimulus presented to the left index finger for each RF/LF stimulus ratio. Curves are cumulative Gaussian functions. Error bars represent SEM. Vertical lines represent mean PSEs.

Simple linear regressions were used to further assess the relationship between skin properties, tactile abilities, and aftereffect magnitude. Those showed strong relations between skin properties and tactile abilities, but no relationship of either with aftereffect magnitude. Linearity of the data as well as normality and homoscedasticity of residuals was visually inspected and approved (normality assessed with Q-Q plot and homoscedasticity by plotting actual residuals against predicted residuals) and residual independence was given (all $p > .05$ in Durbin-Watson test). Hydration and elasticity were highly correlated ($r = 0.69$, $p > .001$). Results of the first linear regression analysis indicated that hydration significantly explained 20.5% of the variance in tactile sensitivity, $F(1,33) = 9.49$, $R^2 = 0.21$, $p = .004$, with a standardized regression coefficient of -0.48, p = .004 (Fig. 8A), indicating lower sensitivity thresholds with higher levels of hydration.

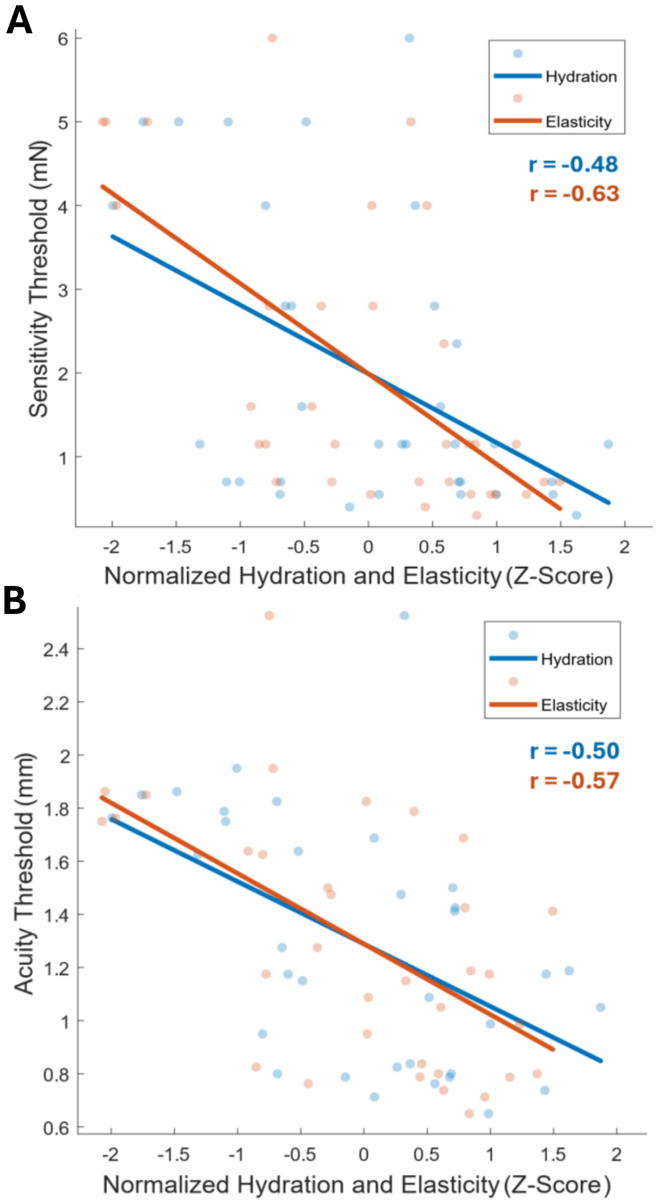

Figure 8. (A) Scatterplot including separate lines representing the linear regression of sensitivity (monofilament detection) on hydration and elasticity. For visualization reasons, hydration and elasticity are given as z-values. (B) Scatterplot including separate lines representing the linear regression of acuity (ridge size in grating orientation discrimination) on hydration and elasticity.

Additional regressions indicated that hydration significantly explained 20.30% of the variance in spatial acuity, $F(1, 33) = 10.92$, $R^2 = 0.23$, p = .002, with a standardized regression coefficient of -0.50 (Fig. 8B), indicating lower acuity thresholds with higher levels of hydration. Further, elasticity significantly explained 37.4% of the variance in tactile sensitivity, $F(1, 33) = 20.75$, $R^2 = 0.37$, $p = <.001$, with a standardized regression coefficient of -0.63 (Fig. 2A), indicating lower sensitivity thresholds with higher levels of elasticity. Similarly, elasticity explained 30.4% of the variance in spatial acuity, $F(1, 33) = 15.39$, $R^2 = 0.34$, $p < .001$, with a standardized regression coefficient of -0.57 (Fig. 8B), indicating lower acuity thresholds with higher levels of elasticity. In contrast, none of the regressions involving aftereffect magnitude as the dependent variable reached significance, i.e. hydration, elasticity, tactile sensitivity did not meaningfully explain variance in aftereffect magnitude (all $p > .52$) (Fig. 9).

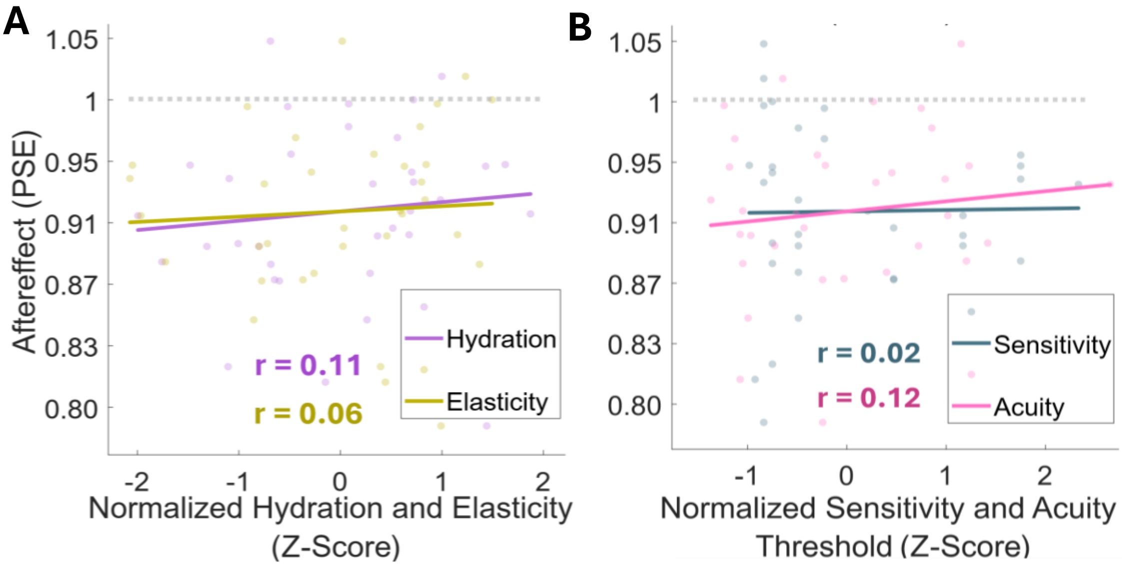

Figure 9. (A) Scatterplot including separate lines representing the linear regression of aftereffect magnitude (lower values indicate stronger magnitude) on hydration and elasticity. (B) Scatterplot including separate lines representing the linear regression of aftereffect magnitude on sensitivity and acuity. Aftereffect values are computed as the difference value between distance adaptation and control condition. Calculations are done on the log-PSEs, those are transformed back to ratios and given here for intuitive reasons.

3.4 Discussion

In this study we assessed inherent interindividual differences in skin properties and their relation to basic tactile abilities. Further, we assessed a potential relationship with tactile adaptation aftereffects, namely the tactile distance aftereffect. Specifically, we investigated whether interindividual differences in skin hydration and elasticity are associated with substantial differences in tactile sensitivity and spatial acuity and whether these in turn affect the individual susceptibility to tactile distance aftereffects. We found that indicators of skin health, i.e. higher hydration and elasticity, were related to improved tactile perception, i.e. higher tactile sensitivity and spatial acuity. These findings underline the importance of biophysical skin properties for tactile perception, particularly for detecting light pressure and discriminating spatial structures. The magnitude of the tactile distance aftereffect on the other hand seems to be mostly independent from both skin properties and the measures of tactile sensitivity and acuity. This suggests that certain perceptual processes such as adaptation might be rather independent from differences in sensory responses at the initial peripheral level, but interindividual differences in their expression might rather stem from cortical idiosyncrasies.

Our findings on the positive relationship between hydration and elasticity with tactile ability align with existing literature while also extending it, as previous research mostly either involved artificially altered skin properties via moisturizing agents (Lévêque et al., 2000; Sakaguchi et al., 2024; Samain-Aupic et al., 2023; Verrilo et al., 1998) or venous occlusion (Hudson et al., 2015), incorporated other perceptual objectives such as discrimination of compliance (Li & Gerling, 2012), focused on changes in the context of aging (Deflorio et al., 2023; Hamasaki et al., 2018; Jobanputra et al., 2020; Skedung et al., 2018), or investigated the consequences of skin mechanics for friction and vibro-temporal interactions without including psychophysical measurements (Gerhardt et al., 2008; Pasurmaty et al., 2011; Sakaguchi & Konyo, 2024). We here demonstrate that a priori interindividual differences in skin disposition of young adults correlate with their ability to detect light pressure and recognize the orientation of fine structures. Notably, given that skin properties like hydration and elasticity decline with age due to reduced collagen and elastin (Pailler-Mattei et al., 2013), and tactile precision declines with age mostly due to a decrease in afferent density (Vega-Bermudez & Johnson, 2004), this afferent density might be suspected as a confounding variable driving the effect, with skin properties merely representing covariates. However, as our sample is confined to a single age cohort (age range: 12 years), differences in afferent density due to aging would be marginal and the distinct contributions of skin properties to differences in tactile abilities are reemphasized. Regarding afferent density, one other covariate exists though which we did not explicitly measure: Finger pad area has been suggested to correlate negatively with afferent density (e.g., Dillon et al., 2001), explaining for example gender differences for tactile sensitivity (Peters et al., 2009). Notably, one study suggests hydration (but not elasticity) to correlate negatively with finger pad area (Deflorio et al., 2023). Based on that, one could argue that the afferent density linked to finger pad area might be a confounder, which we cannot partial out. This seems negligible however, as elasticity is strongly related to tactile ability in the data of our study. Further, when including gender as a factor in the linear regressions, which is the main reason for differences on finger pad area differences in young adults (Peters et al., 2009), results do not substantially change (*r*s = -0.62 to -0.46). Taken together, potential confounders related to afferent density seem to be negligible, i.e. differences in tactile abilities observed in the current study are likely to be rooted in individual skin disposition. Notably, despite the narrow age range of our sample, we observed large interindividual variance in tactile abilities. While skin hydration and elasticity accounted for a significant portion of it (~20%), this suggests that additional, yet unidentified factors might be at play.

Further, we initially hypothesized that skin properties might influence aftereffect magnitude in a way that higher sensitivity and acuity, resulting from increased levels of skin hydration and elasticity, would increase the adaptation intensity and thus the subsequent aftereffect. Although this was not the case, one might argue that, alternatively, there is indeed an involvement of skin properties and basic tactile ability in aftereffect expression, but existing effects might simply cancel each other out: i.e., adaptation might be stronger when hydration, elasticity, and resulting tactile abilities are improved; but at the same time test stimuli might be perceived better, hence possibly reducing the aftereffect. The conclusion however that differences in skin properties do not systematically explain interindividual differences in the magnitude of this tactile aftereffect would still be valid. Note that we also checked mediation models to test whether tactile ability mediates a relationship between skin properties and aftereffect magnitude, potentially revealing any suppressed effects. We did not report these for the sake of brevity. As tactile ability neither had a mediating effect nor did it yield a separate prediction value for aftereffect magnitude, we further conclude that it would not mediate a relationship between e.g. afferent density and aftereffect magnitude. Overall, differences in intensity of sensory responses due to individual levels of tactile ability at the initial peripheral level do not seem to substantially contribute to the magnitude of subsequent adaptation aftereffects. If anything, then stronger and external manipulations might be needed to produce such effects, e.g. increasing adaptation duration (Kovács et al., 2007), manipulating application pressure (as an analog to e.g. visual contrast enhancement (Ishihara, 1999), modulating attentional mechanisms (Georgiades & Harris, 2000), or varying the dissimilarity between adaptor and test stimuli. Intrinsic differences in the susceptibility to adaptation-aftereffects might instead be better explained by cortical differences in how sensitive the sensory system is to adaptation, modulating neural responses after prolonged exposure to an adapting stimulus.

There is large consensus that aftereffects are the result of generally advantageous neural adaptation mechanisms, rather than simply representing a failure of the system to accurately depict the world or being mere by-products of ‘fatiguing neurons’: Aftereffects can reflect neural strategies for optimizing perception, including calibration and gain control – which enables maximum use of the limited working range of neurons (Clifford & Rhodes, 2005; Thompson & Burr, 2009). For this reason, understanding why individuals vary in their inherent susceptibility to aftereffects seems particularly interesting, and future studies could tackle this question e.g. by employing neuroimaging studies. Neuron tuning or receptive field size modulation have been previously proposed to be potential mechanisms responsible for tactile distance aftereffects; humans possibly differ in their tendency for these mechanisms.

Our findings reemphasize the importance of an individual’s skin health for the functioning of tactile perception. Results further suggest that interindividual differences in the magnitude of tactile distance aftereffects are not substantially and systematically related to individual skin properties and associated differences in sensory responses. Skin properties hence show differential effects on different levels of tactile perceptual processes. Importantly, we do not exclude the possibility that tactile aftereffect magnitude can be modulated by input intensity, which could be tested in future works via experimental interventions. Interindividual variance in aftereffect magnitude though might rather be caused by inherent differences in the susceptibility to adaptation processes rather than peripherally caused input variations. One could speculate that these inherent tendencies might apply more generally to other aftereffects as well, which could be tested by comparing the magnitudes of different aftereffects on individual level. This would underline the stability of such cortically evolving processes.

4. Humans flexibly use visual priors to optimize their haptic exploratory behavior

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Humans can use prior information to optimize their haptic exploratory behavior. Here, we investigated the usage of visual priors, which mechanisms enable their usage, and how the usage is affected by information quality. Participants explored different grating textures and discriminated their spatial frequency. Visual priors on texture orientation were given each trial, with qualities randomly varying from high to no informational value. Adjustments of initial exploratory movement direction orthogonal to the texture's orientation served as an indicator of prior usage. Participants indeed used visual priors; the more so the higher the priors' quality (Experiment 1). Higher task demands did not increase the direct usage of visual priors (Experiment 2), but possibly fostered the establishment of adjustment behavior. In Experiment 3, we decreased the proportion of high-quality priors presented during the session, hereby reducing the contingency between high-quality priors and haptic information. In consequence, even priors of high quality ceased to evoke movement adjustments. We conclude that the establishment of adjustment behavior results from a rather implicit contingency learning. Overall, it became evident that humans can autonomously learn to use rather abstract visual priors to optimize haptic exploration, with the learning process and direct usage substantially depending on the priors' quality.

4.1 Introduction

Haptic perception is an inherently active process. Humans typically adjust their exploratory behavior to the current task and present objects to achieve optimal perceptual performance and to behave most efficiently (Kaim & Drewing, 2011; Lederman & Klatzky, 1987; Tanaka et al., 2014). Closed-loop processes based on sensory signals partly enable this motor adaptation: Sensory information is gathered and integrated over the sequential exploration process and used for movement adaptation (Saig et al., 2012; Weiss & Flanders, 2011). For instance, when trying to judge the ripeness of an avocado, you are likely to adjust your executed force after each indentation to maximize the intake of sensory information about the fruit's compliance while trying not to squish it too harshly. In many situations, humans do not only rely on their gathered haptic information but additionally have sources for prior information about the objects they are going to interact with: Prior information can e.g. arise from recent interactions with similar objects (Kaim & Drewing, 2011), be semantic (for instance, verbal), or stem from visual input (Johansson & Cole, 1992; Zoeller et al., 2019) Regarding motor control in general, such prior information can help to adjust motor behavior already before and during initial object contact (Wolpert & Flanagan, 2001). Previous studies could show for example that participants incorporated prior information about weight in their lifting and grasping behavior (Johansson & Cole, 1992). For exploratory behavior specifically, studies demonstrated that participants explored stimuli with higher initial peak forces when they expected harder as compared to softer stimuli (Zoeller et al., 2019) or when they expected lower differences between the stimuli's compliances (Kaim & Drewing 2011). Prior information hence seems to play a role for haptic exploratory movement control as well. For visual information in particular, findings are inconclusive so far: It has been observed that humans adapt their initial indentation force in reaction to explicit visual information on a stimulus' compliance; but this adaptation did not resemble the same tuning behavior as evoked by other predictive or sensory signals (Zoeller et al., 2019). The authors suspected that explicit and implicit prior information lead to different influences on exploratory behavior, which could explain the conflicting research evidence. The current study thus extends previous findings by systematically investigating whether humans use rather abstract, i.e. implicit prior visual information for optimizing their subsequent haptic exploration, elucidating factors that modify the usage, and examining the flexibility of the process. For that, we assess the usage of prior visual information on texture orientation for adjustment of initial movement direction.

