

Chapter 2

Active Movement Reduces the Tactile Discrimination Performance

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Abstract Self-performed arm movements are known to increase the tactile detection threshold (i.e., decrease of tactile sensitivity) which is part of a phenomenon called tactile suppression. Today, the origin and the effects of tactile suppression are not fully understood. Tactile discrimination tasks have been utilized to quantify the changes in tactile sensitivity due to arm movements and to identify the origin of tactile suppression. The results show that active arm movement also increases tactile discrimination thresholds which has never been shown before. Furthermore, it is shown that tactile sensitivity drops at approximately 100 ms before the actual arm movement. We conclude that tactile suppression has two origins: (1) a movement related motor command which is a neuronal signal that can be measured 100 ms before a muscle contraction. This motor command is the origin for the increase of the discrimination threshold prior to the arm movement and (2) task irrelevant sensory input which reduces tactile sensitivity after the onset of the arm movement.

2.1 Introduction

One of the brain's major challenges is to filter task relevant from task irrelevant information. Mechanisms which filter out irrelevant information are suggested to exist across many sensory systems [1] and the perceptual consequences are in some cases well understood.

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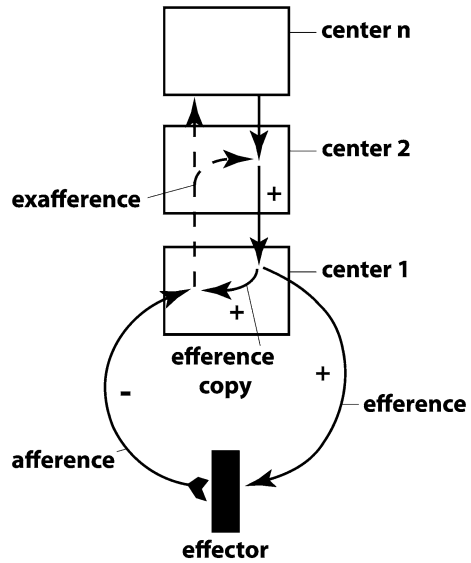
Tactile suppression, a decrease in tactile sensitivity during active limb movement, seems to be a phenomenon that results from some form of filtering. In everyday life, the sense of touch has to deal with a vast amount of sensory information. One can speculate that tactile information may be divided into two groups of information types in order to keep the brain's workload low: task relevant and task irrelevant. During normal body movements, for example, many sensory inputs are generated by one's clothing rubbing on the skin, air flow due to limb movements and others. These tactile stimuli are usually perceptually unimportant for our behavior and most of the time they remain unconscious. Here, tactile suppression seems to reduce tactile sensitivity in order to keep tactile stimulation, which results from self performed movement, low.

Intuitively, one would expect the brain to filter out irrelevant stimuli in order not to be involved in processing information which is irrelevant for a specific task. Hypothetically, two kinds of information filters may be possible:

- (1) Active filters, whereby the neural system is actively preprocessing information and then separating relevant from irrelevant information. An active filter needs processing power. This processing power should be lower than that which would be needed to process the irrelevant information in order to lower the brain's workload. As an analogy one can see it as a spam filter where messages which contain suspicious keywords are filtered out before they will be sent from one server to the other through the World Wide Web.
- (2) Passive filters can filter out information using a fixed criterion. Passive filters are suggested to be part of the peripheral nervous system or early stages of the central neural system. In this case, only little processing capacity is necessary, if at all. As an example one could see it as an instance that filters out messages that have only a small file size, without reading the content of the message.

Filter mechanisms have already been identified, for example, in the visual system. Saccadic suppression is a phenomenon whereby visual sensitivity is decreased during ballistic eye movements (so-called saccades) and may be seen as a visual analogue to tactile suppression, because both phenomena reduce the amount of sensory information during active movement [2–4]. Saccades generate rapid image changes on the retina, which are not of importance, comparable to the tactile stimuli (e.g., cloth rubbing on the skin) caused by limb movements. Saccadic suppression can easily be demonstrated if an observer is standing in front of a mirror. If he is looking into his left and subsequently into his right eye, he will not perceive any eye movement. To explain this phenomenon it has to be assumed that the sensitivity of the visual system must be decreased during saccades, which was already claimed by Helmholtz (1867) [5]. A mechanism which explains the functioning of saccadic suppression is the reafference principle [6], in which a copy of the motor command (efference copy) is compared with the afferent signal (reafference) that comes from an effector (e.g., muscle). Normally, both signals cancel each other out on the level of the center 1 (Fig. 2.1). If the signal strength of the afference becomes too small or too big due to an external influence, then a proportion of the afferent signal remains (exafference). This is the signal for object motion.

Fig. 2.1 Schematic illustration of the reafference principle. With kind permission from Springer Science+Business Media: [6], Fig. 2.4. A center may be seen in this context as a general level of information processing



It is still unknown whether both, tactile and visual suppression, share only the sensory consequences, i.e., decrease of sensory abilities during body movements, or whether the decrease in sensitivity is due to common underlying processes where body movement interacts with perception in the same way independent of the sensory modality. The phenomenon of sensory suppression will be explained by means of the saccadic suppression which is well understood [7, 8].

In previous studies, effects of saccadic suppression, i.e., the decrease of visual sensitivity, were identified and underlying mechanisms have been proposed as it is shown in the following brief overview:

Sperry (1950) [9] suggested that corollary discharges of motor patterns into the sensory system may be crucial for the adjustment of a visually stable world during saccades. This theory is a variation of the reafference principle.

Holt (1903) [10], creator of the inflow theory, claims signals from proprioceptors of the extraocular muscles to be responsible for a blocking of visual centers. Thus, according to Holt the visual system is calibrated by sensory signals and not by eye movement motor commands.

Richards (1969) [4] proposed that shear forces, during saccades, between the retina and the vitreal body induce a blocking of the information stream through the optic nerve. This may explain the drop in visual sensitivity but not the adjustment of a stable visual world.

Matin (1974) [8] suggested that the time in which the photoreceptors are exposed to light (i.e., a visual stimulus) is too short, due to the high motion velocity of the eyes during saccades. The photoreceptors would not rise above threshold.