Haptic texture exploration is typically performed by moving the fingertips laterally across an object's surface for multiple times (Lederman & Klatzky, 1987). This produces small patterns of vibrations, i.e. temporal cues, that enable humans to discriminate fine textures by their microgeometry (Hollins & Risner, 2000) and spatial cues that are based upon spatial variability in skin deformation by the texture. Spatial cues have been shown to dominate the perception of coarse textures (Weber et al., 2013). To investigate texture exploration in psychophysical experiments, groove/ridge gratings are being widely used. Those consist of periodically repeating grooves and ridges, often arranged with a concise orientation. Their roughness is mostly affected by changing inter-element spacing (groove width), element width (ridge width) or their spatial frequency (Lederman & Taylor, 1972) with increased roughness perception, the larger the separation is. The intake of temporal cues during exploration of these gratings can be maximized by moving orthogonal to the gratings' orientation. Lezkan & Drewing (2018a) showed that indeed, movement direction in spatial frequency discrimination is optimized accordingly: In their experiment, participants had to haptically discriminate grating pairs and the movement data revealed that they adapted the directions of their final finger movements orthogonal to the texture orientations. This implies that they exhibited adaptation behavior based on sensory information gathered over the course of the exploration. In a follow-up experiment, this adaptation behavior was found to be beneficial in terms of perceptual precision. In the current study, we used a similar method and examined whether visual priors on grating orientation, presented before each trial, evoke similar adjustments of movement direction as in (Lezkan & Drewing, 2018a) but, importantly, already at initial contact. We focused on the initial movements' direction as it can be assumed to be hardly affected by haptic sensory feedback. Thus, it is a suitable indicator of the usage of the visual priors.

The role of information quality for the priors' usage was in the focus of Experiment 1. Note that most results of this experiment have been pre-published in a conference paper (Jeschke et al., 2022) and are being reinvestigated with further experiments in the current study. Oftentimes, sensory input is noisy, lossy, or unreliable due to e.g., memory decay, attentional processes, or physical conditions of the environment. Many researchers have addressed the question on how the human nervous system combines and integrates different sources of (multi)sensory information and what role their reliability (inverse variance) plays in this context (Alais & Burr, 2019; Ernst & Banks, 2002; Ernst & Bülthoff, 2004; Jacobs, 1999; van Beers et al., 1999; Wada et al., 2003). They demonstrated that the brain often functions similar to a maximum-likelihood integrator, combining different sources of sensory information by weighting them according to their reliability (Alais and Burr, 2019; Ernst & Banks, 2002; Ernst & Bülthoff, 2004). Thus, humans maximize the information they gather from their environment, reducing perceptual errors and negative behavioral consequences resulting from wrong decisions. Bayesian models for multisensory integration additionally take prior information into account, which is again weighted by its reliability. They have been successfully applied to many sensorimotor problems (Berniker & Koerding, 2011; Koerding & Wolpert, 2004). Based on these frameworks and findings on motor control we presumed that the usage of visual priors for exploratory movement adjustments might also depend on their quality; quality here refers to the level of precision at which information can be derived from the visual input. As haptic exploration has been demonstrated before to be an inherently adaptive process (Kaim & Drewing, 2011; Lederman & Klatzky, 1987; Tanaka et al., 2014), it seems plausible that humans also take the quality of prior information into account when using it for movement preparation. To test this, we presented visual priors that randomly differed in their quality each trial, ranging from high to no informational value, and indicated the orientation of upcoming haptic gratings (Fig. 10C). We aimed to artificially induce quality variations in the priors to imitate abovementioned real-world influences such as e.g. movement artifacts, insufficient illumination, low resolution of an image, or deficient visual acuity of an observer. We hypothesized that the presentation of informational visual priors leads to movement adjustments at initial haptic contact and expected stronger movement adjustments towards orthogonal when individuals receive priors of higher as compared to lower quality. This behavior was well reflected in the data, but not yet fully established in the first quarter of the session, suggesting that some learning is required first.

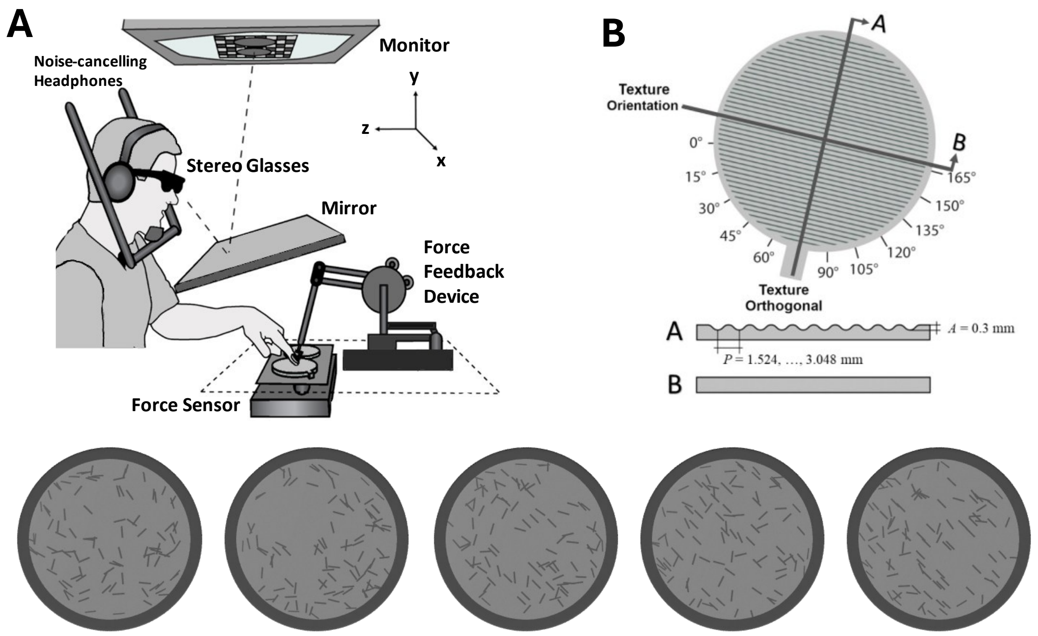

Figure 10. Setup and Stimuli. (A) visuo-haptic workbench. (B) Haptic stimulus in orientation 165°. (C) Examples of visual priors with qualities 0%, 15%, 25%, 35%, and 50% (from left to right) in orientation 135°. Based on pilot studies in which participants judged the orientation of those priors, we manipulated their qualities by varying the percentage of line segments following the same orientation as the gratings' ridges while the remaining ones were randomly oriented.

In Experiment 2, we further investigated the flexibility with which the priors are used by examining another potential moderator of the adaptation process: the task demands. Task demands have been demonstrated to affect participants' exploratory process in other contexts: Participants executed higher forces when indenting stimulus pairs which had smaller differences in their compliance (Kaim & Drewing, 2011). Moreover, findings in the field of vision research suggest that task demands shape the execution of eye movements: The size of the functional visual field was shown to shrink with increasing task demands during visual search (Yung & Hulleman, 2013) and observers seemed to prefer strategies facilitating efficient scanning when being confronted with more difficult tasks (Pomplun et al., 2013), cf. (Kurz et al., 2017). Here, we asked whether task demands influence the usage of visual priors for optimization of haptic exploratory behavior by implementing two levels of task demand, which were established implicitly by presenting trials of the same level in one block. Hence, an effect of task demand on prior usage would be caused by a predictive process: Individuals would expect a certain task demand for the upcoming trial and possibly adjust their subsequent behavior accordingly. The presentation order of the blocks was counterbalanced between participants. For "high demand" trials, stimulus pairs had smaller differences between their spatial frequencies and thus were more difficult to discriminate than "low demand"- pairs. For economic reasons, we only incorporated three (equidistant) levels of visual quality. We hypothesized that higher demands lead to higher extents of adjustment behavior in reaction to the priors; resembling a compensation mechanism for the increased effort that is needed to interpret the haptic sensory signals while trying to achieve a satisfying performance (Hong & Newell, 2008). However, results revealed no increase of initial movement adjustments when task demands were higher, suggesting that task demands do not have a rapidly modulating predictive effect on the direct usage of the priors. Higher demands were however associated with other compensation mechanisms such as prolonged exploration durations. Notably, we observed a trend suggesting that certain initial learning conditions, i.e. higher task demands in the initial experimental block, might foster the establishment of movement adjustments and their prevalence throughout the session.

In Experiment 3 we aimed to explore the flexible nature of the observed adaptation behavior from a different perspective: Instead of assessing the direct usage of the priors, we here focused on the establishment of the adjustments. For that, we investigated the role of the priors' visual quality during establishment of adjustment behavior and the mechanism that underlies the establishment. Based on the experience-dependent effects on movement adjustments observed in the previous experiments, we speculated that a form of contingency learning might enable the adjustment behavior. “Contingency” describes a conditional probabilistic relation between two events/stimuli; many studies have demonstrated that humans can detect and use contingency to make predictions and infer causal relationships (De Houwer & Beckers, 2002): high probabilities of an event B given Event A enhance learning (De Houwer & Beckers, 2002), while lower probabilities, i.e. lower contingencies, can hinder the learning process (Forrin & MacLeod, 2018). Lower-quality visual priors in our study indicate less precisely the orientation of an upcoming haptic texture and hence yield lower predictability for the following orientation. Results from the first experiment confirm this, as the low-quality prior (15%) did not produce substantial adaptation behavior. Hence, we consider less frequent presentations of medium-to high quality priors (and more frequent lower-quality priors) as a reduced contingency of the visual priors’ orientation and the haptic stimulus orientation and tested whether this affects the learning of the pairing and consequently the establishment of movement adjustments. As influences on the establishment of prior usage can only be studied in between-participant designs, the sample of Exp. 2 served as the first group (high contingency, 0%, 25%, 50% priors) and the sample of the following Exp. 3 as the second group (low contingency; 0%, 15%, 50% priors). Hence, we used the same experimental procedures in both experiments. We hypothesized that the extent of adjustment behavior will be substantially reduced with low as compared to high contingency. Indeed, participants in the low-contingency group exhibited almost no adjustment behavior anymore; even when prior quality was high. Not only the direct prior usage, but also the learning process hence seems to crucially depend on the priors’ quality. Taken together, the results from the three experiments suggest that optimization behavior is implicitly established when deemed sufficiently useful, and the direct usage of priors is flexibly adjusted.

4.2 Methods

4.2.1 Experiment 1

Participants

Due to the very strong effect size reported for the movement adjustments over the course of an exploration of similar grating stimuli ($d_z = 1.1$) (Lezkan & Drewing, 2018a), we expected a medium-to-large effect ($f = .35$) for the current experiment. Based on that, we conducted an a priori sample size calculation for a power of 80% and an alpha of 5%. The projected sample size was N =14 for the within-participants factor of a repeated-measures ANOVA (G*Power; Erdfelder et al., 1996) Hence, 16 right-handed students from Justus-Liebig University Giessen participated (10 female, mean age: 22.6 years, range: 18-27 years). Participants had normal or corrected-to-normal vision and reported no tenosynovitis in the past and no motor or cutaneous impairments. We confirmed that participants had no sensory deficits by conducting a two-point discrimination test; all had two-point discrimination thresholds lower than 3 mm on their index fingers (Johnson & Phillips, 1981). They were naïve to the purpose of the experiment, provided written informed consent and received financial compensation (8€/hour). The experiment was approved by the local ethics committee Lokale Ethik-Kommission des Fachbereichs 06 (LEK-FB06) and conducted in accordance with 2013 Declaration of Helsinki, except for preregistration.

Setup and stimuli

Participants sat at a custom-made visuo-haptic workbench (Fig. 10A). It consisted of a PHANToM 1.5A haptic force feedback device (spatial resolution: 0.03 mm, temporal resolution: 1000 Hz; used only to track finger position), a force sensor to collect data of the normal force when the participant touches the stimulus (682 Hz, resolution: 0.05 N), and a 24" computer screen (120Hz, 1600 × 900 pixel). Participants looked at the screen through a mirror while wearing stereo glasses (Nvidia 3D Vision 2, viewing distance 40 cm). The visual setup displayed 3D scenes aligned with the haptic workspace in front of the participant and prevented them from seeing their hand. Grating stimuli were displayed as light grey cylindrical discs on a dark green checkerboard. At the same positions two real stimuli were placed side-by-side with a force sensor underneath. A small sphere (diameter: 8 mm) represented the participants' finger position in the scene. It disappeared while they touched the stimulus. A chinrest stabilized their head position. Via a spherical magnet fixed at the fingernail, the right index finger was connected to the PHANToM, allowing to move the finger in all axes with a maximum amount of freedom in a 38 × 27 × 20 cm^3 workspace and leaving the fingertip free for bare-finger exploration. Devices were connected to a PC where C++- based custom software controlled the experiment and processed the data. Passive noise-cancelling headphones and white noise were used to mask any acoustic noises, The haptic stimuli consisted of four 3D-printed grating stimuli (Fig. 10B; printer: Stratasys Objet 30 Pro, resolution: 600 × 600 × 1600 dpi). We printed 4 mm high (z-axis) grating discs with a texture diameter of 90.7 mm (100.7 mm including the rim). A handle (10 × 5 mm) helped the experimenter arranging the stimuli before each trial. Each stimulus consisted of a groove pattern following a sine-wave function in height z (x):

$$z = \frac{1}{2} A \sin \frac{2\pi x}{P} + \frac{1}{2}$$

Stimuli all had the same amplitude *A* of 0.3 mm and differed only in their period *P*. They had periods of 1.524 mm, 2.032 mm, 2.540 mm, and 3.048 mm. Stimuli with adjacent periods were compared, resulting in three pairs in total. Every pair was presented in 6 possible orientations relative to the observer (15°, 45°, 75°, 105°, 135° and 165°; for 0°, ridges would be parallel to the body, see Fig. 10B). As visual priors, visual representations of the grating stimuli were displayed on the screen with a texture made of 100 dark grey line segments (8 × 1 mm) on their top side (Fig. 10C). The textures indicated the orientation of the upcoming haptic gratings and were displayed before exploration. The quality of the priors was manipulated by varying the percentage of line segments following the same orientation as the gratings' ridges while the remaining lines segment were randomly oriented. Pilot studies (*N*=16 in total) had demonstrated that participants perceived the orientation of such stimuli excellently when 100% to 50% of the line segments were identically oriented. Variance in answers systematically increased only with lower percentages. Hence, we presented visual stimuli with percentages of 50% or lower.

Design and Procedure

We varied the quality of prior visual information on stimulus orientation in five steps (50%, 35%, 25%, 15%, and 0% [= no information]). The haptic stimuli (and consequently the visual priors) were presented in 6 possible orientations (15°, 45°, 75°, 105°, 135° and 165°). Three different pairs of stimuli with adjacent periods were presented in both possible left-right assignments. Participants had to accomplish a two-alternative forced choice discrimination task: On each trial they explored two stimuli, starting equally often with the left and right stimuli, and had to decide which one had the higher spatial frequency. Overall, each participant conducted 360 trials in randomized order (5 qualities × 6 orientations × 3 pairs × 2 stimulus location × 2 start location). We implemented a break of 3 minutes every 60 trials. In total, the experiment took ca. 3.5 h. During each single trial, prior information was displayed for 2500 msec before participants were allowed to begin with the haptic exploration. The exploration was initiated by a beep sound. To indicate where participants should start, one of the two visual stimulus representation-discs was highlighted in yellow. They were instructed to use the typical movement scheme for the exploration, i.e. stroking over the surface (Lederman & Klatzky, 1987), and to switch between stimuli as often as desired. After the exploration they indicated which stimulus they had perceived to be of higher frequency by pressing a virtual button above it. White noise was presented through the headphones during the whole experiment to mask any exploration sounds. Before starting with the main experiment, participants performed eight test trials with 0% prior information textures and separate stimuli, which were not used in the main experiment, to familiarize themselves with the task. Participants filled out a questionnaire after the experiment which purpose was to check whether they had paid attention to the visual prior information and intentionally used it for movement adjustments. This contained three questions: 1) Did you actively pay attention to the visuals that were displayed at the beginning of each trial? 2) If yes, did you change your behavior in reaction to them and if so, how? 3) Did you feel discomfort at any point during the experiment? The last question served as a check-up for the feasibility of the design in general. Participants were not informed about the relationship between visual priors and the gratings' orientation beforehand.

Data Analysis

All datasets generated and analyzed during the current study are available at https://doi.org/10.5281/zenodo.7639118. We analyzed movement directions of the initial, middle and last movement ("strokes") in the exploration of each stimulus pair. A stroke was defined by a single unidirectional exploratory movement across the grating. In case of an even number of total strokes, the later of the two possible ones was defined as the middle stroke. A custom-written algorithm segregated single strokes from movement data when the participants' finger was touching the stimulus area with at least 0.1N of force for > 200 msec. We detected strokes as continuous movements either from one texture border to another or between two movement turns, being extracted by zero crossings in the 1st order derivatives of the x- or z-position over time. Movement direction was determined as the orientation of the line connecting start and end point (x and z coordinates) of each stroke. Movement directions were processed as axial data and thus ranged only between 0° - 180°. All stimulus orientations were aligned with 0° to collapse data over trials. We calculated circular histograms of initial movement directions (bin size: 10°) separately for each visual quality condition. Each histogram displays how many times participants moved in a specific direction. For statistical analyses, we focused on the initial strokes. Movement directions were analyzed using the MATLAB Circular Statistics Toolbox (Berens, 2009): We used V-tests on the distributions of individual average movement directions per visual quality condition and separately for the initial, middle and last movements to test whether the distribution is not uniform (= all directions are equally likely) but rather has a specified mean direction of 90° (= optimal adaptation behavior). The middle and last strokes are analyzed mostly to allow for replication of previous findings (Lezkan & Drewing, 2018a). Significant test statistics imply a deviation from uniformity in the suspected direction. Additionally, we compared proportions of close-to-orthogonal initial strokes (90° ± 15°) between quality conditions across participants using a repeated measures analysis of variance (ANOVA) with the within-participant factor Visual Quality. This range served as an indicator for a general drift of movement direction. The specific range has previously been used to detect movement changes over the course of an exploration (Lezkan & Drewing, 2018a) and seemed feasible the current analysis as well, as we did not expect more distinct and precise movement adaptations in reaction to the priors than in reaction to gathered haptic sensory information and because we aimed for data that can be linked to those previous findings. A more conservative criterion (90° ± 10°) led to the same conclusions. Hence these results are not reported in the paper. To evaluate the establishment of movement adjustments over the course of the experiment, we focused on the percentage of close-to-orthogonal strokes when visual quality was very high (50%). We split data into the four chronological quarters of the experimental session (Trial 1-90, Trial 91-180, Trial 181-270, Trial 271-360) and analyzed it using a repeated measures ANOVA with the within-participant factor Quarter (Quarter 1-4). As we did not intent to conduct an in-depth analysis of the time course but were interested whether the adaptation behavior appears immediately or rather needs some time to get established, we decided to only analyze the condition that likely produced the most pronounced adaptation behavior, thus potentially revealing the strongest differences. Whenever the assumption of sphericity was violated, the *p*-values of the respective ANOVA were Greenhouse-Geisser adjusted (Greenhouse & Geisser, 1959).

4.2.2 Experiment 2

Participants

Following similar power considerations as for Experiment 1, 18 right-handed students from Justus-Liebig University Giessen participated (14 female, mean age: 23.05 years, range: 19-28 years.). They were naïve to the purpose of the experiment and had not participated in the previous experiment.

Setup and stimuli

The setup was identical to that of Experiment 1. Here we used 8 haptic stimuli in total, resulting in 4 pairs (two for each demand condition). The two "low demand" pairs were defined by a difference of ~ 0.5 mm between their periods (ca. 2 Weber fractions [44]): Their stimuli had periods of 1.524 mm versus 2.032 mm and 2.540 mm versus 3.048 mm. "High demand" pairs had a difference of ~ 0.25 mm between their periods (ca. 1 Weber fraction): 1.92 mm versus 2.16 mm and 2.40 mm versus 2.64 mm. The mean of all periods of the "high demand" stimulus set was the same as the one of the "low demand" stimulus set and all periods of one set were equidistant to each other.

Design and Procedure

For economic reasons, as visual quality was not the main focus anymore, the experiment included only the three quality conditions 0%, 25% and 50%. We chose these levels as they were equidistant to each other with regards to the percentage of line segments following the same direction as the upcoming grating. Additionally, the design included two levels of task demand. The level of task demand was established implicitly by presenting trials of the same condition in one block, with 4 alternating blocks in total (ABAB/BABA design). The number of sessions starting with the "low demand" and the "high demand" condition was counterbalanced and randomized across participants. The instructions, task and procedure during the trials were the same as in Experiment 1. Each of the two demand conditions consisted of 144 trials in random order (3 qualities × 6 orientations × 2 pairs × 2 start position × 2 stimulus position), so that each participant conducted 288 trials in total. The experiment took on average 2.5 hours and breaks were implemented after every block (72 trials).

Data Analysis

Movement directions were extracted in the same way as described for Experiment 1. We also did the same analyses on these data as in Experiment I, except for that the overall ANOVAs on close-to-orthogonal strokes included three factors: the within-participant factors Visual Quality (0%, 25%, 50%) and Task Demand (low/high) and the between- participant factor Order (low first/hard first), to explore whether there is a difference between participants that started the experiment with the low versus the high demand block. Although the trial number per quarter was not the same as in Exp. 1, we again split data into the four chronological quarters of the experimental session and conducted the same ANOVA, as we aimed to check for a general trend rather than to compare exact time courses between experiments. If anything, we would expect higher differences especially between the first and last quarter due to the smaller number of trials in this experiment and consequently its first quarter.

4.2.3 Experiment 3

Participants

Exp. 3 focused on studying prior learning in comparison to Exp. 2. Starting from the strong effect of the priors' quality on their direct usage found in Experiment 2, we expected at least medium-sized effect of the priors' quality on the prior learning process (f = .25). Based on that, we conducted an a priori sample size calculation for a power of 80% and an alpha of 5%. The projected sample size was 28 for the within-between interaction of a repeated-measures ANOVA (G*Power; Erdfelder et al., 1996). We decided for a sample size of *N* = 14 in addition to the *N* = 18 of Experiment 2. Accordingly, 14 right-handed students from Justus-Liebig University Giessen participated (9 female, mean age: 25.29 years, range: 19-29 years). They were naïve to the experiment's purpose and had not participated in the previous experiments.

Design and Procedure

The setup, stimuli and procedures were similar to those of Exp. 2 except that we used the visual quality conditions 0%, 15%, and 50% (instead of 0%, 25%, and 50% as in Exp. 2). We chose the 15% condition here, as it was the lowest of the previously implemented quality conditions and in line with that, produced the lowest adaptation behavior in Experiment 1.

Data Analysis

We applied the same data analyses as for Exp. 2. In addition, we compared proportions of orthogonal initial strokes of Experiment 2 (high contingency) and 3 (low contingency) separately for 0% and 50% quality-trials with two Bonferroni-corrected Welch-tests. We used Welch-tests instead of checking for an interaction effect with an ANOVA here in order to account for unequal sample sizes and -variances.

4.3 Results

4.3.1 Experiment 1

In Experiment 1, we studied the role of information quality for the priors' usage in haptic frequency discrimination (Jeschke et al., 2022). Participants spent on average 5.5 seconds (*SD* = 1.36) per trial on the stimuli, performed 6.6 strokes (*SD* = 2.67), switched 1.7 times (*SD* = 0.37) between them and gave 91.1 % correct responses (*SD* = 8.88%). Correct responses did not depend on the priors' Visual Quality; $F(4,60) = 0.18$, $p = .95$, $\eta^2_p = 0.03$ in repeated-measures ANOVA of arcsine-transformed percentages (i.e., the arcsines of their square-roots). Likewise, movement variables such as number of strokes, switches between stimuli, or time spent on stimuli did not differ between quality conditions (all *p*s >.12). We plotted angular distributions of movement directions of all initial movements (in the following: "strokes") separately for each visual quality condition (Fig. 11A-E). Bonferroni-corrected V-tests on deviations from uniformity were performed on distributions of individual average movement directions per quality condition, and separately for the first, middle, and last strokes. For initial strokes, results indicated movement adjustments towards orthogonal for the 25%, 35% and 50% quality conditions, but not for the 0% and 15% quality condition (0%: $V = 7.26$, $p = .08$, 15%: $V = 6.56$, $p = 0.18$, 25%: $V = 11.71$, $p < .001$, 35%: $V = 9.54$, $p < .001$, 50%: $V = 9.15$, $p < .001$). For individual average movement directions of middle and last strokes in a trial (not depicted), distributions of all quality conditions deviated significantly towards orthogonal (all $p < .001$, all $V > 11.37$).

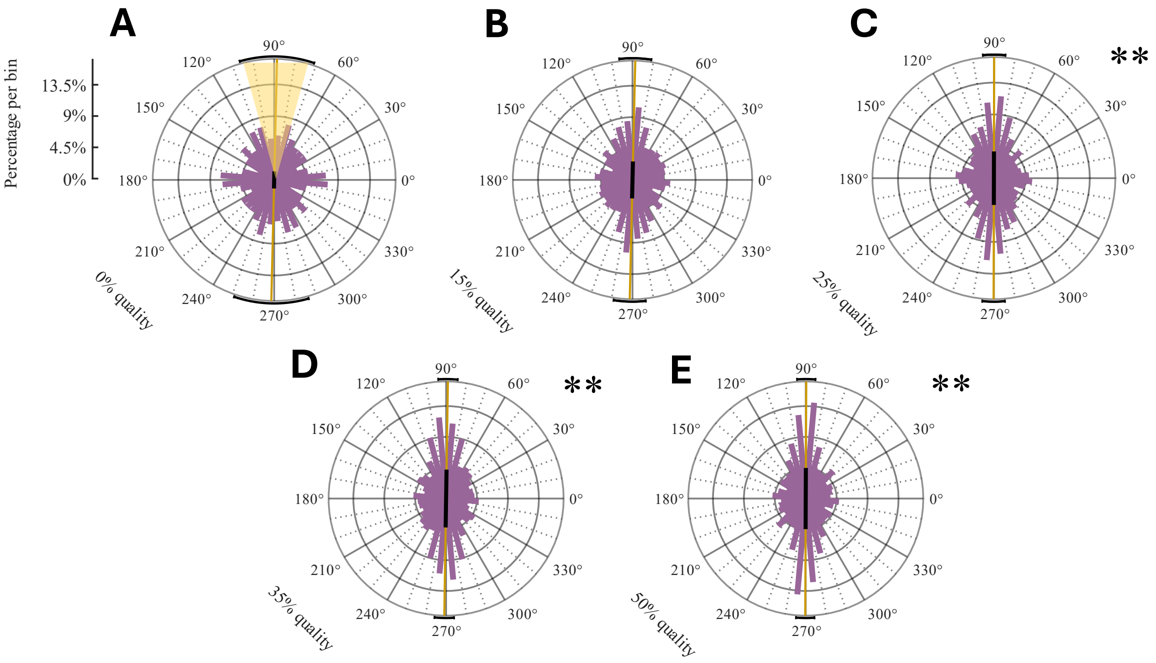

Figure 11. Experiment 1: Initial movement direction histograms for each quality condition including all participant data. Bin size: 10°. Textures were aligned to a 0° orientation. Possible movement directions varied only between 0–180° and were mirrored on the lower part of each figure. Orange lines indicate mean directions, black bars in the center of each circle represent resultant vector lengths. Black circle segments mark the 95% confidence interval of the mean direction. Yellow cone in (A) marks the 90°± 15° area of movement directions.

Proportions of movements close-to- orthogonal to the texture's surface 90° (± 15°) (see Fig. 11A) among all initial strokes across participants (Fig. 12A) entered an ANOVA with the within-participant factor Visual Quality. As expected, proportions of orthogonal initial strokes were higher with higher visual qualities, $F(4, 60) = 4.39$, $p = .036$, $\eta^2 = 0.23$. The proportional increase of orthogonal strokes in reaction to priors of increased visual quality was confirmed by a linear trend, $F(1,15) = 6.11$, $p = .026$, $\eta^2 = 0.29$, analyzed with a linear contrast on the proportions of orthogonal strokes across the quality conditions. For middle and last strokes, that is after gathering sensory information on grating orientation, proportions of orthogonal strokes did not differ between quality conditions, $F(4,60) = 2.33$, $p = .11$, $\eta^2 = 0.14$, and $F(4,60) = 1.52$, $p = .28$, $\eta^2 = 0.09$, respectively. Same patterns were found for the individual mean resulting vector lengths of initial, middle and last strokes, being indices of variance in movement direction, which also entered ANOVAs with the within-participant factor Visual Quality (Supplementary Information Section I, Fig. S1), corroborating the evidence. Finally, we observed that prior usage was established during the beginning of the experiment;

proportions of orthogonal initial strokes for trials with high visual quality (50%) entered an ANOVA with the within-participant factor Experimental Quarter (Fig. 12B). There was a significant main effect, $F(3,45) = 4.92$, $p = .005$, $\eta^2_p = 0.25$, with proportions of the first quarter of the session being smaller than those of the second quarter, as Bonferonni-corrected post-hoc tests revealed, $t(15) = 2.73$, $p = .02$ (three tests, adjacent levels compared, other *p*s > .50). In the questionnaire, only two participants reported that they were aware about the visual priors indicating the orientation of the upcoming haptic stimulus and that they intentionally adjusted their movements accordingly, i.e. by moving orthogonal to the indicated orientation. All others responded “no” to the first question (i.e., whether they actively paid attention to the visuals).

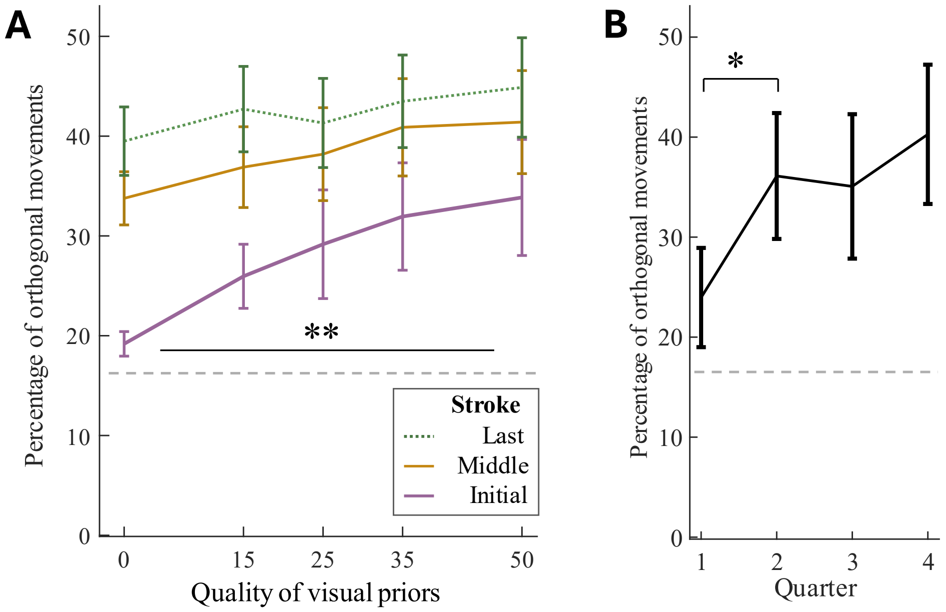

Figure 12. Experiment 1: Percentages of orthogonal movements. (A) Average percentages of orthogonal movements and standard errors for each quality condition and movement type. (B) Percentages of initial orthogonal movements for trials of highest quality (50%) for each chronological quarter of the experiment. The dashed grey line represents chance level (entirely uniform movement distribution, 16.67%).

4.3.2 Experiment 2

In Experiment 2, we studied the role of task demands. Participants spent on average 10.85 seconds (*SD* = 3.16) per trial on the stimuli, performed 14.78 strokes (*SD* = 5.74), switched 2.48 times (*SD* = 0.68), and gave 90.2 % correct responses (*SD* = 7.09%). Participants executed more strokes during more demanding trials as compared to less demanding ones, $t(1,17) = 2.89$, $p = .011$, $d = 0.36$, switched more often, $t(1,17) = 3.55$, $p = .002$, $d = 0.54$, and spent more time on the stimuli, $t(1,17) = 2.64$, $p = .017$, $d = 0.50$; but kept their response accuracy constant, $t(1,17) = 0.74$, $p = .47$, $d = .02$. Again, none of those variables differed between visual quality conditions (all $p > .08$). We plotted angular distributions of movement directions of initial strokes separately for each visual quality condition and the two demand conditions (Fig. 13A-F). Bonferroni-corrected V-tests on deviations from uniformity were performed on the distributions of individual average movement directions per quality and demand condition, and separately for initial, middle, and last strokes. For initial strokes of both the low and high demand condition, significant tests indicated adjustments towards orthogonal movement for the 25% and 50% quality conditions, but not for the 0% condition (low demand: 0%: $V = 7.55$, $p = .09$, 25%: $V = 10.18$, $p < .001$, 50%: $V = 8.96$, $p = .015$, high demand: 0%: $V = 6.70$, $p = .27$, 25%: $V = 11.65$, $p < .001$, 50%: $V = 11.64$, $p = .015$. For middle and last strokes, distributions of all quality and demand conditions significantly indicated adjustment towards orthogonal (all $p < .001$, all $V > 14.28$).

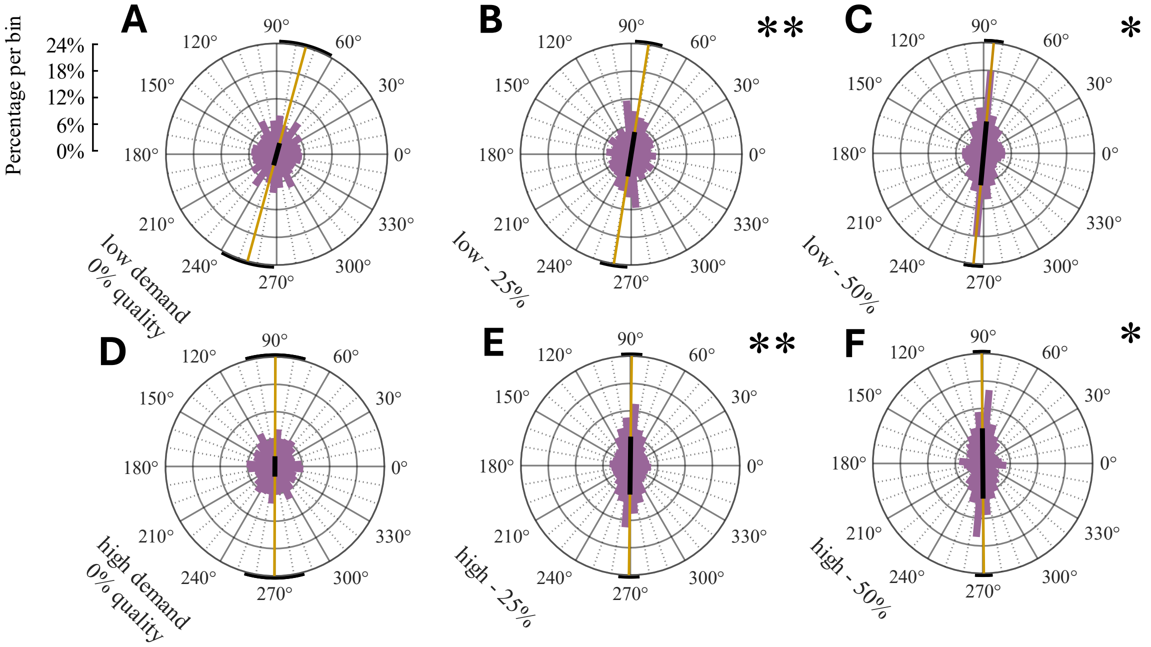

Figure 13. Experiment 2: Initial movement direction histograms for each quality*demand condition including all participant data.