Finally, Mackay (1970) [11] has shown that rapid image motion itself (as it occurs during saccades) can induce a suppressing effect, while the eyes remain stationary.

Any of these hypotheses can only partially explain saccadic suppression. Despite the attempt to define the origin of saccadic suppression, many researchers were investigating the effects, occurring during suppression, and the resulting perceptual properties. Apart from propagation of a complete loss of visual sensitivity during saccades, evidence for partial sensitivity modification is found. For example, it was reported that saccadic suppression mainly affects motion perception [12], whereas other characteristics, such as contrast detection of high-frequency or equiluminant gratings remain unaffected [2, 3, 7, 13, 14]. Investigations regarding the perception of intrasaccadic motion give further insight into the directional sensitivity of perception. Ilg & Hoffmann's study [7] showed by changing the direction of intrasaccadic motion relative to the direction of the eye movements that subjects perceived the intrasaccadic movement after the saccade. The perceived motion velocity was decreased and also the threshold amplitude was increased compared to perception without eye movement. Most interestingly they did not find changes in threshold amplitudes if the image motion was presented in the same direction as the eye movements were orthogonally. They conclude that saccadic suppression is mediated by a delayed processing of retinal information in the CNS during saccades and is independent of parameters like saccade amplitude or eye motion direction.

To identify whether saccadic suppression results from a central signal as it is proposed by [9] or [6], or whether visual motion caused by the eye movement itself is inducing the visual masking effect during saccades is a major question. Researchers have found some indication that both are acting on the same cortical mechanisms. An interesting finding, that supports the idea of a central mechanism, is the early action of saccadic suppression, that is the finding that suppression precedes visual motion analysis [12] and contrast masking [3]. The time course for the loss of sensitivity has been shown to begin as early as 50 ms before the onset of saccades, has the highest sensitivity reduction at or shortly before the start of saccades, diminishes during saccades, and vanishes after the end of saccades [15].

The tactile sense shows also sensitivity changes during self-performed movements. Referring to the visual phenomenon it is called tactile suppression or tactile gating whereby tactile stimulation during self-produced body movement is felt less intensely than stimulation during not self-produced movements. A well-known version of this filtering effect is that you cannot tickle yourself [16–20] or at least the sensation of self-tickling is less powerful. This can be interpreted to serve as a strategy to reduce the brain's workload by keeping out uninformative stimuli. As it is supposed in other sensory systems, separating sensory information due to its task relevance can reduce the workload of the brain and is supposed to be a major goal of tactile gating [21].

How tactile suppression is generated is not fully understood, yet. However, two major mechanisms are thought to be involved in decreasing tactile sensitivity during self-motion. Firstly, as in saccadic suppression, the reafference principle [6] is claimed to mediate tactile suppression [22]. Sensory consequences of self-performed movements can be predicted precisely [16, 20] and can therefore be cancelled out. Unpredicted stimuli will not be cancelled and become accentuated. Secondly, it has been shown that the motor command, which is responsible for the

execution of muscle contraction, induces a blockade between the peripheral- (PNS) and the central nervous system (CNS) [23]. Thus, afferent sensory information is filtered out due to this sensory gating.

Similar to saccadic suppression, it is reported for tactile suppression to be selective for decreasing the sensitivity only for a subset of tactile features while others seem to be unaffected. Most studies report on an increased detection threshold during active movement [22, 24–28], while the discrimination threshold is stated to remain unchanged [24, 25, 29].

In most of the studies on tactile gating, changes in detection and discrimination thresholds have been investigated by applying electrical stimuli to the skin or by directly stimulating nerves. Intensity ratings were utilized to determine the thresholds. However, this method has two major disadvantages: (1) Electrical stimulation is not common in real life. This stimulation is hardly comparable to tactile sensing as it is experienced during tactile exploration. Manipulative finger movements, for example, generate multiple kinds of stimuli such as normal force, shear force or vibration. Electrical stimulation however does not stimulate mechanoreceptors specifically. (2) Electrical stimulation provides the possibility to investigate intensity discrimination but it does not permit for directional changes of moving stimuli. Moving stimuli for example, which occur during any tactile exploration are hardly possible to be simulated by electrical stimulation.

Previous findings, that tactile detection threshold changes during active movement but discrimination threshold does not, may be an exceptional case of intensity ratings of electrical stimulation.

To investigate whether active movement affects the tactile discrimination threshold, real life tactile stimuli which occur during tactile exploration are utilized (i.e., normal and tangential forces). Normal forces can be generated if one is tapping on a rough surface and the skin is indented perpendicular to the skin surface. In this study, normal forces will be generated by a set of Braille generators, consisting of pins which can be extended vertically. Tangential forces (i.e., forces parallel to the skin surface) appear during almost any tactile manipulation, for example if one is rubbing the finger on a surface. In this study they are generated with a tangential force device, consisting of a pin which is able to move on a horizontal x/y -plane. The fact that it can be changed in intensity but also in direction makes it a good stimulus to investigate the effect of active movement on tactile sensitivity of moving stimuli. This provides the possibility not only to study the effect of movement on tactile sensitivity but also a basic phenomenon of motion perception, namely, the involvement of movement prediction on the amount of sensitivity decrease. Considering the reafference principle, described above, it seems plausible that the arm movement direction may be taken into account to modulate tactile sensitivity in a direction specific manner. Thus, tactile stimulus motion along the same direction of the arm movement may be attenuated because the sensory consequences of a self performed arm movement are predicted and canceled out [16–18]. Tactile motion perpendicular to the arm movement may be less predictable, because they hardly ever appear in a real environment and thus, the sensory system may have been hardly ever confronted with perpendicular tactile movement. The unpredictability of these

stimuli may increase the perceptibility which would result in a higher sensitivity for stimuli which move perpendicularly to the arm movement.

Tactile gating, however, suggest a general decrease in sensitivity since it is simply blocking the information transfer to the central nervous system, caused by a motor command. Consequently, any sensory information will be blocked which results in a lower amplitude of sensory signals in the somatosensory cortex leading to a lower quality of the tactile stimulus.

The aim of this study is to measure qualitatively and quantitatively tactile sensitivity changes during arm movement under real life conditions. That is, utilizing realistic tactile stimuli combined with natural arm movements. Furthermore, the predictability of tactile stimuli and its effect on the directional sensitivity changes will be investigated.

2.2 Experiment 1: Sensitivity Reduction vs. Predictability of Arm Movement

The aim of this experiment was to investigate whether tactile sensitivity changes for different tactile motion directions relative to the direction of an arm movement. This was done by simulating a tactile exploration scenario in which one is sliding the index finger over a surface. Tactile motion, generated by a pin which moves parallel to the skin surface, was applied to the fingertip. Such tangentially moving stimuli are present during most tactile manipulations and were combined with a simple forward movement of the arm. The tactile stimuli can be changed in their motion direction so that they move in line with the direction of arm motion or with an angular offset. By measuring the discrimination threshold for deviations of the tactile motion direction during or in the absence of arm movements it is possible to investigate the following question:

Is there a change in the tactile discrimination threshold during active arm movements or will it be unaffected as it is claimed in previous studies. Today, the prevailing view is that active movement increases the tactile detection threshold but not the discrimination threshold.

If the discrimination threshold changes as a result of active arm movements, two hypotheses will be tested regarding the sensory consequences of tactile suppression:

- (1) If the prediction of sensory consequences is taken to cancel out self performed sensory input and thus, to alter tactile sensitivity during active movement, then differences in the discrimination threshold during self-performed arm movements should occur. If the motion direction of the tactile stimulus and the arm movement are congruent (i.e. tactile consequences are predictable) the discrimination threshold should be higher than if both stimuli move in orthogonal directions (i.e. tactile consequences are not predictable).
- (2) If tactile gating is a major factor that causes tactile suppression, then no difference in the discrimination threshold should occur. The gating effect is expected

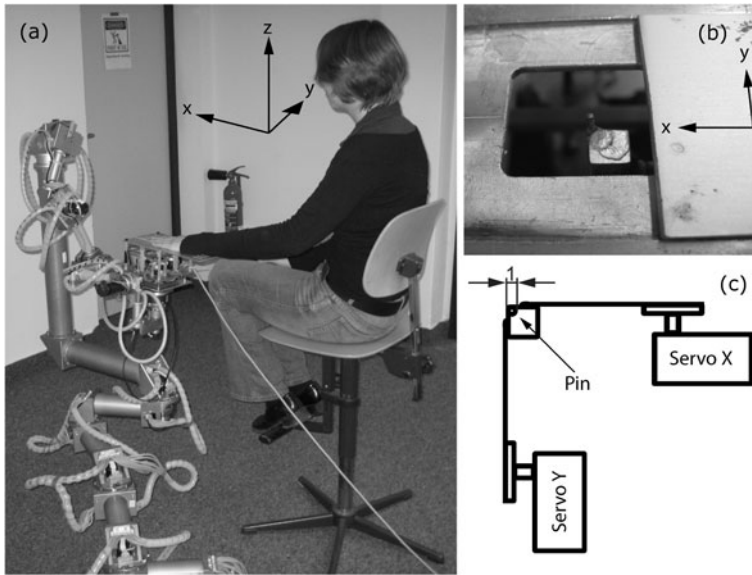


Fig. 2.2 (a) Participant seated in front of the kinesthetic (ViSHaRD 10) and the tactile device. (b) Close-up view of the pin of the tactile motion device. (c) Schematic diagram (top view) of the tactile motion device. Two servo motors are generating the pin motion in x and y direction. Pin diameter is 1 mm. Pin is at the level of the cover plate

to reduce any tactile input, regardless of the motion direction of the arm and the tactile stimulus.

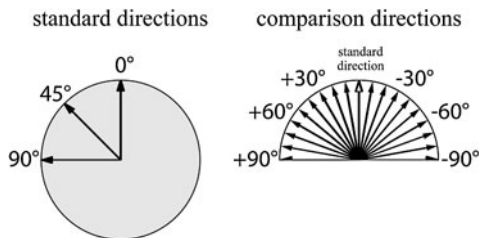
2.2.1 Methods

Twelve right-handed, participants (seven male, five female) participated for pay (8€/h). Ten of them were naïve to the purpose of the experiment. Participant age ranged from 19 to 35 years (average 26 years). None of them reported previous injuries or impairment of tactile sensitivity of the finger tip. The experiments were approved by the local ethics committee.

A custom made hyper-redundant kinesthetic display, called ViSHaRD 10 (for details see [30]), was used to provide kinesthetic force feedback to the operator's hand and to track its position (Fig. 2.2). As a tactile stimulator a custom made tactile motion device was utilized to generate tactile stimuli that move parallel to the skin (for details see [31]). A metal pin moved radially on the x/y plane to exert tactile motion stimuli. The radius of tactile motion is 1 mm. The maximal pin velocity is 10 mm/s. Figure 2.2 shows the tactile device in use (a) with a close up view of the pin area (b) and a schematic diagram of the top view of the pin (c).

The tactile motion device was mounted on the kinesthetic device in order to couple kinesthetic and tactile stimulation. For our experiment the free moving space

Fig. 2.3 Possible directions of the standard and the comparison stimuli. The *left panel* shows the three standard directions (0° , 45° , 90°); the *right panel* shows the possible comparison directions relative to the standard directions



of the kinesthetic device was limited to one degree of freedom (1 DOF) along the x axis.

Participants were sitting on a bar stool in front of the setup. Their left hand was fixed to the cover plate of the tactile device. Adhesive tape was used to ensure the fixation of the hand and to prevent unintentional hand movements during the experiment. Thus, the position of the index finger was kept constant during all the experimental conditions. Participants were instructed to move the arm of the force feedback device by pushing it with the thenar eminence in order to keep the finger free of force throughout the experiment. The distal phalanx of the left index finger is not supported by the device's cover plate. To ensure full skin stretch and to prevent that the pin slides over the finger tip, the metal pin which mediated the skin stretch was glued with a minimal amount of cyanoacrylate to the tip of the index finger. Sight of the index finger was prevented by cardboard blinds. The lateral surfaces of the tactile device were covered with cardboard to prevent sight of the device's mechanics.