Proportions of orthogonal initial strokes entered a three-way mixed-design ANOVA with the within- participants factors Visual Quality (0%, 25%, 50%) and Task Demand (high vs. low) (Fig. 14) and the between-participants factor Order (participants that started the experiment with the low demand-block vs. those that started with the high demand-block). The proportion of orthogonal initial strokes was again higher with higher visual qualities, $F(2, 32)$

= 6.83, $p = .014$, $\eta^2_p = 0.30$), confirmed by a linear trend, $F(1,17) = 7.13$, $p = .016$, $\eta^2_p = 0.30$. There was no main effect of Task Demand, $F(1, 16) = 0.33$, $p = .57$, $\eta^2_p = 0.02$. The main effect of Order, $F(1,16) = 3.67$, $p = .073$, $\eta^2_p = 0.19$, marginally failed to reach significance. This trend might though suggest that participants show stronger adjustments when starting with high demand trials as compared to starting with low demand trials (Fig. 15A). None of the three possible interaction effects were significant (all $p > .16$). Proportions of close-to-orthogonal movements among middle and last strokes entered three-way mixed-design ANOVAs with the within-participants factors Visual Quality and Task Demand (see Fig. 15) and the between-participant factor Order (Fig. 15B,C). For middle strokes, there was no main effect of Visual Quality, $F(2,32) = 2.46$, $p = .10$, $\eta^2_p = 0.13$ or Task Demand, $F(1,16) = 1.04$, $p = .32$, $\eta^2_p = 0.06$, but a main effect of Order, $F(1,16) = 5.09$, $p = .038$, $\eta^2_p = 0.24$, suggesting stronger adjustments of later movements when participants were initially confronted with the more demanding block. The interaction effect of Quality and Order was significant, $F(2,32) = 4.93$, $p = .014$, $\eta^2_p = 0.23$, moderating the magnitude but not the direction of the Order-effect (other interaction effects all $p > .27$). For last strokes, only the main effect of Order reached significance, $F(1,16) = 6.01$, $p = .026$, $\eta^2_p = 0.27$ (all other $p > .06$). Proportions of orthogonal initial strokes of trials with high visual quality entered a one-way repeated measures ANOVA with the within-participants factor Quarter, which gave no significant result, $F(3,51) = 0.954$, $p = 0.392$, $\eta^2_p = 0.05$ (Quarter 1: $M = 30.93$, $SD = 17.71$, 2: $M = 36.00$, $SD = 22.87$, 3: $M = 35.78$, $SD = 26.69$, 4: $M = 37.77$, $SD = 29.55$).

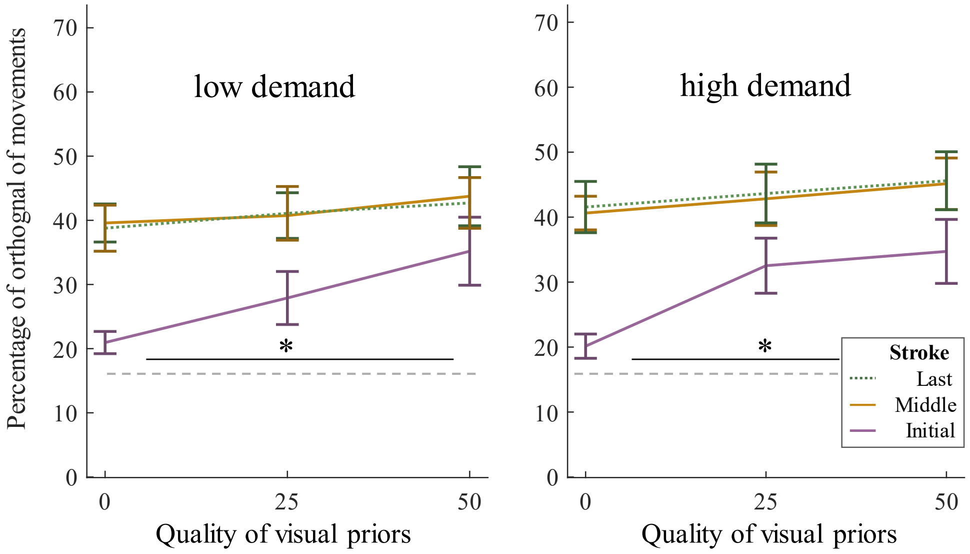

Figure 14. Experiment 2. Average percentages of orthogonal movements and standard errors for each quality condition and movement type, for each demand condition separately.

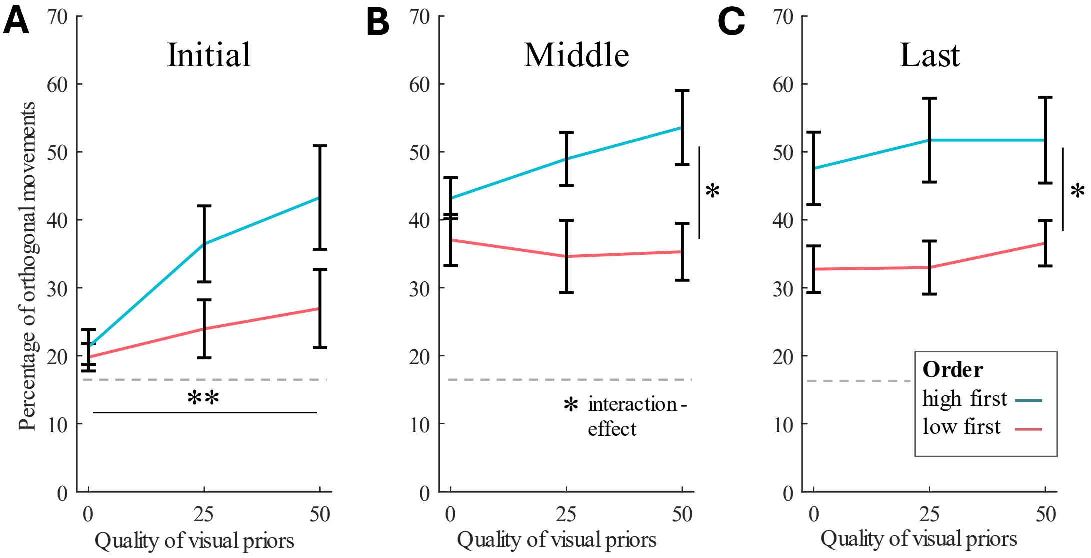

Figure 15. Experiment 2. (A) Average percentages of orthogonal initial movements and standard errors for each quality condition of participants starting with low demand block vs. high demand block. (B) Percentages for middle movements. (C) Percentages for last movements.

4.3.3 Experiment 3

In Experiment 3, we replicated Exp. 2 but with a reduced contingency between high-quality visual priors and haptic information to study establishment of motor adjustment. Here, participants spent on average 6.23 seconds (*SD* = 2.02) per trial on the stimuli, performed 8.36 strokes (*SD* = 3.74), switched 2.03 times (*SD* = 0.49) and gave 87.1 % correct responses (*SD* = 6.48%). Again, participants executed more strokes during more demanding trials, $t(1,13) = 2.45$, $p = .03$, $d = 0.36$, spent more time on the stimuli, $t(1,13) = 2.66$, $p = .02$, $d = 0.50$, but kept their response accuracy constant, $t(1,13) = 0.70$, $p = .50$, $d = 0.02$.

In V-tests, distributions of initial strokes did not significantly deviate from uniformity in most conditions, suggesting hardly any optimization of movement behavior (high demand, 0%: $V = 4.82$, $p = .51$, 15%: $V = 3.02$, $p = 1$, 50%: $V = 6.88$, $p = .075$, low demand: 0%: $V = 6.27$, $p = .135$, 15%: $V = 2.37$, $p = 1$, exception 50%: $V = 7.53$, $p = .033$, Fig. 16). This is strongly distinct from the movement adjustments observed in Exp. 2 with higher contingency. For individual average movement directions of middle and last strokes, again all distributions deviated significantly from uniformity as had been the case in Exp. 2 (all $p < .001$, all $V > 11.65$).

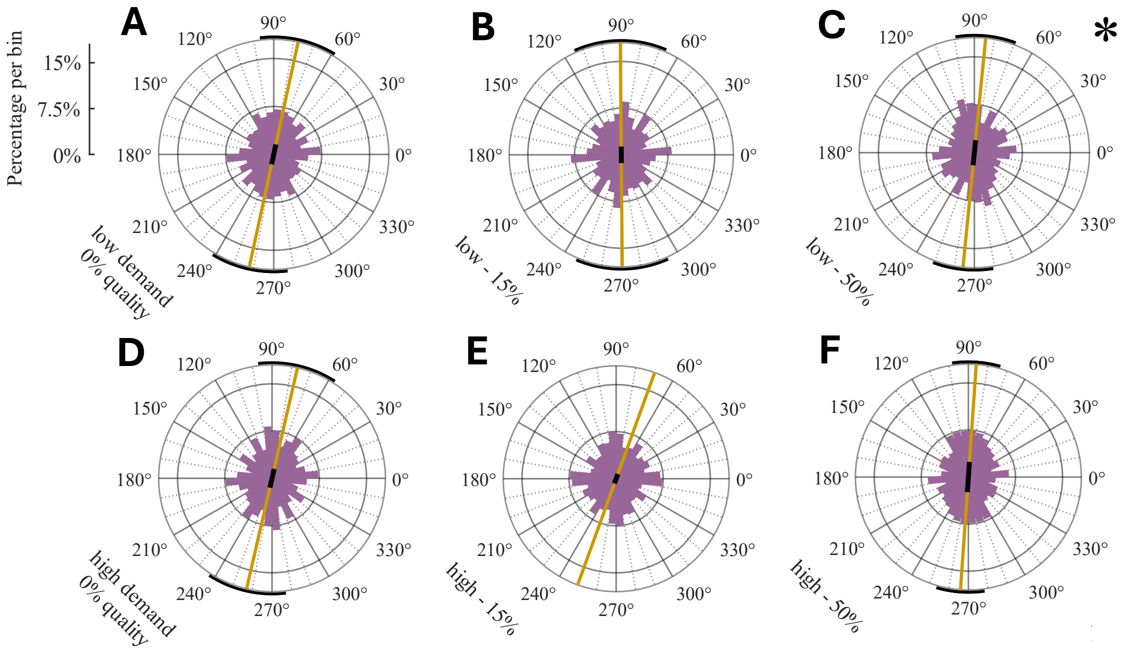

Figure 16. Experiment 3: Initial movement direction histograms for each quality*demand condition including all participant data.

In line with this lack of initial adjustment, we did not find significant effects in proportions of orthogonal initial strokes neither in a three-way mixed-design ANOVA with the within-participant factors Visual Quality and Task Demand and the between-participants factor Order, nor when analyzing adjustment in different quarters of the experiment (all $p > .189$; see Supplementary Section II for details, cf. Fig. 17A). Most importantly, we compared proportions of orthogonal initial strokes of Experiment 2 and 3 (Fig. 17B) with two Bonferroni-corrected Welch-tests. Welch tests are an alternative to independent sample t-tests when sample sizes and -variances are unequal. For 0% quality trials, proportions did not differ between the two experiments, $t(1, 24.87) = 0.29$, $p = 1$, $g = 0.1$. For 50% quality trials, proportions were significantly higher for Exp. 2 than for Exp. 3, $t(1,19.81) = 2.6$, $p = 0.034$, $g = 0.85$.

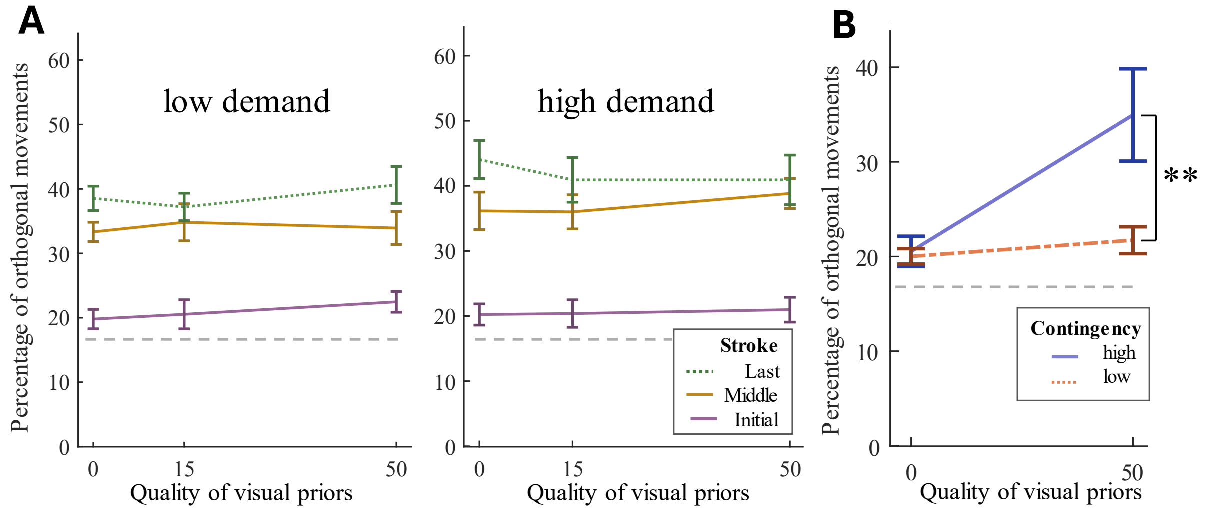

Figure 17. Experiment 3. (A) Average percentages of orthogonal movements and standard errors for each quality condition and movement type, for each demand condition separately. (B) Average percentages of initial orthogonal movements for 0% and 50% visual quality trials of Experiment 2 (high contingency) and 3 (low contingency).

Finally, proportions of orthogonal middle and last strokes from Exp. 3 entered three-way mixed-design ANOVAs with the within-participants factors Visual Quality and Demand and the between-participants factor Order. In contrast to Exp. 2, results revealed no effect of Order, $F(1,12) = 1.45$, $p = .25$, $\eta^2_p = 0.10$, but a main effect of the factor Demand, $F(1,12) = 5.65$, $p = .035$, $\eta^2_p = 0.32$, suggesting higher adjustments when task demands are higher. There was again no main effect of Visual Quality, $F(2,24) = 0.56$, $p = .595$, $\eta^2_p = 0.01$, and no interaction effect (all $p > .07$). For last strokes, no effect reached significance (all $p > .12$).

4.4 Discussion

In the current study we aimed to clarify whether humans use visual priors for exploratory movement adjustments, enabling optimization of sensory information gathering. We also asked whether this behavior can be further moderated by the quality of the priors and the present task demands, and which mechanism is likely to enable the behavior. Experiment 1 (Jeschke et al., 2022) demonstrated that indeed, visual priors indicating a texture's orientation produce orthogonal movement adjustments at initial contact similar to those that typically occur over the course of an exploration (Lezkan & Drewing, 2018a). Additionally, it became evident that the higher the priors' quality, the more pronounced the movement adjustments become. This is in line with a number of empirical findings and motor control models which suggest that sensory and prior information are weighted and used according to their reliability (Flanagan et al., 2008; Mugge et al., 2009; Tassinari et al., 2008). We conclude that this principle also applies to the usage of prior (visual) information for exploratory movement preparation. Our findings thus underline the dynamic and adaptive nature of active touch: When having access to prior visual information of sufficient quality, humans use it to employ more efficient exploratory strategies. Notably, only 2 out of 16 participants reported having intentionally used the visual priors or at least having paid attention to them. This could seem surprising as the importance of active attention to the relevant signals in a task has been widely claimed in the field of perceptual learning (Ito et al., 1998; Shiu & Pashler, 1992). However, several studies also provide evidence for the effectiveness of perceptual learning processes without the observer's awareness and active attention (Schmidt et al., 2007; Watanabe et al., 2001). Whether the process takes place despite the observers' unawareness or whether their unawareness is required, remains an open question. This is particularly interesting as Zöller and colleagues observed force-tuning behavior in reaction to implicit prior information (from recurring presentation of stimuli) but found no clear effects for explicit semantic and visual information (Zoeller et al., 2019). They argued that a reason for this could be the potential of explicit knowledge to interfere with automatic responses (Masters, 1992). It might be worth investigating which behavioral consequences less abstract variants of visual priors such as highly naturalistic stimuli or even explicit instructions would provoke in our paradigm. Additionally, we observed an experience-dependent change of the amount of close-to-orthogonal movements in reaction to visual priors of high visual quality. During the first quarter of the experimental session, participants showed substantially less adjustment behavior as compared to the following quarter. This suggests that the underlying process is not fully based on pre-existing interpretations of the visual system but rather a learned behavior: (implicit) knowledge about the pairing of visual and haptic stimuli is gradually established, with the movement adjustments in reaction to the priors possibly being reinforced by a more convenient exploration experience.

In Experiment 2, we replicated the findings regarding the effect of the priors' quality on their usage for exploratory movement adjustment. The focus however was on the potential effect of task demands: We hypothesized that higher task demands might be associated with a stronger usage of the priors for movement adjustments as a mean to compensate for impeded haptic discriminability (Hong & Newell, 2008; Kaim & Drewing, 2011). When analyzing the difference between the low and high-demand trials from a within-participant perspective, we did not observe any substantial differences regarding the amount of orthogonal movements. Notably though, higher task demands were related to a higher number of total strokes, more changes between stimuli, and longer times spent on the stimuli; which most likely reflect compensatory mechanisms. Hence, the lack of effect is presumably not caused by an unsuccessful manipulation of the demands. Task demands thus seem to not have a rapidly modulating predictive effect on the use of the priors. Instead, we observed a trend suggesting that participants who were initially confronted with the more demanding block showed more pronounced adjustment behavior throughout the session. This would imply that tasks demands rather affect the learning process instead of the direct prior usage. The initial task demand was also related to an increased intake of sensory information, reflected by a higher proportion of orthogonal later strokes when participants began with the more demanding block. This has not been observed before and could underline the initial demand's relevance for movement optimization during prolonged tasks; however it might be mainly caused here by the initial movement adjustments mentioned before. For an in-depth investigation of especially those initial movement adjustments, a between-participant design would be more feasible. Manipulating other task demands by e.g. restricting the exploration duration could also be of interest for this aim (Zoeller & Drewing 2020). Surprisingly and in contrast to Experiment 1, the extent of movement adjustment did not substantially change over the course of the current experiment; the observed adaptation was mostly finalized within the first quarter of the session. Thus, the learning of adjustments seems to evolve rather quickly. The lack of time-dependency here could also be partly caused by the fact that half of the participants began the experiment with the more demanding block, in line with observed trend of increased adaptation behavior for this group.