White noise presented via headphones effectively masked the noise caused by the mechanics of the kinesthetic and tactile devices. Two IBM-compatible PCs (one for the tactile and one for the kinesthetic device) controlled the stimulus presentation, data collection and pin motion of the tactile device, using custom programmed applications.

The tactile stimulus was a pin stroke generated by the tactile motion device. A single stroke consisted of a tactile motion in the forward and backward direction of one metal pin, starting and ending at a center position of the tactile device. The amplitude of the pin movement was 1 mm in length for each direction with a velocity of 10 mm/s resulting in a stroke presentation time of 200 ms. Stroke directions are characterized by their radial deflection as illustrated in Fig. 2.3.

Three standard orientations were chosen for the tactile strokes, i.e., 0° (towards the finger tip) 45° and 90° . Each standard orientation was paired with a set of 19 comparison strokes ranging from $\pm 90^\circ$ around the standard direction in steps of 10° (Fig. 2.3). An 84%-discrimination threshold was measured for every standard direction using the method of constant stimuli in a two-interval forced-choice paradigm. The discrimination task was performed in three experimental conditions, which were "static", "active" and "passive" (see below). Each of the three experimental conditions comprised twelve repetitions of each standard and its 19 comparison strokes (the order of the intervals in which the pairs of strokes were presented was randomized) resulting in 228 trials per condition. All the trials were presented in three blocks of 228 trials each. Each block lasted about 20 minutes. Between each

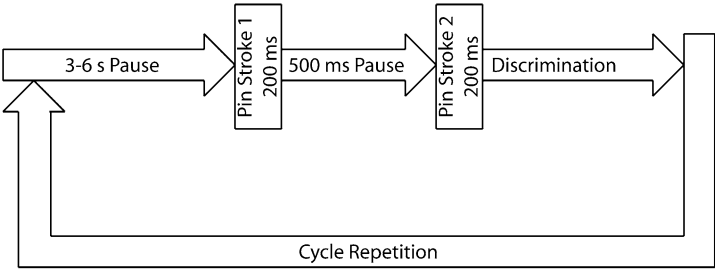


Fig. 2.4 Schematic flow chart of a trial in the “static” condition

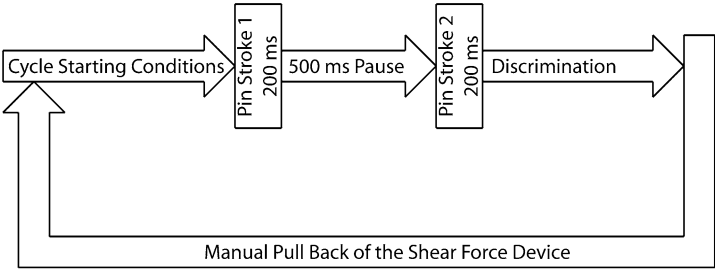


Fig. 2.5 Schematic flow chart of a trial in the “active” condition

block there was a 5 minute break. So collecting data for one condition lasted a bit more than an hour per subject. All three conditions were tested for all subjects on different days. The order of conditions (i.e., static, passive, active) was randomized.

To investigate the effect of active arm movement on the perception of moving tactile stimuli, three arm movement conditions were introduced under which the tactile task was performed.

“Static” condition (Fig. 2.4): In this condition participants kept their arms in a rest position during tactile stimulation. A trial started by switching a rotary switch of the input device. After a delay between three and six seconds the sequential presentation of both pin-strokes (200 ms per pin-stroke) started. Both pin-strokes were separated by a 500 ms pause. Participants indicated whether the second stroke was shifted clockwise or counterclockwise with respect to the first stroke by switching the rotary switch of the input device, after which the next trial started automatically.

“Active” condition (Fig. 2.5): In the “active” condition participants performed an active arm movement. During the arm movement they received the tactile stimulation. From a resting position, which was adjacent to the subject, the setup had to be pushed forward within a velocity range of 0.2 and 0.3 m/s. This velocity had to be achieved within 10 cm from the starting position to trigger the pin movement. A velocity which was faster or slower than specified resulted in no tactile stimulus and the trial had to be redone. After entering their judgment using a custom made response box participants had to pull the arm of the force feedback device back to the starting position and the next trial was initiated.

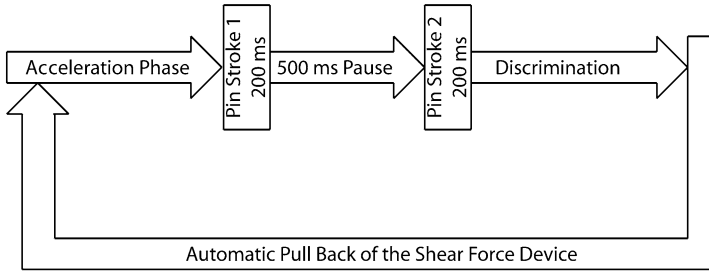


Fig. 2.6 Schematic flow chart of a trial in the “passive” condition

“Passive” condition (Fig. 2.6): The procedure in the “passive” condition was very similar to the “active” condition since the mechanical arm movements were identical. In the “passive” condition, however, the kinesthetic device applied a force resulting in a forward movement which drags the participant’s arm along a trajectory. The force was increasing with the distance from the starting position to ensure a smooth acceleration. The goal was to achieve a velocity of 0.3 m/s within 8 cm from the starting position. The tactile strokes were executed after accelerating subject’s arm to a velocity of 0.3 m/s and after covering the first 8 and 19 cm of the arm movement resulting in the same stroke output duration as in the other conditions. If subjects did not reach this velocity criterion within the given limits no stroke was elicited. This, however, never happened indicating that subjects did not actively slow down the robotic arm which means that there was no force applied by the user.

The participant’s task was to discriminate the motion direction of two successively presented strokes on the finger pad. More precisely, they were instructed to report whether the second stroke was deviated clockwise or counterclockwise relative to the first stroke.