Interestingly, response accuracy remained constant across different conditions of visual prior quality in both the first and the second experiment. This might seem unexpected, as the prior usage should benefit perception in order to be deemed as behavior optimization. One reason for this lack of effect might be a ceiling effect, as response accuracy was relatively high overall and that we used a rather rough performance measure here only, and not a sensitive measurement of the just-noticeable-differences as in (Lezkan & Drewing, 2018a). Another reason could be that the task involved completely unrestricted haptic exploration, allowing participants to use other strategies to maximize performance. Still though, one might then suspect certain other parameters related to exploration efficiency to be affected by prior quality; such as the number of movements and changes between stimuli or the total time spent on the stimuli. Although this was also not reflected in the data, it is possible that exploration strategies differed in subtle and even individually different ways. Importantly, orthogonal movements have already been shown to improve perceptual precision (Lezkan & Drewing, 2018a). Hence, the current study did not focus on explicitly assessing the merit of the prior usage in the context of task performance or exploration efficiency, but rather on investigating whether the presentation of visual priors elicit movement adjustments at all.

In Experiment 3, we investigated the role of the priors' quality in the learning of adjustment behavior. For that, we presented lower- instead of the medium quality priors. As these lower-quality priors yielded the lowest informational value and have been shown produce the lowest adaptation behavior in Experiment 1, this manipulation can be construed as decreasing the contingency between visual priors and haptic information. The overall lower contingency was shown to deteriorate the establishment of movement adjustments: The results revealed no substantial movement adjustments as a reaction to the visual priors, reflecting an even stronger impairment of movement adaptation than previously expected. Direct comparisons showed that participants executed fewer close-to-orthogonal initial strokes during Exp. 3 than in Exp. 2. As the only methodological difference between the two experiments was the variation of quality conditions, we conclude that higher proportions of low-quality priors affect the learning process similar to how a lower contingency affects the learning of a pairing of two events (de Houwer & Beckers, 2002): a certain minimum contingency of priors and haptic stimuli seems crucial for the learning and thus for establishing adjustment behavior in the first place. This suggests that when a potential source of prior information does not yield sufficient informational value, this source is not used for the preparation of subsequent haptic exploration. This neglect possibly minimizes behavioral errors, as behavior is not adjusted according to e.g. ambiguous information. Especially because the visual priors in our paradigm are rather abstract and indirectly related to the upcoming stimulus as they yield information on its orientation but not the spatial frequency itself, the learning process might be sensitive to such changes in the overall contingency. Still, one could suspect a delayed, slower learning of the priors' relevance in comparison to Experiment 1 and 2 and thus later onsets of adaptation behavior. However, the extent of adaptation behavior – or rather the lack thereof - did not change over the course of the session. This is in line with previous research: in Forrin & MacLeod (2018), the contingency learning effect disappeared when contingency was reduced to a certain threshold. The results on the one hand reemphasize that a learning process enables the adjustment behavior, as the usage of optimal priors should not be that strongly affected if mainly pre-existing interpretative processes would be the basis. For less abstract and more naturalistic stimuli, this might be different; plausibly, their presentation would provoke immediate adjustments of exploratory behavior. Mostly, the results underline the relevance of the priors' quality: The disparity between priors of differing qualities regarding their value for our perceptual system and their assigned weight in the process of movement preparation became even more evident. One could have argued that when only considering the first experiment's results, low quality priors might actually evoke movement adjustments as well; but simply in a suboptimal way. This might yield the same effect on behavioral level (movement variability) but surely would have different implications. The last experiment demonstrates that at least before the adjustment behavior is established, priors differing in their quality seem to be in fact treated inherently different from each other. Whether this is still entirely true for the direct usage once the behavior is established, cannot be answered with utter certainty yet. It also remains open what the actual "shape" of movement adjustments looks like, i.e., whether the majority of movements tend to drift to the orthogonal axis or if some movements directly are adjusted onto the more or less orthogonal axis while some are not. Although we observed - unsurprisingly - no effect of task demands on the usage of priors, we found higher task demands to be associated with more pronounced adjustments for later movements in the last experiment. The observed immediate effects of task demand are in line with previous research showing that task demands evoke spontaneous exploratory movement optimizations (Kaim & Drewing, 2011) directed at the intake of sensory information. This process thus seems to be more prone to be influenced by task demands than the more complex link between usage of priors which in turn improves the intake of sensory information.

In the present study we demonstrated that humans autonomously learn to use rather abstract visual prior information for optimization of their haptic exploration process. It became evident that the learning process as well as the direct usage of the visual priors strongly depend on the priors' quality. Specifically, the number of stroking movements orthogonal to a texture's orientation was increased when visual priors indicated the orientation of the upcoming haptic stimulus; the more so the higher the priors' quality. The effect of visual quality on the direct usage of the priors is in line with assumptions of motor control models and related empirical findings, as more reliable information is supposed to be given a higher sensory weight in the process of movement preparation and execution (Berniker & Koerding, 2011; Koerding & Wolpert, 2004). In order for the adjustment behavior to establish in the first place, a minimum contingency of high-quality visual priors and haptic stimuli appeared to be required. Unexpectedly, higher task demands did not increase the direct usage of the priors. Instead, the task demands that participants were initially confronted with seemed to possibly affect the establishment of adjustments as a whole. Due to the fast, but gradual establishment of prior usage and the fact that participants did not necessarily have to show subjective awareness (Cheesman & Merikle, 1986) about the priors' purpose, the establishment of the prior usage appears to resemble a rather implicit learning process. Eventually, findings on how humans use prior information for exploratory movement control can be applied in the field of neurorobotics to improve object recognition or - manipulation of autonomous agents (Higy et al., 2016; Martinez-Hernandez et al., 2017). The optimization of exploration processes could improve information gathering, allowing for more efficient and more accurate decision-making.

5. Look first, feel faster: Prior visual information accelerates haptic material exploration

A similar version of this manuscript has been published in: Jeschke, M. & Drewing, K. (2025). Look first, feel faster: Prior visual information accelerates haptic material exploration. I-Perception, 16(5). https://doi.org/10.1177/20416695251385816

Humans use distinct exploratory procedures (EPs) in active touch which are typically specialized for materials with particular properties: e.g. pressing for deformable objects like cushions; or stroking to test a fabric's smoothness. Further, humans can use abstract visual priors for fine-tuning of exploratory movement parameters such as exploration direction. We here test the usage of visual priors in the planning of material-specific EPs, using real-life materials and a naturalistic visual virtual reality (VR) environment. We show that humans are better in selecting specialized EPs at initial touch when they have access to valid prior visual information on the material: They used specialized EP earlier, with higher probability, and explored materials for a shorter time. We conclude that visual prior information increases the efficiency of haptic explorations by anticipatory planning of appropriate movement schemes.

5.1 Introduction

Humans employ specialized movements, so-called exploratory procedures, tailored to the object being interacted with and the information they aim to retrieve: e.g. rubbing movements for coarse textures, rotating for granular materials, or normal pressing for deformable objects (Lederman & Klatzky, 1987). These movements are further fine-tuned regarding force or velocity based on serially gathered sensory info (Katircilar & Drewing, 2023, Weiss & Flanders, 2011). Additionally, predictive mechanisms enable movement preparation before initial contact: For example, humans use abstract visual priors to tune exploratory movement direction at initial contact during grating exploration (Jeschke et al., 2024). Here, we test the usage of visual priors for the selection of appropriate exploratory procedures and assess this in a more naturalistic setting involving real-life stimuli and a VR environment. Regarding real-life material properties, humans derive high-level expectations on mechanical material properties from basic visual images (Wijntjes et al., 2019), which is why we deemed it plausible to observe improved haptic exploration in reaction to static visual information about upcoming materials. Specifically, we asked: Does prior visual information on an upcoming material guide haptic exploration by supporting the selection of specialized haptic exploratory procedures?

5.2 Methods

We implemented a two-interval forced choice task: 14 participants were instructed to freely explore two haptic stimuli with their dominant hand (setup: Fig. 18A). Each trial, the two stimuli consisted of the same material; either sandpaper, sand, or sponge (Fig. 18B). Participants judged which one was rougher/more coarsely grained/more compliant. Explorations were filmed (60 Hz webcam). For each material, there were three possible stimulus pairs varying in discriminability (70%, 80%, 90% accuracy in piloting): sandpapers differing in roughness via grit size, sand samples differing in granularity via particle sizes, or sponge-stimuli differing in Young's modulus. Participants wore a head-mounted display which visually presented a simplified duplicate of the scene in front of them: The haptic stimuli were represented as white boxes and their hand by a oval-shaped object. At the beginning of each trial, the white boxes changed appearance and displayed the type of the upcoming haptic material; or, in 50% of all trials, nonsense-visual information, consisting of all materials combined (Fig. 18C). The onset of these visual stimuli indicated the beginning of the trial: Participants could now begin their exploration (Fig. 18E). As soon as they reached towards the stimuli, the boxes turned white again (signaled by a tracker at participants' wrist). After exploration of both stimuli, participants verbally reported their decision. The order and number of trials was randomized and counterbalanced regarding information type (informative/nonsense), material type (sandpaper/sand/sponge), stimulus pair (three pairs) and stimulus position (left/right) (36 trials in total). Movement recordings of the firstly explored stimulus were analyzed, because these provide insights on the merits of prior visual information. Recordings were manually decoded by an experienced rater with regard to EP type at initial contact (pressure, stroking, rubbing, running through, stirring, rotating, tapping, pulling), onset times of the first EPs that are specialized for the respective material (rubbing and stroking for sandpaper; running through, stirring, and rotating for sand; tapping and pressure for sponge) (Fig. 18D) (Cavdan et al., 2021; Lederman & Klatzky, 1987), and the exploration duration for the first stimulus. Crucially, the rater was fully blinded regarding the experimental condition (informative visual priors/nonsense) due to the randomization across trials and the fact that visual stimuli were only presented to the participants via the VR glasses. Onsets of initial material-specific EPs were defined as the time that passed between the beginning of the reaching phase (simultaneous to when prior visual information disappears) until the beginning of the first movement segment belonging to those initial EPs which are specific for the respective explored material.

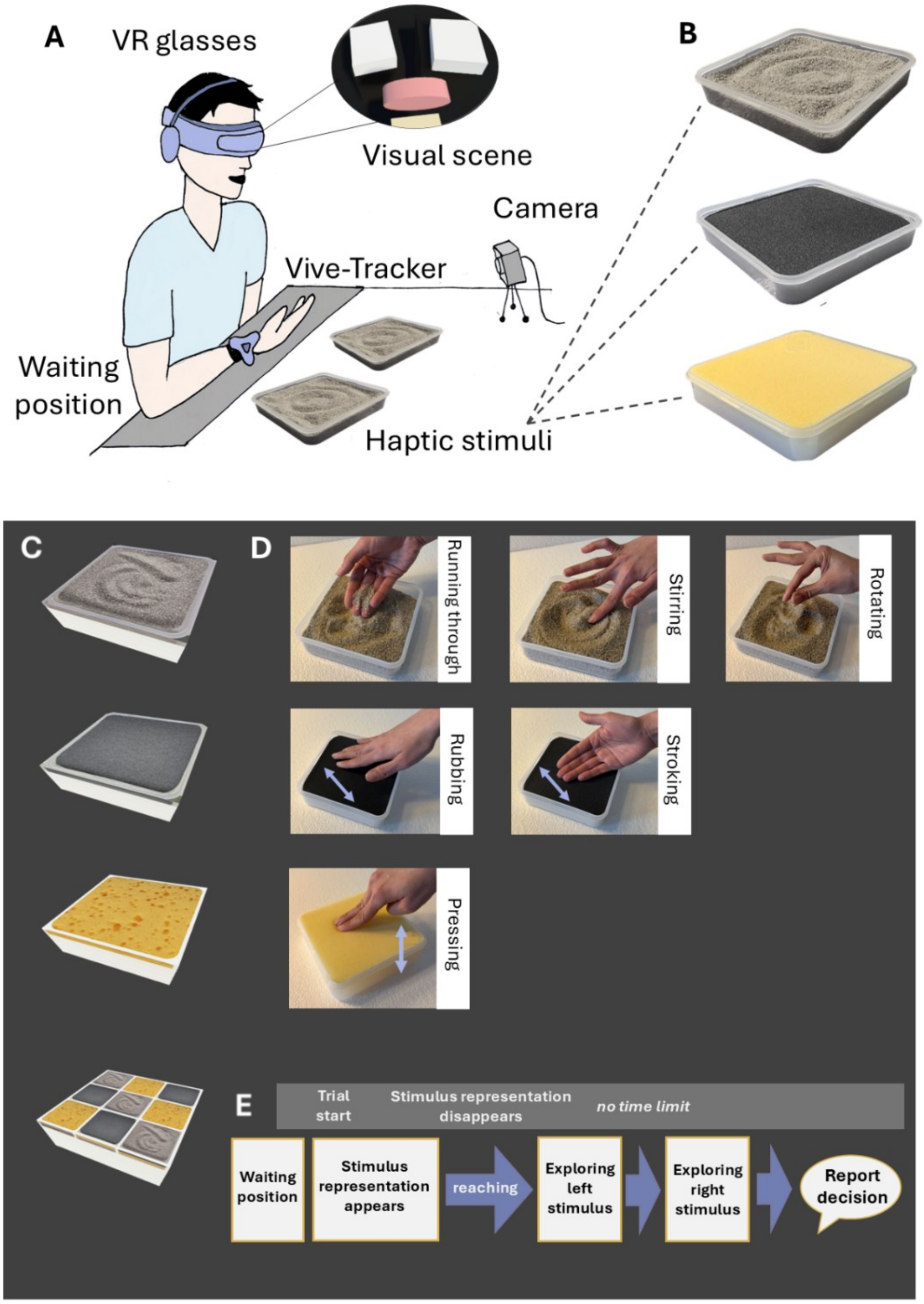

Figure 18. (A) Experimental setup: HTC VIVE HMD and HTC VIVE tracker. (B) Haptic stimuli, attachable to the table with Velcro® strips at the bottom of each container and at the respective position on the table. (C) Corresponding visual stimulus representation and nonsense visual information. (D) Specialized EPs for each material (one row for each material, respectively). (E) Experimental procedure.

5.3 Results

Onsets of initial material-specific EPs were earlier with informative visual priors, $t(13) = 8.34$, $p = <.001$, $d_z = 2.23$, Fig. 19A; i.e., participants reached quicker and employed the appropriate movement scheme sooner. Generally, participants almost always and thus more often used material-specific EPs at initial contact with informative visual priors, $t(13) = 2.56$, $p = .012$, $d_z = 0.68$ (informative: $M = 97.15\%$, $SD = 5.43$; nonsense: $M = 91.10\%$, $SD = 11.23$). With nonsense priors, participants sometimes used tapping movements initially. With informative priors, total exploration time spent on the first stimulus was reduced as compared to nonsense priors, $t(13) = 4.49$, $p = <.001$, $d_z = 1.20$, Fig. 19B. This decrease likely demonstrates the advantage of specialized EPs, reflecting optimized gathering of sensory signals. Participants showed constant response accuracies across conditions, which is expectable as unrestricted exploration tasks allow compensation in various ways, $t(13) = 1.06$, $p = .308$ (informative: $M = 81.24\%$, $SD = 9.93$; nonsense: $M = 77.01\%$, $SD = 10.20$).

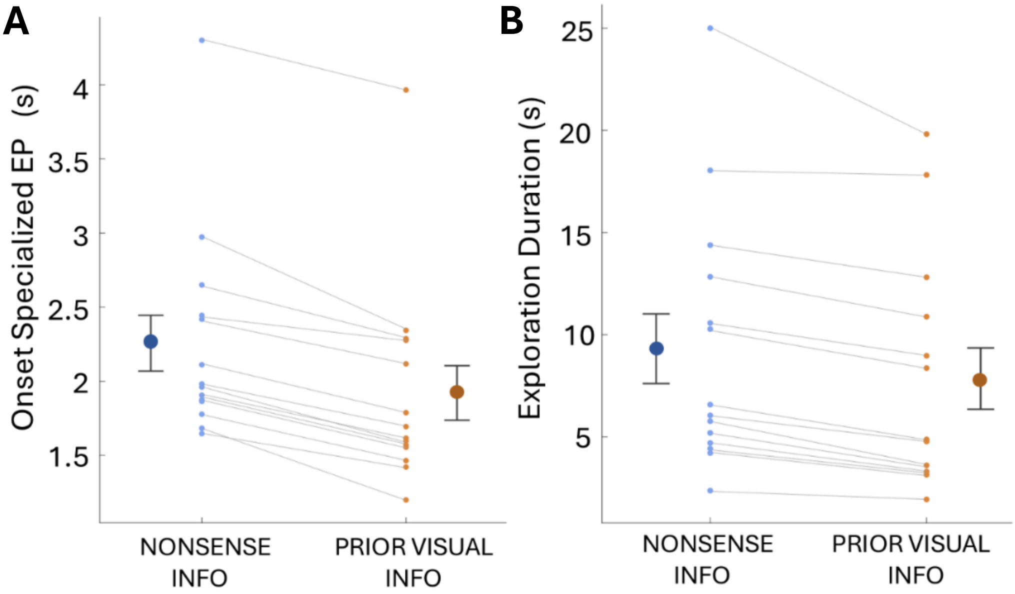

Figure 19. (A) Average onset of those initial EPs that were specialized for the current material. Error bars indicate standard error of the mean. Faint dots connected with lines display individual participant values for the two conditions. (B) Average exploration duration.

5.4 Discussion

We conclude that visual prior information increases the efficiency of haptic explorations by anticipatory planning of appropriate, holistic movement schemes beyond the fine-tuning of movement parameters previously shown. Behavioral optimization might further depend on the type of provided information (e.g., explicit or implicit), or on the complexity of visual input (e.g., static or dynamic). The default initial exploratory procedure in absence of any prior information might be light tapping, which maximizes sensory intake while minimizing risks such as potential injury. This may reflect a general strategy across species and could be paralleled for example by whisking behavior in rodents (e.g. Hartmann 2001). In total, this experiment underlines both the benefit of prediction in active touch and the advantage of specialized exploratory movements. These insights might have valuable applications in neurorobotics, where optimizing exploration processes via the exploitation of visual prior information could support object recognition and -manipulation in autonomous agents.

6. Humans terminate their haptic explorations according to an interplay of task demands and motor effort

A similar version of this manuscript has been published in: Jeschke, M., Metzger, A., & Drewing, K. (2024). Humans Terminate Their Haptic Explorations According to an Interplay of Task Demands and Motor Effort. In: Kajimoto, H., et al. Haptics: Understanding Touch; Technology and Systems; Applications and Interaction. EuroHaptics 2024. Lecture Notes in Computer Science, vol 14768. Springer, Cham. https://doi.org/10.1007/978-3-031-70058-3_7. (Reproduced with permission from Springer Nature)

Haptic exploration is an inherently active process by which humans gather sensory information through physical contact with objects. It has been proposed that humans generally optimize their exploration behavior to improve perception. We hypothesized that the duration of haptic explorations is the result of an optimal interplay of sensory and predictive processes, also taking costs such as motor effort into account. We assessed exploration duration and task performance in a two-alternative forced-choice spatial frequency discrimination task under varying conditions of task demand and motor effort. We manipulated task demands by varying the discriminability of virtual grating stimuli and manipulated motor effort by implementing forces counteracting the participants' movements while switching between stimuli. Participants were instructed to switch between stimuli after each swipe movement. Results revealed that higher task demands lead to higher numbers of exploratory movements (i.e. longer exploration duration), likely reflecting a compensatory mechanism that enables participants to attain a certain level of task performance. However, this effect is reduced when motor effort is increased; while low and medium task demands yield similar numbers of movements regardless of related motor effort, higher demands are not associated with increased numbers of movements when the required motor effort is high. In conclusion, the extent to which increased task demands are compensated via the extension of an exploration seems to depend on the motor costs that the agent is confronted with.

6.1 Introduction

Humans gather sensory information about objects, materials, or textures via active touch, i.e. by haptic exploration. Previous research has illustrated the adaptive nature of such explorations with various examples: In texture perception for instance, humans systematically use different scanning velocity patterns depending on the perceptual task (Tanaka et al., 2014) or they gradually adjust their movement direction to the orientation of grating textures over the course of an exploration (Lezkan & Drewing, 2018a); or in curvature perception, participants update their contact force according to the present surface curvature (Weiss & Flanders, 2011). The adjustments of those exploration parameters serve as optimization mechanisms, increasing task performance (Kaim & Drewing, 2011; Lezkan & Drewing, 2018a; Metzger & Drewing, 2020) and efficiency of explorations (Jeschke & Drewing, 2023). Another parameter that might be subject to optimization is the duration of haptic explorations, i.e. the time individuals dedicate to touching and perceiving objects. The amount of time spent on an exploration can drastically differ across situations and objectives: Humans might be rather quick when checking for keys in their pocket or lifting the milk package to check whether it is empty, though explorations might take longer when they do woodwork and investigate the smoothness of edges, or when surgeons inspect tissues and organs during procedures.

Humans typically conduct serial exploration with repetitive movements, i.e. multiple indentations for deformable objects or swiping and rubbing movements for rough surfaces (Lederman & Klatzky, 1987). The percept then results from the integration of the sensory information gained during each of these single movements (Metzger et al., 2018). Prolonged exploration, i.e. the extension of the exploration over space and time, was shown to increase perceptual reliability (Drewing et al., 2011; Lezkan and Drewing, 2018b; Giachritsis et al., 2009; Louw et al., 2005; Metzger & Drewing, 2017) (up to a saturation point). This is consistent with the Maximum Likelihood Estimation (MLE) model of optimal integration of information (Ernst & Bülthoff, 2004). More recent (modified Kalman filter-) models also take memory limitations into account (Lezkan & Drewing, 2018b; Metzer & Drewing, 2021) and hence are able to explain why the increase in the percept's reliability in a prolonged exploration is overestimated by the MLE model (Lezkan & Drewing, 2014).

Various factors have been previously shown to produce or affect optimization behavior (e.g., adjustment of contact forces and movement orientation) during haptic explorations, such as the (expected) task difficulty (Kaim & Drewing, 2011), the availability of prior information (Jeschke et al., 2022; Zoeller et al., 2019), or motivational factors related to the individual relevance of the task and goal (Lezkan et al., 2018). However, it is not yet clear how these factors interact in determining the time after which individuals decide to terminate their exploration. Given that the spatiotemporal extension of a haptic exploration increases the differential sensitivity of an agent, we could predict that the exploration would be extended in response to increased task demands to maintain a certain level of task performance. As the benefits of the extension of the exploration come at a cost of additional motor effort, we could also predict that it has a counteracting effect on the exploration length.

It is widely established in fields such as ecology and economics that costs and benefits are central determinants of behavior, combined to form a utility function that can guide choices (e.g., Kahnemann & Tversky, 2013). This principle has been demonstrated to apply to motor control as well, with motor effort being represented as costs which humans seek to minimize and weigh up against potential positive outcomes (Rigoux & Guigon, 2012): Motor control has been shown to be an optimal process derived from the maximization of the weighted differences between anticipated rewards and motor efforts, i.e. energetic expenditure, with examples such as walking, flying, or reaching (e.g., Shadmehr et al., 2016). Extending this concept to the gathering of haptic information, we speculate that haptic explorations are similarly governed by closed-loop and open-loop optimization processes following the principles of established utility frameworks for decision and motor control with regards to cost-benefit discounting. More concretely, when being confronted with higher motor costs, humans should terminate their exploratory behavior earlier than when being confronted with lower motor costs. In line with this, humans typically stop their exploration before reaching the abovementioned saturation point of task performance (Giachritsis et al., 2009; Louw et al., 2005; Metzger & Drewing, 2021): Motor costs appear to be a plausible reason why humans would display this premature termination behavior. Here we assessed the exploration duration as a function of task demands and the motor effort required to explore an object.

In our experiment, participants in each trial explored two virtual gratings (rendered by a force-feedback device) and decided which one had higher spatial frequency. Exploration duration can be operationalized in multiple ways, e.g. as the overall time spent on the exploration, the length of movement trajectories, or as the number of (repetitive) movement segments that are being executed. Here, we operationalized duration as the number of individual swiping movements over the stimuli (= swipes). Participants were instructed to switch after every swipe, which yields maximum perceptual performance by minimizing “memory loss” (Lezkan & Drewing, 2014) and allows for thorough control of motor effort. Motor effort was manipulated by implementing forces that counteract the participants’ movements when switching between the virtual stimuli. Task demand was manipulated by varying the discriminability of the stimuli. We hypothesized that with increasing task demands, the exploration duration would increase, resembling a compensatory mechanism. Further, we expected increased motor efforts to reduce the expected utility of an exploration extension, leading to earlier termination of the exploration when compared to lower motor efforts.

6.2 Methods

Participants

Previous studies that investigated optimization processes in exploratory movement control oftentimes reported large effect sizes (e.g., Jeschke et al., 2022; Lezkan & Drewing, 2018). A sample size calculation for a large effect (f =.40), a power of 80% and an alpha of 5% yields a sample of 12 for a three-level within-participant factor of a repeated measures ANOVA (G*Power; Erdfelder et al., 1996). In the present study, 12 right-handed students from Justus-Liebig University Giessen participated (8 female, 4 male, age 19-35 years, mean: 24.89 years). None of them reported motor or sensory impairments. All participants were naïve to the purpose of the experiment, provided written informed consent, and received financial compensation (8€/hour). The experiment was approved by the local ethics committee LEK FB06 and conducted in accordance with 2013 Declaration of Helsinki, except for preregistration.

Setup and Stimuli

The setup (Fig. 20A) consisted of a Geomagic Touch™ haptic force feedback device (spatial resolution: ~ 0.055 mm, temporal resolution: 1000 Hz). This was embedded in a virtual-reality environment to guide the participants through the experiment while preventing them from seeing their actual interaction with the haptic device. For this, we used the HTC Vive Pro Eye virtual head-mounted-display (HMD; 1440 × 1600 pixels per eye, 90 Hz; HTC Corp., Xindian, New Taipei, Taiwan). The experiment was implemented and programmed using Unity (Version 2021.2.7f1; Unity Technologies, Inc., San Francisco, CA, USA), SteamVR (Version 2.1.9), the Unity Experiment Framework package (Version 2.2.1, Brookes et al., 2020) and the Haptics Direct Unity Plugin (Version 1.0; 3D Systems). It was run on a custom-built desktop PC (Intel Core i9-12900KF CPU at 3.2 GHz, 64 GB RAM, Dual NVidia GeForce RTX3080 GPU).

The visual scene (Fig. 20B) consisted of the two virtual stimuli, two response buttons above the stimuli (grey cubes), and the bright green stylus that participants used to interact with the objects. The stimuli bases were rendered in white while the ridges were invisible. As soon as participants moved the pen over the ridge area, the stylus became invisible as well. Thus, no information on movement velocity or the spatial frequency of the stimuli was visually revealed to them via movement characteristics of the stylus. A semi-transparent pink ellipsoid object was permanently placed between the two stimuli to remind participants of the prescribed switching movement trajectory (arc-like motion over the ellipsoid) and prevent them from carelessly moving too close to the stimuli during the transportation phase. The virtual stimuli were simulated by the force feedback device by applying reaction forces ($\overrightarrow{F_P}$) as a function of the 3D-position of the end effector. The force magnitude is directly proportional to the indentation depth (i_p) of the virtual stimulus and its spring constant (K), i.e. its stiffness. The direction of the indentation is computed by Unity's built-in 3D physics engine (Nvidia PhysX 3.4). The force direction is normal to the texture's surface at the contact point ($\vec{n}_P$):

$$\overrightarrow{F_P} = \vec{n}_P \times \left|\overrightarrow{F_P}\right|, \ \left|\overrightarrow{F_P}\right| = K \times i_P \qquad (1)$$

The virtual grating stimuli all consisted of a 10 × 4 × 0.5 cm rectangular cuboid and 0.1 × 40 × 0.05 mm cylindrical segments (= ridges) on their top side (Fig. 20C). The distance between the centers of adjacent ridges (= period) defined the spatial frequency and differed between stimuli. Amplitude and ridge width was constant. With constant stimulus sizes, higher spatial frequencies would always be characterized by higher absolute number of ridges. To partly decouple the spatial frequency from the absolute number of ridges, we varied the length of the ridged stimulus area between trials. The length of the ridge area could comprise ca. 7 cm, 5.5 cm, and 4.5 cm (slightly varying depending on the respective period), with each size appearing equally often in randomized order. At the front and back ends of each stimulus, there were areas without ridges: 2.5 × 4 cm at the front end, being the starting area, and 0.5, 2, or 3 × 4 cm at the back end, depending on the length of the ridged area. The stimulus set comprised two reference stimuli with periods of 10.84 mm and 13.38 mm. For each demand-level, reference stimuli were paired with comparison stimuli of either +/- 2.54 mm period (high demand), +/- 3.81 mm (medium demand), or +/- 4.45 mm (low demand), resulting in 4 stimulus pairs for each demand level. The stimulus pairs were selected after examination of psychometric functions derived from a pilot-study (N = 5): their differences corresponded to discrimination performances of about 65%, 75%, and 85%. Throughout the experiment, brown noise was presented via the headset's headphones and additional white noise was played from a speaker directly above the force feedback device.

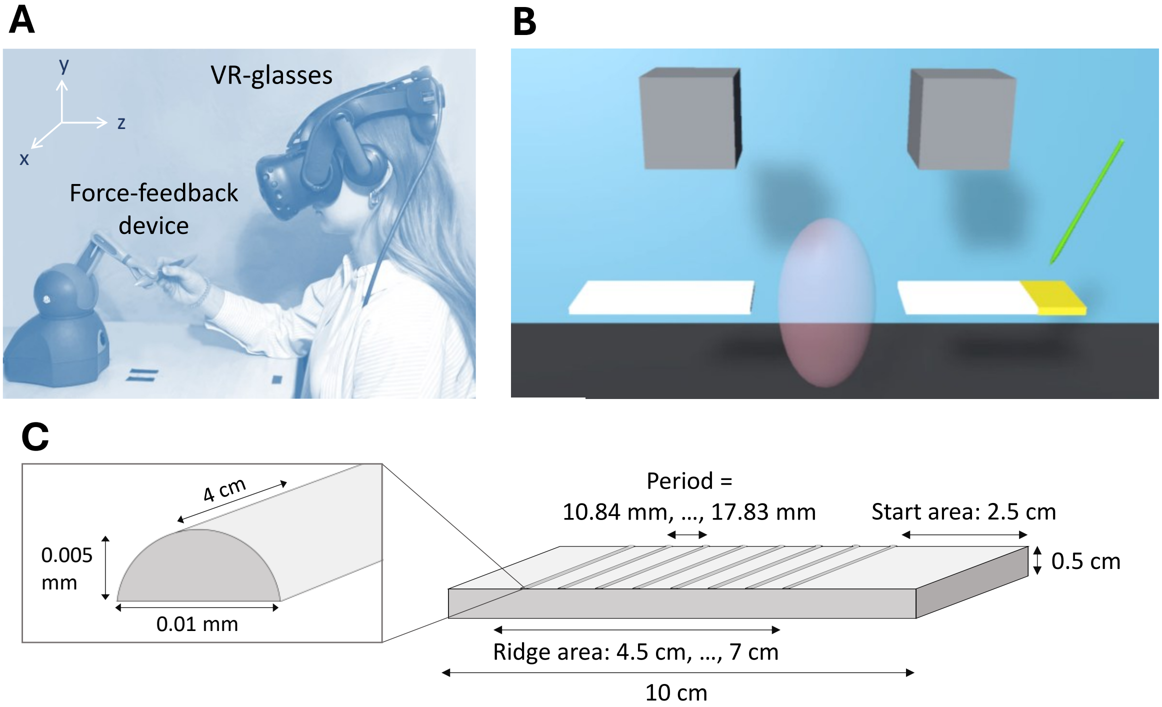

Figure 20. (A) Setup. (B) Visual scene (before participant touches the stimulus for the first time in a trial), yellow area indicates start stimulus. (C) Schematic depiction of virtual stimulus.

Design and Procedure

The experimental design was a 3 (Demand) × 3 (Motor Effort) - design, with 3 × 3 × 4 (stimulus pairs) × 6 (repetitions) = 216 trials in total. The experiment was split in two blocks. Each block contained 3 repetitions of the trial types and the trial order was randomized within each block. There was a break of 15 minutes between the blocks and a break of 5 minutes in the middle of each block. All in all, the session took about 2 hours. In each trial, participants had to complete a two-alternative forced choice (2AFC) discrimination task, in which they had to successively explore two grating stimuli and decide which one had a higher spatial frequency. To ensure a reasonable level of effort in the completion of the task, we provided participants with a monetary incentive (i.e., they received points for correct responses, which could amount to max. total 8.64 €). After every 10 trials, the number of accumulated reward points was displayed (3 s), to not give immediate performance feedback after each trial. The starting area of the respective stimulus on which participants were supposed to begin the exploration was highlighted in bright yellow before each trial until they first touched it (Fig. 20B). Exploration began equally often on the left and right stimulus, in randomized order. This was also the case for the position of the reference stimulus. As indicated via the starting area, exploration always began at the "outer" area of a stimulus towards the "inner" area (with regards to the visual scene). Participants were instructed to switch to the other stimulus after one swipe. Here again, exploration started at the outer area and ended in the inner area. Thus, the switching movement was sufficiently long to allow for proper manipulation of motor effort. Participants were free to switch as often as desired. To log their decision, they had to touch the virtual button (cube) above the respective stimulus that they perceived to have the higher spatial frequency, triggering the next trial to begin. We manipulated „motor effort" by implementing forces counteracting the participants' movement when switching from one stimulus to the other. Thus, when a participant finished one swipe, lifted the stylus up, and moved to the other stimulus, the device exerted a constant force Fx of either 1.7 Newton (high effort), 0.85 N, (medium) or 0 N (baseline) along the x-axis of the device in the opposite direction of the movement vector. Thus, participants had to put a constant additional effort into moving from one stimulus end area to the other stimulus start area. The force was only active > 1.5 cm above and next to the stimuli, to ensure that the sensory perception during exploration was not directly affected by e.g. increased muscular effort. The onsets and offsets of the counterforce were not abrupt; the force linearly increased/decreased from zero to the respective value and vice versa by 3.6N/s. Participants were instructed that they should never touch the stimuli while switching. To standardize the switching movement, they were additionally instructed to make an arc-like motion and avoid the semitransparent pink capsule object between the two stimuli. This way, the switching movement comprised a minimum distance of ~ 22 cm.

Before each session, participants had a familiarization phase for the HMD and the force-feedback device and a subsequent training phase of about 10 minutes (10 practice trials) to practice the movement coordination. During training and experimental trials, we aimed to keep scanning velocities relatively constant between and especially within participants at around 100-120 mm/s to avoid any potential confounds (Boundy-Singer et al., 2017; Gamzu & Ahissar, 2001; Louw et al., 2005; Smith et al., 2002). This target velocity has been observed to occur naturally and was proven feasible during piloting. While moving over the stimulus, the velocity was continuously tracked and averaged over the last previous 250 ms for smoothing. Whenever the average value exceeded or fell below the threshold of 180 mm/s or 60 mm/s respectively, an acoustic warning signal was played (low pitch tone or high-pitched beep tone, duration 300 ms). We kept the criterion relatively liberal, enabling participants to mainly focus on the task rather than on the movement execution. Consequently, the training phase also helped with automatizing the prescribed velocity. It additionally gave a rough orientation on how much force participants should exert during stimulus contact. This was verbally instructed by the experimenter, who received visual feedback on the current reaction forces of the device (desired range: approx. 0.4-1 N). After the experiment, participants filled out a brief questionnaire to check whether they noticed any behavioral changes in reaction to the motor effort manipulations.

Data analysis

Raw data of individual observers is available at https://doi.org/10.5281/zenodo.10370635. Data analysis was performed using MATLAB (Version R2020b). Raw data comprised the positions of the end effector represented as Cartesian coordinates in three-dimensional space, the movement velocities, and the participants' responses. The number of swipes was derived from the position of the end effector, i.e. the number of times that the effector changed from one stimulus area to the other stimulus area + 1. We compared the number of swipes using a two-way repeated measures analysis of variance (ANOVA) with the within-participant factors Task Demand and Motor Effort. Likewise, we analyzed the average response accuracy. As a manipulation check, we also assessed whether there were systematic differences in the average movement velocities between the different conditions, conducting a similar ANOVA as the previous ones. Whenever the assumption of sphericity was violated, the *p*-values of the respective ANOVA were Greenhouse-Geisser adjusted (Greenhouse & Geisser, 1959). The assumption of normality (tested with the Shapiro-Wilk test) was not violated (all $p > .07$).