2.2.2 Results

The left panel of Fig. 2.7 depicts the mean thresholds of the three experimental conditions and the three standard directions. For a statistical analysis individual thresholds were entered into a 3×3 ANOVA with the factors “condition” (static, passive, active), and “direction” (0° , 45° , 90°). The main factor of “condition” was significant ($F(df, df) = 16.9$, $p < 0.001$). A subsequent t-test showed that there is a significant difference between the “static” and “passive” ($t(df) = -5.0$, $p < 0.001$) and between the “active” and “static” ($t(df) = 5.6$, $p < 0.001$) condition. The anisotropy for direction in any of the three conditions did not reach significance. That is, performance is equally worse within a given arm movement condition (active, passive, static), independent of whether the stroke direction is inline with the direction of arm movement or not. The right panel of Fig. 2.7 shows the same data collapsed over standard direction. Mean thresholds across subjects (for stroke direc-

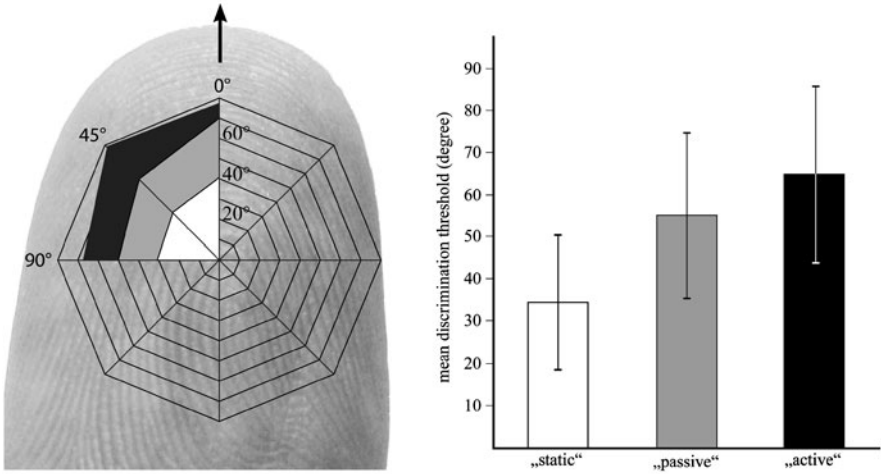


Fig. 2.7 *Left:* 84% discrimination thresholds in the coordinates of the finger tip (projected on the palm of the finger): Thresholds are depicted as a function of stroke direction. 0° corresponds to standard strokes in forward direction, 90° to standard strokes perpendicular to it. Thresholds are averages across participants. The *arrow* indicates the direction of the arm movement. *Right:* Mean across subject’s discrimination thresholds and standard directions of each experimental condition. Error bars depict standard deviations of mean across subjects

tion) are 34.7° in the “static” condition, 55.6° in the “passive” condition and 65.4° in the “active” condition.

2.2.3 Discussion

The aim of this experiment was to investigate changes of tactile discrimination performance during arm movements. Our main finding is that tactile discrimination performance changes significantly due to active arm movement. This is in contrast to previous studies where discrimination thresholds were tested for electrical stimulation [24], vibrotactile stimulation [25] or tactile pattern discrimination [29]. In these studies, indications for an increase of discrimination thresholds were reported but they did not reach significance.

Our results show that arm movements have a considerable effect on tactile perception on the finger. Discrimination performance is best when the arm is unmoved and becomes worst when the arm is moved actively. An intermediate performance level is reached in the “passive” condition. Statistically, the discrimination performance in the “passive” condition does not differ from those in the “active” and “static” condition. This intermediate performance during “passive” motion is most likely caused by consciously or unconsciously moving the arm in order to follow the actively stirred robotic arm. An active arm movement, however, implies the presence

of a motor command which causes a tactile suppression. Analyzing the velocity profile of passive movements shows that the specified velocity is always achieved. This suggests that the proportion of the unwanted active arm movement component and hence the motor command is relatively low which leads to a smaller suppression of tactile sensitivity. Even if participants were distinctively instructed not to act in favor of the robotic movements, one can hardly prevent participants from doing so.

Analyzing the discrimination thresholds with respect to the standard directions of stimulus motion shows no perceptual anisotropy at the fingertip. Drewing et al. [31] utilized the same tactile motion device as it is used in the actual study. They also discovered no significant perceptual anisotropy at the finger tip. Thus, the fact that the same device was used in both studies and no perceptual anisotropies were found strongly indicates that the discrimination performance at the finger tip is equal, independent of the arm movement and the stimulus direction.

In addition to answering the main question, namely, that active arm movement can increase the discrimination thresholds it is possible to make further suggestions regarding the origin of tactile suppression. The results show that the increase of the discrimination threshold is independent of the relative motion direction between the tactile stimulus and the arm. This supports the hypothesis that tactile suppression is the result of a gating effect, caused by a motor command, rather than the reafference principle. For the validation of the reafference principle it would have been expected to find a correlation of discrimination threshold change and arm movement direction. To get further evidence in favor of a gating mechanism to be responsible for tactile suppression, we need to show that tactile suppression depends on a collocation of tactile and kinesthetic information. From the actual results it is not possible to claim the involvement of a motor command in tactile suppression. The observed changes in the discrimination threshold could also be caused by the different workloads in the different arm movement conditions. In the “static” condition, participants had to perform the tactile task alone whereas in the active condition they also were instructed to move their arm within a specified velocity range. This can be seen as an additional task which may lead to a reduced performance in the tactile task during tactile arm movements. This issue will be investigated in Experiment 2 where the tactile task and the arm movement were performed contralaterally.

2.3 Experiment 2: Bilateral Control

Arm movements have been shown to affect the discrimination threshold. The results of Experiment 1 suggest an active arm motion (i.e., the involvement of muscle contraction) to be responsible for this decrease in tactile sensitivity. To strengthen this hypothesis, the possibility that an increased workload, associated with the arm movement, is responsible for the observed increase in discrimination threshold has to be excluded.

Two hypotheses will be tested in this experiment:

- (1) The increase of the discrimination threshold in Experiment 1 may be due to a higher workload and participants are facing difficulties in a simultaneous conduction of both tasks (arm movement and tactile discrimination). If this were the case than by splitting the tasks between the different body sides should produce the same result as in Experiment 1. If anything this dual tasking should increase the workload and exaggerate the differences between the conditions.
- (2) If, on the other hand, the observed discrimination threshold in Experiment 1 is caused by the motor command responsible for the arm movement, then the thresholds in all arm movement conditions should be the same, because the tactile task is now essentially independent from the motor task.