6.3 Results

The average numbers of exploratory movements can be seen in Fig. 21A. A two-way repeated measures ANOVA with the within-participants factors Task Demand (low, medium, high) and Motor Effort (baseline, medium, high) showed that a higher number of movements was executed when task demands were increased, $F(2,22) = 4.65$, $p = .021$, $\eta^2_p = 0.30$, confirmed by a linear trend, $t(22) = 2.9$, $p = .008$. There was no significant main effect of Motor Effort, $F(2,22) = 1.79$, $p = .19$, $\eta^2_p = 0.14$, but an interaction between the two factors, $F(4,44) = 3.76$, $p = .01$, $\eta^2_p = 0.26$. Bonferroni-corrected post-hoc tests (36 pairwise comparisons) revealed that for Baseline Motor Effort, more movements were executed in the High Demand condition than in the Low Demand condition, $t(11) = 4.54$, $p = .001$, $d = 0.83$. For High Motor Effort, this was not the case ($p > .99$). For High Demand, in line with that, more movements were executed in the Baseline Effort condition than in the High Effort condition, $t(11)= 3.65$, $p = .022$, $d = 0.65$. Trivially, more movements were executed for Baseline Effort/High Demand than for High Effort/Low Demand, $t(11) = 3.47$, $p = .035$, $d = 0.73$. For Low Demand, the amount of movements did not differ regardless of the Effort level, all $p > .99$ (same for all other 33 comparisons). In summary, participants extended their explorations in reaction to higher task demands, but only when motor effort was low. Average accuracies entered a similar repeated measures ANOVA (Fig. 21B), which revealed a main effect of Task Demand, $F(2,22) = 13.01$, $p = <.001$, $\eta^2_p = 0.54$, with accuracies decreasing with increasing task demand, confirmed by a linear trend, $t(22) = 5.08$, $p = <.001$. No main effect of Motor Effort, $F(2,22) = 0.34$, $p = .072$, $\eta^2_p = .03$, and no interaction effect, $F(4,44) = 0.78$, $p = 0.55$, $\eta^2_p = 0.07$, was found. As intended, participants kept their movement velocities rather constant across conditions, resulting in no significant main effect of Task Demand on the average velocities, $F(2,22) = 0.12$, $p = 0.89$, $\eta^2_p = 0.01$, no main effect of Motor Effort, $F(2,22) = 2.58$, $p = .1$, $\eta^2_p = 0.19$, and no interaction effect, $F(4,44) = 0.57$, $p = .69$, $\eta^2_p = .05$.

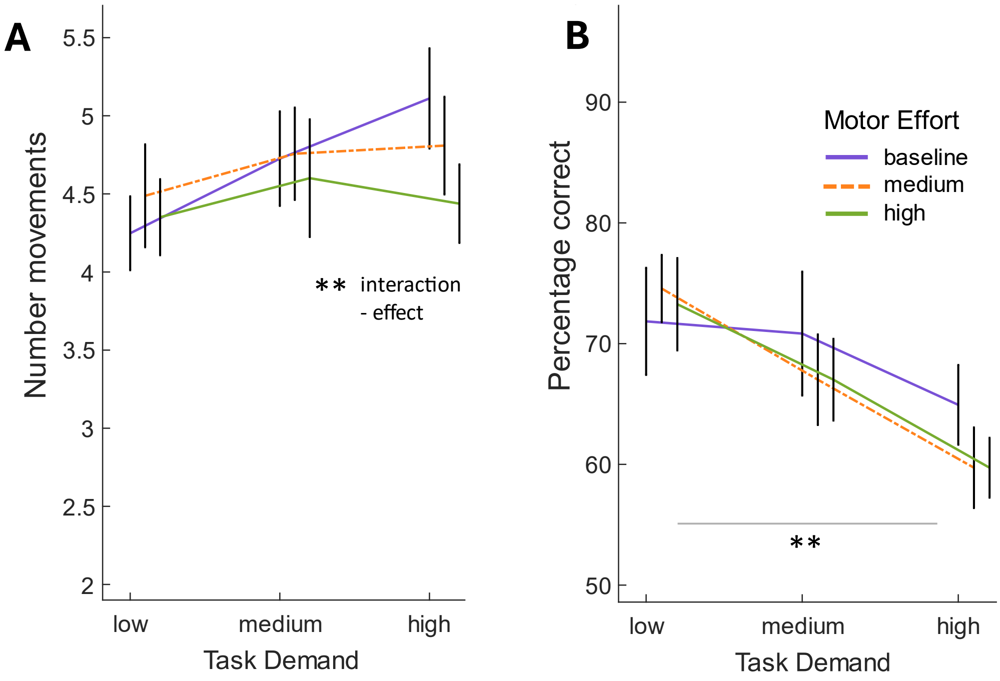

Figure 21. Results. (A) Exploration duration (number of swiping movements) as a function of task demands separately for all motor effort conditions. (B) Task performance (average percentage of correct responses) as a function of task demands separately for all motor effort conditions. Error bars represent the standard error of the mean.

6.4 Discussion

The current study provides evidence that humans adjust the duration of their haptic exploration as a function of both task demands and the motor efforts that are associated with the execution of the exploration. When confronted with higher task demands, participants extended their exploration by executing more exploratory movements. This likely constitutes an adaptation mechanism serving perception/task performance–given that previous literature showed that extension of exploration generally leads to an increased sensitivity of the agent (Drewing et al., 2011; Giachritsis et al., 2009; Lezkan & Drewing, 2018b; Louw et al., 2005). The effect though seems to strongly depend on the motor effort participants must exert during the execution of their exploration, as it disappears when the associated motor effort is high. While participants devoted the same number of movements to less demanding trials, they did not extend their exploration during the more demanding trials anymore. Furthermore, higher task demands were associated with reduced accuracies, demonstrating successful manipulation of task demands. However, one could expect an interaction effect with motor effort here as well, with stronger effects of task demands when motor effort is increased, resulting from the lack of the observed adaptation behavior. This what not the case though, possibly due to other, e.g. attentional compensatory mechanisms.

With this study, we hope to provide a first cornerstone for a comprehensive understanding of how humans adapt their haptic exploration strategy with respect to the extension of the exploration. In light of our findings, we theorize that humans adjust the duration of their exploration according to the principles of an expectancy × value framework (see e.g., Tolman, 1955). Herein, the utility of the extension of an exploration would be derived from the expected task performance, which in turn consists of the agent’s perceptual ability and the task demands at hand, combined with the value that is associated with a correct task performance (e.g. monetary reward, positive consequences). Thus, higher task demands would be compensated with extended explorations due to expected task performance differences. Additionally, aligning with motor control literature (Shadmehr et al., 2016), motor costs would be discounted with the expected utility. The accumulated costs increased with increasing motor efforts, while the (intrinsic) reward stayed constant. Consequently, the expected utility of an exploration extension would be reduced due to the changed ratio of (expected) motor costs and reward, leading to earlier termination of exploration behavior.

Even though it seems plausible that the observed effect of the effort manipulation is a result of cost-benefit-weighting, there are more banal alternative explanations. One would be the mere exhaustion of the participant, i.e. a ceiling effect due to physical restrictions of their bodies. This might produce an absolute limit of exploration duration, only manifesting itself in higher task demand trials due to the necessary exploration durations being longer. More extensive assessments could rule this out, but while the progressing fatigue over time might have some moderating effect, it does not seem likely that it is the main driving force for the observed behavior. Participants did not report that they noticed immense exhaustion of their arm or changes in their behavior. One might still wonder why the motor effort manipulation affects the behavior when task demands are high but does not affect it when demands are low. A possible explanation could involve the expected utility of the exploration segments/swipes. As task demands increase, the exploration duration needed for a consistent task performance also increases. Hence, when exploring a very demanding stimulus pair, each swipe yields a lower repetition gain, i.e. benefit regarding expected task performance, than when exploring a less demanding pair. Thus, the expected utility of each swipe would be lower for high task demands then for low demands. As a consequence, with the reward (value) staying constant and the utility of each swipe being lower, the increased motor efforts (= increased accumulated costs) would carry higher weights for high demand trials than for low demand trials, thus reducing the expected utility of an exploration extension more. In other words: For high demand trials, one can renounce one or two swipes as a measure for cost reduction without affecting the task performance too drastically. This might possibly not be the case for the low demand swipes, as the impact of e.g. just one swipe less might be immense. Obtaining the individual perceptual performances of each participant as a function of instructed exploration duration would help elucidating on that matter.

Please note that the artificial manipulation of motor effort did not only have unspecific binary effects; it could have been possible that the manipulation is perceived as unnatural and disruptive, so that participants virtually cease to explore as soon as any additional effort is introduced. However, when motor effort was only increased by one level (= medium effort), the participants' behavior only slightly deviated from the baseline level. That is, the impact of the effort- manipulation is likely not dichotomous; we can rather expect a gradual progression of the effect's magnitude, just as we would expect it for the real life. This underlines the feasibility of the experimental procedure. Further, one might speculate that sensory consequences of the counterforce in medium- and high motor effort conditions could have tampered with perceptual performance due to masking effects or conflicts with proper sensory input. However, as the average accuracy for low demand trials does not substantially differ between the baseline and high effort condition, this seems improbable. Finally, an evident peculiarity of the present study is the restricted exploration scheme. Investigating unrestricted explorations could offer valuable insights: One might expect less switching as a reaction to increased efforts and possibly more swipes as a consequence (Metzger & Drewing, 2020). Still, the driving mechanisms would be the same, i.e. cost reduction and cost-benefit weighting; but could be assessed from a different viewpoint.

For future studies, a more thorough examination of the influence of task demands on the duration of haptic explorations might provide interesting insights. Data of the baseline effort condition in the current study suggests a linear relationship between exploration duration and the three implemented levels of task demands. However, it can be expected that exploration duration would at some demand level reach a saturation point, in line with the observed saturation point of task performance as a function of instructed exploration duration (Lezkan & Drewing, 2018b); and because trivially, humans would not explore infinitely long. It is likely as well that the relationship is not linear when task demands are closer to saturation: Task demands might become so high that people terminate earlier again, as the expected utility-gain from an extension could be perceived as insufficient. As every additional movement is associated with costs but would yield only extremely limited information gain due to the very high task demand, the marginal increase in expected task performance might not provide sufficient "incentive", resulting in premature termination of exploration. Additionally, it would be necessary to confirm the derived conclusions in a more naturalistic setting. In this context, one could also tackle the question whether the artificial motor effort manipulation introduces additional cognitive load; although participants did not report notable disturbances in the questionnaire, the perceived unnaturalness of the effort manipulation might yield subtle effects.

Ultimately, we plan to model the trade-off between motor effort and task performance and aim to be able to predict natural exploration duration by also taking motivational influences into account, as these were proven to be crucial in the motor control literature (Rigoux & Guigon, 2012). We expect this to provide fruitful insights: Dissecting the prediction and valuation processes that take place during haptic explorations is worthwhile for both practical and theoretical reasons, as the derived conclusions can inform the development of more efficient and ergonomic human-computer interfaces, improve design choices for haptic experiences, and enhance our understanding of the intricacies of human perception and action.

7. Discussion

7.1 Findings on passive touch

The first half of this thesis dealt with tactile adaptation aftereffects, providing new insights into somatosensory processing of spatially structured tactile features and extending knowledge about the role of peripheral factors in the tactile distance aftereffect. Within study 1, we demonstrated cross-property aftereffects between different spatially structured features (tactile distance, macro-scale roughness, and curvature), effectively revealing shared cortical preprocessing between those. By systematically varying the orientation and location of adaptation and test stimuli, and including a control condition, we localized the effects to early cortical stages and ruled out alternative explanations such as peripheral desensitization or higher-order decisional factors. Cross-property aftereffects between roughness and distance were bidirectional but consistently weaker than within-property effects, indicating that these features rely on a common spatial representation preceding feature-specific analyses. The only other study that employed a conceptually related approach for the tactile domain would be Hollins and colleagues (2001), where high- but not low-frequency vibrotactile adaptation interfered with subsequent discrimination of fine textures (but neither affected the perception of coarse textures). With this, they solidified evidence for a temporal code for the perception of fine textures. Part of our study provides the equivalent to that but or the spatial code; vice versa, one would expect that the perception of very fine textures should be mostly unaffected after distance adaptation. In total, cross-property aftereffect paradigms seem to pose a useful tool for future studies to disentangle somatosensory computations. Gathered insights could ultimately inform models of sensory processing in artificial neural networks and provide a design guide for building artificial haptic systems that jointly encode distance, roughness, and curvature.

For certain aftereffects such as the haptic size aftereffect, previous studies suggest that adaptation conditions can largely affect the aftereffect's magnitude, such conditions being for example the manner of touch (resting/dynamic) (Hidaka et al., 2024) or the posture of the hand and arm (Frisco et al., 2023). Especially for visual aftereffects, some mentioned in the introduction of study 2, stimulus characteristics and attentional factors were shown to yield strong effects with regards to aftereffect magnitude or decay rate (Georgiades & Harris, 2000; Hong & Yoon, 2018; Ishihara, 1999; Roumani & Moutousis, 2020). Based on these findings, we hypothesized that peripheral factors such as individual skin disposition might explain interindividual differences in *tactile* aftereffect expression (here*: tactile distance* aftereffect) as skin properties have previously been found to be related to several basic indicators of perceptual performance. Study 2 however does not provide evidence for this idea as no correlations were found between skin properties and aftereffect magnitude. Importantly, we did observe the expected relationship between skin properties and basic tactile abilities, i.e. the sample did vary in skin disposition to an extent that yielded effects for other perceptual outcomes. This, in turn, gives higher credibility to the null result for the effect of skin properties on aftereffect magnitude (apart from the evident problem that null results only have very limited explanatory power anyway), as one otherwise could have rightfully argued that the sample was simply too homogenous to successfully uncover correlations. Notably, and in line with our findings, the haptic *size* aftereffect has recently been shown to be similar large between young and old adults (Kuroda et al., 2025). Ergo, even despite the fact that older adults display substantially reduced afferent density (Deflorio et al., 2023) and loss in skin quality (Firooz et al., 2012), the aftereffect remained mostly unaffected. It further seems unlikely that peripheral factors would yield more substantial effects for higher level aftereffects, even the opposite. Instead, the cortical susceptibility to adaptation (-aftereffects) might differ between individuals. Trivially, interindividual variance regarding aftereffect strength might ultimately just be noise; however, the possibility that interindividual differences are meaningful remains intriguing (cf., De Haas et al., 2019; Moutsiana et al., 2016; Wang et al., 2024). To examine whether susceptibility to adaptation varies systematically across individuals, one could test correlations between the strength of different tactile aftereffects, compare aftereffect strength across modalities, or assess the test-retest reliability of the same aftereffect. Ideally, these approaches would be complemented by e.g. functional magnetic resonance imaging to identify neural correlates of the behavioral effects (Krekelberg, 2006). To my best knowledge, such within-participant comparisons have not yet been conducted but would allow for fruitful conclusions regarding the stability and potentially idiosyncratic nature of neural adaptation susceptibility.

7.2 Findings on active touch

Study 3, 4 and 5 dealt with optimization processes in haptic perception. By employing a series of differentially controlled behavioral experiments, we were able to decipher exploratory movement parameters such as direction, velocity, duration, switching behavior, and movement types and assess the extent to which they are adjusted in response to prior knowledge and dynamic expectations induced by varying context factors.

Previously, it remained unclear whether exploitation of prior knowledge for exploration optimization only is possible when implicit prior knowledge is induced but not if explicit information is provided; or whether information must be of somatosensory nature and cannot originate from the visual modality. Zoeller and colleagues (2018) found that while implicit prior information on compliance (through blocked presentation) facilitated initial force adaptation during exploration of silicone stimuli, presentation of explicit (verbal or visual) prior information yielded inconclusive results. Addressing this issue, we conducted study 3 and 4: Here, abstract and naturalistic visual priors did elicit behavioral effects with regards to fine-tuning of movements and the preparation of holistic movement schemes. This suggests that humans might indeed leverage visual priors to optimize their explorations, similar to other previously reported sources of information. These contrasting results might at first seem peculiar, as Zoeller et al. even implemented *dynamic* visual priors; which is a feasible approach for a property like compliance (Paulun et al., 2017; Wijntjes et al., 2019); but did not observe the expected effects. Grating orientation (study 3) though is an inherently static property which might explain why static visual priors were sufficient to enable fine-tuning in this case. Further, orientation might simply be easier to interpret and thus more feasible for exploitation than deformability/compliance, where inference ultimately depends on the applied force; which is not visually accessible. Question remains why the (static) visual priors yielded effects regarding exploration of the sponge stimulus in study 4, given that this is analogous to the silicone stimuli. A simple reason might be the naturalistic character of the sponge stimulus: Sponges are everyday objects; their presentation might thus automatically evoke more (useful) associations. Additionally, optimization here involved initial EP type selection, not fine-tuning of forces; this is a very different application. The extent to which visual priors can be exploited (and the affected movement parameters) might hence depend on factors like *stimulus specifics* and *visual information type* (static/dynamic); as well as the priors' "informational value" that is resulting from the relationship between those factors.