Here, all experimental conditions were identical to those in Experiment 1 except that the arm movement and tactile discrimination are separated to contralateral sides. The tactile task still has to be performed with the left index finger, while the right arm was moved.

2.3.1 Methods

Six right-handed, participants (three female) participated for pay. All of them were naïve to the purpose of the experiment. Their age ranged from 22 to 33 years (average 26 years). None of them reported previous injuries or impairment of tactile sensitivity of the finger tip.

Tactile discrimination performance was investigated by conducting the entire set of movement conditions (“active”, “passive” and “still”—as described in Experiment 1) using the same kinesthetic and tactile display as in the previous experiment.

2.3.2 Results

The right panel of Fig. 2.8 shows the results for direction discrimination performance for the three arm movement conditions. Mean thresholds (for stroke direction) were 29.3° in the “static” condition, 35.9° in the “passive” condition and 35.1° in the “active” condition (Fig. 2.8). The mean discrimination thresholds were not statistically significantly different across the arm movement conditions.

The left panel of Fig. 2.8 depicts the mean thresholds of the three experimental conditions and the three standard directions. For statistical analysis individual thresholds were entered into a 3×3 ANOVA with the factors condition (“static”, “passive”, “active”), and Direction (0° , 45° , 90°). The main factor of condition was not significant ($F = 2.4$, $p = 0.158$). As in Experiment 1, there is no perceptual anisotropy for direction in any of the three conditions. That is, performance is equally worse with arm movement, independent of whether the stroke direction is in line with the direction of the arm movement or not.

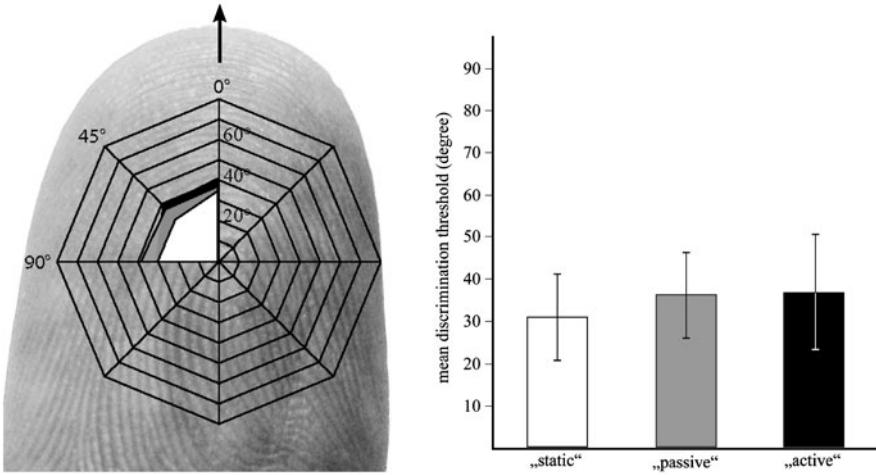


Fig. 2.8 *Left:* 84% discrimination thresholds in the coordinates of the finger tip (projected on the palm of the finger): Thresholds are depicted as a function of stroke direction. 0° corresponds to standard strokes in forward direction, 90° to standard strokes perpendicular to it. Thresholds are averages across participants. *Right:* Mean discrimination thresholds of each experimental condition averaged across standard direction. Error bars depict standard deviations across subjects and conditions

2.3.3 Discussion

This control experiment was conducted to provide further support of the results in Experiment 1, namely, that tactile suppression is mainly caused by a neural gating effect. The origin is supposed to be a motor command which is blocking the transition of tactile information from the peripheral neural system to the central neural system.

The results show that the tactile discrimination threshold at the finger tip does not depend on the direction of the tactile stimulus motion. In addition, discrimination thresholds do not show significant perceptual anisotropies with respect to the arm movement conditions. The mean discrimination thresholds across standard directions reveal that the discrimination performance is equally worse in all arm movement conditions. Here, the mean thresholds (ranging from 29.3° to 35.9°) are at the same level as the mean discrimination threshold of the “static” condition in Experiment 1 (34.7°). This strongly indicates that no tactile suppression occurred in the present experiment.

These results show that active arm movements do not induce tactile suppression per se. By comparing the results of the current and the previous experiments one factor can be identified that is supposed to be necessary to induce tactile suppression; this is the collocation of tactile and kinesthetic input. Only if both types of information are applied to the same body region, a significant drop in tactile sensitivity occurs. A displacement of the motor command to the contralateral side, as it is

shown in the current experiment, results in the same discrimination threshold levels in either movement conditions.

In contrast to the previous experiment, the arm where the tactile stimulus was presented did not move. This means that there might have been a higher signal to noise ratio due to less neural firings during muscle and skin stretch, and there was no motor command which activates muscle contraction. Both are claimed to reduce tactile sensitivity [23, 32] by interfering with the tactile information and by inducing a gating effect, respectively. To identify which of those has a major effect on tactile sensitivity a follow up experiment has to be conducted where the time course of tactile suppression is investigated. The time course of both parameters, spontaneous firing rate and motor command, may show different characteristics. Sensory noise is mainly generated during the arm movement by muscle and skin stretch and, thus, tactile sensitivity should occur from the beginning of an arm movement. On the other hand, a motor command induced gating effect is supposed to occur before the arm movement since the motor command blocks neural pathways during its decent in order to activate the muscle and, thus, generates a block of afferent tactile information.

2.4 Experiment 3: Time Course of Tactile Suppression

In Experiment 1 and 2 it was shown that active arm movements decrease tactile discrimination performance. Furthermore, it was demonstrated that by splitting the tactile and kinesthetic task, discrimination thresholds in all arm movement conditions were essentially the same, suggesting a major impact of a motor command on the discrimination performance. However, to identify whether sensory noise or a motor command is generating tactile suppression, the time course of tactile suppression will be studied. In other studies, gating is reported to occur 60 ms to 100 ms before movement onset whereas others found gating only after movement onset [33–37]. Williams et al. [28] found a decrease in detection performance of weak electrical stimuli applied to a moving finger prior to its abduction which is reported to become significant at 120 ms before the movement onset.

Time courses have never been investigated with mechanical tactile stimuli. Here, a discrimination of pin position in combination with arm movements is investigated. By presenting the tactile stimuli before or during the arm movement it is expected to find changes in the discrimination threshold with respect to the presentation time. Two hypotheses will be examined:

- (1) If a motor command is mainly involved in generating tactile suppression, then the gating effect will occur before the actual arm movement, because the motor command will be sent prior to the muscle contraction, resulting in a neural blockade of afferent tactile information. Thus, tactile suppression will be established before the motor command activates the muscle.
- (2) If sensory noise is mainly responsible for tactile suppression, then a drop in tactile sensitivity will occur after the onset of an arm movement, because prior to the arm movement no additional sensory noise is expected.

2.4.1 Methods

Eight right-handed, participants (five male, three female) participated for pay. All of them were naïve to the purpose of the experiment. Their age ranged from 23 to 32 years (average 26 years). None of them reported previous injuries or impairment of tactile sensitivity of the finger tip.

In contrast to the previous experiments in this chapter, a different tactile display is used. The VirTouch Mouse (VTM) is a commercially available computer mouse containing three Braille modules (each consisting of a 4×8 pin matrix display) that extend plastic pins (diameter of 0.5 mm) normal to the skin surface. The range of pin movement is 1 mm, divided into 16 incremental steps. Figure 2.9 shows the VirTouch Mouse. Utilizing the VirTouch Mouse was necessary due to the need for a temporally short stimulus presentation to investigate the time course. A stimulus presentation consisted of an up and down movement of one pin (overall duration of 60 ms). In Experiment 1 and 2 the presentation of the tactile stimuli in a 2-interval forced-choice (2IFC) paradigm took 900 ms. In order to detect tactile sensitivity changes in a close temporal proximity to the onset of arm movements, this seems to be an inadequate method. Instead, a 1IFC paradigm is used where only one stimulus is presented per trial. This allows for sensitivity measurements in the temporal proximity of the arm movement onset.

The pin extension is regulated by bending piezo actuators. The interface, electrical drivers and the power supply, are integrated. To use the full functionality of the VirTouch Mouse as a tactile display, the development of a custom made device driver software was necessary. This device driver was realized as a RTLinux real time module under special privacy conditions from VTS (Virtual Touch Systems) regarding the transmission protocol of the serial link. In contrast to the previous experiments the VTM was mounted on a kinesthetic robot arm (DeKIFeD 4) in order to move and track participant's arm in space (for details see [38]). This kinesthetic device was built of the same electric motors and gears, resulting in similar kinematic properties as the kinesthetic device (ViSHaRD 10) earlier in this chapter. The free moving space of the kinesthetic device was restricted to one degree of freedom (1 DOF).

In this experiment, the “static”, “active” and “passive” movement conditions are used. In the “active” condition participants had to perform an active arm movement during the pin discrimination task. After a brief tone, which was presented in a temporal window of three to six seconds after the trial start, participants pushed the setup, with a velocity of at least 0.2 m/s. As in the previous experiments, the “passive” arm movement condition was similar to the “active” condition. The crucial difference was that the kinesthetic device was producing a force in a forward or backward direction in order to move participant's arm along these directions. The “static” condition served as a baseline measurement, where no arm movement was required.

Participants were sitting on a bar stool in front of the kinesthetic/tactile setup. Their right hand was placed on the VirTouch Mouse and the distal phalanx of the left



Fig. 2.9 *Left:* Kinesthetic device (DeKIFeD 4) in combination with the tactile device (VirTouch Mouse). *Right:* Close-up view of the VirTouch Mouse containing three Braille modules and proportions of the Braille module. Distances are in millimeters

index finger was placed on the Braille module of the VirTouch Mouse. Two IBM-compatible PCs (one for the tactile and one for the kinesthetic device) controlled the stimulus presentation, data collection and the movement of the VirTouch Mouse in space, using custom programmed applications.

In the present experiment a discrimination task had to be performed where participants had to discriminate two spatially separated pins. The pins were adjacent and had a spatial distance of 1 mm (Fig. 2.9). Either the left or the right pin was lifted during each trial and participant's task was to name whether it was the left or the right one. Thus, the task is criterion free and a direct measure of sensitivity. The order of pin presentation and pin extension was randomized. Seven stimulus intensities were presented ranging from 5 to 11 on a scale of 12 possible steps (12 steps = 1 mm). The same custom made input device as described in the previous experiments was used to enter the responses. In the "active" and the "passive" arm movement condition, tactile stimulation was randomly presented in a temporal range of 200 ms before and 200 ms after the onset of the arm movement in steps of 1 ms. For the analysis the data was pooled in bins of 50 ms. The arm movement was performed for approximately one second.

2.4.2 Results

Figure 2.10 shows the mean proportion of correct answers across subjects. Answers were pooled in 50 ms bins. The dashed grey box depicts the time of the arm movement. The baseline performance of the current tactile discrimination task, which was measured in the "static" condition, was 82% of correct answers (Fig. 2.10, dotted

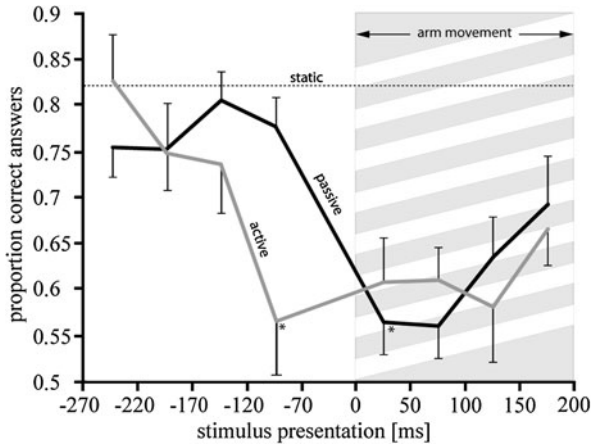


Fig. 2.10 Mean proportion of correct answers of tactile discrimination task in a “static” (*dashed line*), “active” (*grey line*) and “passive” (*black line*) condition. Stimulus presentation times are relative to the onset of arm movement (0 ms). The *dashed grey box* covers the time of the arm movement. Error bars depict standard errors. For demonstrational purposes only half error bars are displayed