One further achievement of the second part of this work was to highlight previously underexplored alignments of exploratory movement optimization with principles of established information processing/motor control models. Specifically, study 3 delivered clear evidence that the quality of prior visual information substantially determined the extent of its exploitation for exploratory movement optimization. This is in line with predictions of (multisensory) information integration models for perception, which are characterized by statistically-optimal reliability weighting (e.g., Hillis et al., 2002; Jacobs, 1999). Likewise, sensory feedback during sensorimotor learning has been previously shown to be weighted by its uncertainty, and motor adaptation over time followed principles of Kalman filtering (Berniker & Koerding, 2011; Mehta & Schaal, 2002; Wolpert et al., 1995). Importantly, it was also found that *prior* knowledge is integrated for subsequent motor control (e.g., Flanagan et al., 2008). In our study, the visual priors facilitated or "triggered" the movement adjustments; adjustments which otherwise would occur only after sensory information has been gathered over the course of the exploration (Lezkan & Drewing, 2018a); with higher probability, the higher the priors' quality. Haptic exploration optimization hence might follow similar principles regarding reliability weighting as information integration in perception and sensorimotor control.

Study 5 further suggested that *motor costs* are taken into account for overall duration of a haptic exploration. For typical cost-intensive tasks like walking, a resource-rational approach has previously been confirmed (e.g., Carlisle & Kuo, 2023; Shadmehr et al., 2016). Studies demonstrated that humans predicted movement costs, which influenced decisions regarding the specific execution of actions such as reaching and grasping before or during performance of those (Christopoulos & Schrater, 2011; Cos et al., 2011; Cos et al., 2014; Huang et al., 2012; Michalski et al., 2020; Morel et al., 2017). Even for eye movements, i.e., metabolic rather low-cost actions, movement parameters have been shown to be influenced by planning and execution costs (for a review see Schütz & Stewart, 2025). Study 5 suggests that motor costs are taken into account during haptic exploration in a similar fashion, which is a fruitful finding as it shows that these principles of resource-rationality apply to larger-scale information gathering processes that involve prolonged goal pursuit; and not only to planning of short-segmented action or rapid perceptual decision making (e.g., Burk et al., 2014) . This conclusion is supported by a conceptually related study, in which participants had to move a cursor with manual handle to reveal information about objects during a visual search task, and higher artificially introduced resistance against the handle movement influenced the search behavior (e.g. reduced travel distance) (Moskowitz et al., 2023). Additionally, study 5 serves as a good example how exploration optimization is based on a tight interplay between information gathering, prediction, and valuation processes. Given that task difficulty and motor costs (both inferred by the participant from the gathered sensory information) systematically influenced termination behavior, it seems likely that based on those signals, humans estimate the utility of a potential exploration extension: Participants would *predict* their potential task performance and the resulting utility of an exploration extension under consideration of the task difficulty and their own capabilities. This would be combined with a motivational factor (in study 5 kept constant) and *discounted* by the motor costs, resulting in the estimated exploration length of highest value. So far, we can of course only assume and infer that the experimental manipulations induced certain expectations and that these in turn triggered optimization processes; ultimately, we aim to combine data from the unrestricted exploration task with an experiment assessing performance as a function of instructed exploration length (for the same participants); this would allow for modeling whether actual termination of exploratory behavior corresponds to the exploration length of maximal value on an individual basis.

7.3 Broader Perspectives

The principle of adaptivity underlying the perception-action loop, evidenced by a large body of research introduced in sections 1.3 and 1.4 and underscored by the studies 3-5 of this dissertation, carries one implication that is less frequently discussed. Lifelong experience enables humans to learn and estimate contingencies between motor actions and sensory experience, improving data-gathering behavior and property estimation (cf., Gehb et al., 2019; Preißler et al., 2021; Schwarzer & Jovanovic, 2024); but without regular engagement in active touch, these capacities may possibly decline. The writer Gaby Hinsliff described in the Guardian: “I increasingly notice the disappearance of small ways in which humans used to engage tangibly and effortfully with their world but now don’t; a growing physical distance between people and stuff” (Hinsliff, 2015; as cited in Gross, 2019). Certain procedures like winding up a watch have almost become extinct, she argues. 10 years later, one can easily come up with many other such developments, from small changes such as the disappearance of manual buttons on stoves or cars to voice recording instead of typewriting and handwriting (though other motor skills likely emerge meanwhile through, e.g., gaming). But just as specific motor skills might undergo changes (for a review see, e.g., Heuer, 2016), “haptic skills” might erode (or not develop properly in the first place, e.g., Mohamed et al., 2023) when exposure is less needed or provided, (due to, e.g., online-shopping or digital instead of physical modeling), and explorations would become less efficient. Further, there might be *inherent* interindividual differences in how sophisticated one's "enactive approach" is, even due to some a priori biological disposition. Anecdotally, while observing participants handling certain materials, one can witness the most absurd and time-consuming movements (albeit having given clear instructions on the property that is needed to be estimated). After this observation, one might ask whether some humans are naturally more efficient "active perceivers" than others and wonder what else this might correlate with. As of now, there are no systematic attempts of establishing a construct like "haptic skill" which explicitly involves the tendency or ability to efficiently gather haptic information, and it would of course be difficult to do so (independently from peripheral factors); but it would allow for capturing interindividual differences with regards to sensorimotor knowledge/their enactive approach due to pathologies, aging, training, or inherent tendencies (cf., "need for touch scale", Peck & Childers, 2003).

One potential future application, noted within Study 3 and 4 but not explored in detail, is enactive sensing for autonomous robotic systems. Artificial tactile sensing has substantially progressed over the last decades, particularly through the development of sensor technologies (for reviews, see Darghahi & Najarian, 2005; Hao et al., 2022; Luo et al., 2017). Further, adaptation in terms of motor control has reached an impressive level, allowing stable control under perturbations during walking, grasping, or lifting objects of different weights or varying surface frictions via slip detection (e.g., Burdet et al., 2014; Dang & Allen, 2014; Kumar et al., 2022; Liang et al., 2024; Nazari et al., 2023; Steingrube et al., 2010). However, adaptation in the context of active haptic information gathering remains more limited. Despite some promising attempts of combining continuous feature extraction, feature integration, and reciprocal control strategy (Fishel & Loeb, 2012; Fleer et al, 2020; Funabashi et al., 2018; Ottenhaus et al., 2018), robotic haptic exploration is still largely static or repetitive (for a review see e.g. Seminara et al., 2019), lacking the kind of dynamic, fine-tuned, and purposive exploratory movements observed for humans as outlined in section 1.4. In particular, the kind of multimodal facilitation demonstrated in Studies 3 and 4 has rarely ever been implemented in autonomous systems. Current approaches have achieved visuo-tactile integration for perceptual computations (e.g., Babadian et al., 2023; Falco et al., 2017; Xiong et al., 2024; Xu et al., 2024), or multimodal motor planning (Guo et al., 2017; Sun et al., 2016; Yamaguchi & Atkeson, 2019), but they seldom extend to guiding or optimizing the dynamic exploratory process itself (though see Eiband et al., 2019; Yuan et al., 2018). As such, implementing active visuo-haptic exploration of materials into robotic biomimetic systems may offer a promising approach to increase their data-gathering efficiency.

7.4 Conclusion

This dissertation examined predictive mechanisms that operate at varying levels of sensory processing, and which shape both the percept itself as well as the reciprocal relationship between action and perception. We found that neural adaptation can affect tactile perception more broadly than previously assumed, crossing property boundaries and revealing shared primitive cortical preprocessing mechanisms for spatially structured features. Regarding active touch, we identified new parallels with established information processing and motor control models, advancing our understanding of (visuo-) haptic exploratory procedures. Specifically, we found humans to dynamically optimize their haptic explorations through the usage of visual priors: they flexibly used prior information of varying quality to guide initial exploratory movements and holistically select more efficient strategies. Furthermore, exploration duration seems to be strategically terminated based on cost-benefit expectations weighing task demands against motor effort, suggesting an ecologically rational process for haptic perception.

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Supplementary Information

Humans dynamically use visual priors to optimize their haptic exploratory behavior

Section I

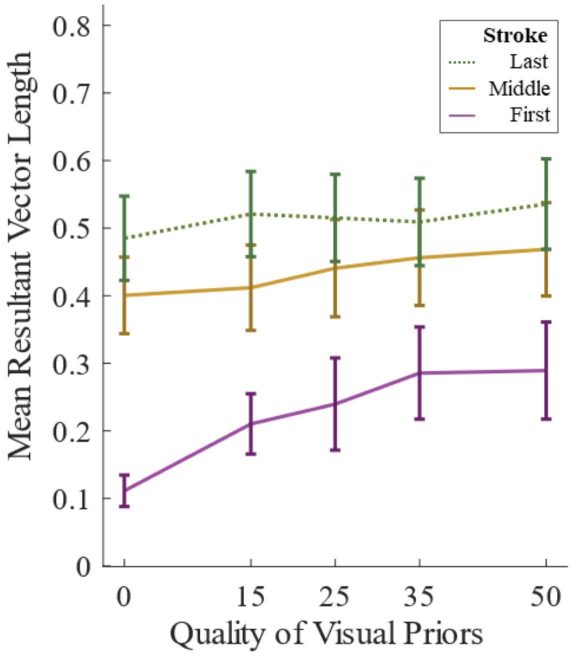

Figure S1. Average mean resultant vector lengths and standard errors for each quality condition and movement type.

In Experiment 1, the mean resultant vector length $\bar{R}$ of each participants' initial movement directions for each visual quality condition entered a repeated measures ANOVA to compare the variance of movement directions between quality conditions. $\bar{R}$ is the vector length of the mean direction $\bar{\theta}$ of a circular distribution. It varies between zero and one; an $\bar{R}$ near one implies that there is little variation in movement directions and the data is concentrated around the mean direction $\bar{\theta}$. Vectors were longer with higher visual qualities, i.e. variability of the initial movements' directions decreased with higher visual quality, $F(4, 60) = 4.81$, $p = .03$, $\eta^2 = 0.24$ (Greenhouse-Geisser adjusted), confirmed by a linear trend, $F(1,15) = 6.16$, $p = .025$, $\eta^2 = 0.30$. For middle and last strokes, there was no effect of visual quality, $F(4, 60) = 2.22$, $p = .08$, $\eta^2 = 0.13$, and $F(4, 60) = 1.74$, $p = .15$, $\eta^2 = 0.10$, respectively.

Section II

In Experiment 2, there was again a significant main effect of Visual Quality on the mean resultant vector lengths of initial strokes, *F*(2, 32) = 7.01, *p* = .007, η^2_p = 0.32 (Greenhouse-Geisser adjusted), confirmed by a linear trend, *F*(1,17) = 8.19, *p* = .01, η^2_p = 0.33, (0%: *M* = 0.18, 25%: *M* = 0.28, 50%: *M* = 0.34), but no main effect of Task Demand, *F*(1,16) = 0.63 , *p* = .439, η^2_p = 0.03, or Order, *F*(1,16) = 2.96 , *p* = .10, η^2_p = 0.16, and no interaction effect, all *p* > .20.

Section III

For middle and last strokes, there was no effect of visual quality, *F*(2, 32) = 0.92, *p* = .41, η^2_p = 0.05, Movement, *F*(1,16) = 0.20, *p* = .66, η^2_p = 0.01, or Order, *F*(1,16) = 4.45 , *p* = .051, η^2_p = 0.22, but a main effect of Demand, *F*(1,16) = 8.79, *p* = .009, η^2_p = 0.36, (low: *M* = 0.49, high: *M* = 0.54), an interaction effect of Movement and Demand, *F*(2, 32) = 4.86, *p* = .04, η^2_p = 0.23, an interaction effect of Movement, Visual Quality and Order, *F*(2, 32) = 7.01, *p* = .006, η^2_p = 0.28, but no other interaction effect (all *p* > .06).

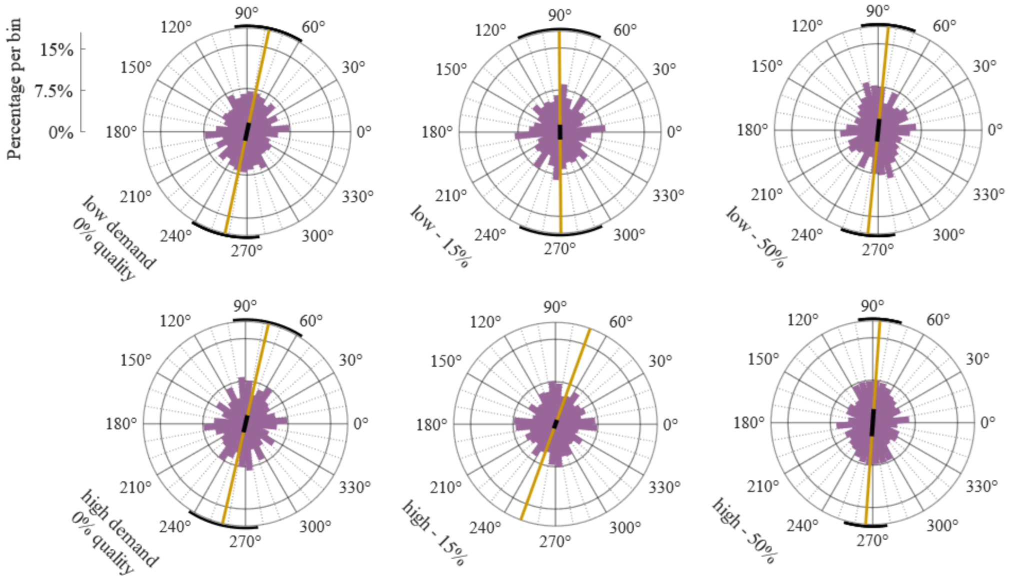

Figure S2. Initial movement direction histograms for each quality*demand condition including all participant data of Experiment 3.

List of all Publications

Journal articles

Jeschke, M., Azañón, E., & Drewing, K. (under review). Shared early processing of distinct tactile features. *iScience*

Jeschke, M. & Drewing, K. (2025). Look first, feel faster: Prior visual information accelerates haptic material exploration. *I-Perception*, *16*(5). https://doi.org/10.1177/20416695251385816

Jeschke, M., Zoeller, A. C., & Drewing, K. (2024). Humans flexibly use visual priors to optimize their haptic exploratory behavior. *Scientific Reports*, *14*(1), 14906. https://doi.org/10.1038/s41598-024-65958-6

Scheffels, J. F., Kräling, H., **Jeschke, M.,** Kalbe, E., & Kessler, J. (2022). Erfassung exekutiver Funktionsstörungen mit dem Kölner-Exekutiv-Test. *Zeitschrift Für Neuropsychologie, 33*(2), 71–83. https://doi.org/10.1024/1016-264X/a000354

Conference articles

Jeschke, M., E. Azañón, E., & Drewing, K. (2025). The Relationship Between Biophysical Skin Properties, Tactile Ability, and the Distance Adaptation-Aftereffect. IEEE World Haptics Conference (WHC), Suwon, Korea, Republic of, 2025, pp. 115-122, https://doi.org/10.1109/WHC64065.2025.11123197.

Jeschke, M., Metzger, A., & Drewing, K. (2024). Humans Terminate Their Haptic Explorations According to an Interplay of Task Demands and Motor Effort. In: Kajimoto, H., et al. Haptics: Understanding Touch; Technology and Systems; Applications and Interaction. EuroHaptics, Lille, France, 2024. Lecture Notes in Computer Science, vol 14768. Springer, Cham. https://doi.org/10.1007/978-3-031-70058-3_7

Jeschke, M., Drewing, K., & Azañón, E. (2023). The Tactile Distance Aftereffect Transfers to Roughness Perception. IEEE World Haptics Conference (WHC), Delft, Netherlands, 2023, pp. 8-13, https://doi.org/10.1109/WHC56415.2023.10224476

Jeschke, M., Zöller, A.C., & Drewing, K. (2022). Influence of Prior Visual Information on Exploratory Movement Direction in Texture Perception. In: Seifi, H., et al. Haptics: Science, Technology, Applications. EuroHaptics 2022. Lecture Notes in Computer Science, vol 13235. Springer, Cham. https://doi.org/10.1007/978-3-031-06249-0_4

Conference abstracts

Jeschke, M., Azañón, E., & Drewing, K. (2025). Revealing similarities in somatosensory processing of tactile distance and curvature with adaptation-aftereffects. Tagung experimentell arbeitender PsychologInnen (TEAP), Frankfurt am Main, Germany.

Jeschke, M., Metzger, A., & Drewing, K. (2024). Motor costs, monetary reward, and task demands determine haptic exploration duration. European conference on visual perception (ECVP), Aberdeen, Scotland.

Jeschke, M. & Drewing, K. (2024). Termination of haptic exploratory behavior is affected by motor effort and task demands. TEAP, Regensburg, Germany.

Jeschke, M. & Drewing, K. (2023). Prior static visual information on material properties increases the efficiency of a subsequent haptic exploration. Vision Sciences Society conference, St. Pete Beach, Florida (US).

Jeschke, M. & Drewing, K. (2023). Haptic exploratory movement adjustment to prior visual cues depends on their quality and frequency. TEAP, Trier, Germany.

Jeschke, M., Zoeller, A., & Drewing, K. (2022). How prior visual information affects exploratory movement adaptation in texture perception. ECVP, Nijmegen, Netherlands.

Jeschke, M., Scheffels, J.F., Kalbe, E., & Kessler, J. (2019). TWIST(A/B): Eine ökonomische Stroop-Variante zur Bestimmung exekutiver Funktionen. Kongress der Deutschen Gesellschaft für Neurologie, Stuttgart, Germany.

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“I hereby declare that I have prepared the thesis at hand independently and without undue aid or the use of any resources other than those indicated within the thesis. All parts of my thesis taken either verbatim or analogously from the published or unpublished works of or based on oral communications with others are indicated as such. Regarding all aspects of my scientific inquiries as they appear in my thesis, I have upheld the tenets of good scientific practice as laid out in the "Satzung der Justus-Liebig-Universität Giessen zur Sicherung guter wissenschaftlicher Praxis" and complied with the precept of ethics, data protection and animal welfare. I declare that I have neither directly nor indirectly given monetary or any other valuable considerations to others in connection with the thesis at hand. I declare that I have not presented the thesis at hand, either in an identical or similar form, to an examination office or agency in Germany or any other country as part of any examination or degree. All materials from other sources as well as all works performed by others used or directly referenced within the thesis at hand have been indicated as such. In particular, all persons involved directly or indirectly in the development of the thesis at hand have been named. I agree with the screening of my thesis for plagiarism via offline or online detection software.”

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Gießen, 15.10.2025