line). Two main differences of the discrimination performance in the “active” and “passive” movement can be identified: First, the discrimination performance in the “active” condition (grey line) is continuously decreasing, beginning from the earliest stimulus presentation time (83% correct in the first bin). The lowest discrimination performance (57%) is observed in the time bin of 120 ms to 70 ms prior to the movement onset ($F(df, df) = 13.3, p < 0.01$). A subsequent t-test indicates a significant drop below the baseline from the time 120 ms to 70 ms prior to the arm movement ($t(df) = -4.3, p = 0.004$). After the movement onset, performance remains at a low level and even increases slightly, without reaching significance. Secondly, the “passive” condition (black line) shows a decrease in discrimination performance from a plateau (ranging from 75% to 81% correct answers), whereby the percentage of correct responses are not significantly different across the bins. The biggest drop (57% correct answers) can be observed in the time from the movement onset to 50 ms after movement onset ($F = 10.1, p = 0.016$). In this time bin the first significant drop occurs below the baseline ($t = -7.5, p < 0.001$). Subsequently, discrimination performance rises again but was not significantly different from the lowest performance level.

The proportion of correct answers reaches a maximum of 0.81 of the “passive” condition. A significant drop occurs in the time 0 ms/50 ms which corresponds to the onset of the passive arm movement. Here, the proportion of correct answers drops to a mean of 0.57. Tactile sensitivity represented by the proportion of correct answers increases after 100 ms but did not reach significance. By contrast, in the “active” condition, the proportion of correct answers drops significantly from an initial proportion of 0.83 to 0.57, occurring at a time of 70 ms to 120 ms prior to the

arm movement. Also in this movement condition, tactile sensitivity rises after the arm movement has begun. Again, this rise does not reach significance.

2.4.3 Discussion

The goal of this experiment was to identify whether the decrease in tactile discrimination threshold can be addressed to a motor command that is generated during active arm movements or due to sensory noise caused by receptor activation by muscle and skin stretch during arm movement. Comparing the time course of tactile discrimination performance in the “active” and “passive” arm movement condition shows major differences: In the “passive” condition, a statistically significant drop in performance occurred from the beginning of the arm movement indicating that mainly sensory noise was interfering with the tactile target signal. A lower signal-to-noise ratio leads to a poorer discrimination performance. It may be speculated that a motor command interferes with the tactile information after the onset of arm movement. This will be further investigated in Experiment 4.

In the “active” arm movement condition, the strongest decrease in tactile discrimination performance appears in a time range between 70 ms to 120 ms prior to the arm movement. This speaks for a motor command to induce tactile gating and thereby establish a blockade at the neural border of the peripheral nervous system (PNS) and central nervous system (CNS). Such a blockade is supposed to decrease the amount of tactile information which is transmitted to the somatosensory cortex. Consequently tactile sensitivity is being decreased. Our results are in line with a neurophysiological study in awake monkeys by Seki et al. [23], who found that presynaptic inhibition is the result of descending motor commands, typically 400 ms before movement onset.

One observation in Fig. 2.10 provides an opportunity for speculation. In both arm movement conditions, the “active” and the “passive”, a recovery of tactile discrimination performance occurs, starting between 50 ms and 150 ms after the onset of the arm movement. The performance increase may be explained by the end of the acceleration phase of the arm movement. A lower arm acceleration results in lower forces required from the arm and thus, a weaker motor command is involved.

In Experiment 1, tactile stimuli were presented about 300 ms after the onset of the arm movement, depending on the arm movement velocity. Nevertheless, a strong increase of tactile discrimination threshold can be observed. However, according to the results in Experiment 3, tactile sensitivity should be almost recovered by that time. Since the observed recovery of tactile discrimination did not show a statistically significant difference from the lowest performance near the onset of the arm movement this could be an artifact. Furthermore, a recovery of tactile sensitivity was never reported in other studies [28, 33–37, 39, 40].

In summary the results suggest that in the “active” arm movement condition a descending motor command causes a drop in tactile discrimination performance. In the “passive” arm movement condition a drop in tactile discrimination threshold

can be observed only after the start of the arm movement. This drop may have two origins. First, sensory noise is originating in the muscles and the skin. Secondly, participants could support the forward movement of the kinesthetic device by actively moving their arms without taking notice. To distinguish between the two and pinpoint the origin of the drop in sensitivity we used electromyography (EMG) in a final experiment.

2.5 Experiment 4: Time Course of Muscle Contraction

It has been shown that active arm movements lead to a decrease in tactile sensitivity and that motor commands may play a major role in this. A decrease in tactile sensitivity during passive arm movement, which occurs after the onset of the movement, has to be further investigated to identify whether it originates from sensory noise or from unconscious muscle contraction. Here, an electromyographic (EMG) measurement is conducted to determine the timing of muscle activity and compare it to the drop in tactile sensitivity. The aim is to investigate whether the muscle activity precedes or follows the onset of the arm movement. Thus, two hypotheses will be investigated:

- (1) A motor command which precedes the arm movement supports its suppressing effect on tactile performance.
- (2) If the motor command does not proceed then it is unlikely that a motor command modulates tactile sensitivity and sensory noise.

2.5.1 Methods

Four right-handed, participants (three male) volunteered. All of them were naïve to the purpose of the experiment. Their age ranged from 25 to 38 years (average 30 years).

Subjects were sitting in front of the same setup as described in Experiment 3. They had to perform only the kinesthetic task. 40 trials were performed, half of them in the “active” arm movement condition and half of them in the “passive” arm movement condition. In the “active” condition subjects had to move the arm forward after a visual go signal had occurred. In the “passive” condition participants’ arm was moved by the kinesthetic device.

EMG activity of the right *Musculus triceps brachii* (for two participants) or the right *Musculus deltoideus* (for the remaining two participants) was measured using surface electrodes of 10 mm in diameter (Fig. 2.11). Different subjects showed different muscle activities (*M. triceps brachii* vs. *M. deltoideus*). This could be due to differences in participant’s posture which made it necessary to activate either muscle to move the arm forward. One pair of electrodes (12 cm center-to-center inter-electrodes distance) was placed centrally with respect to the muscles after cleaning

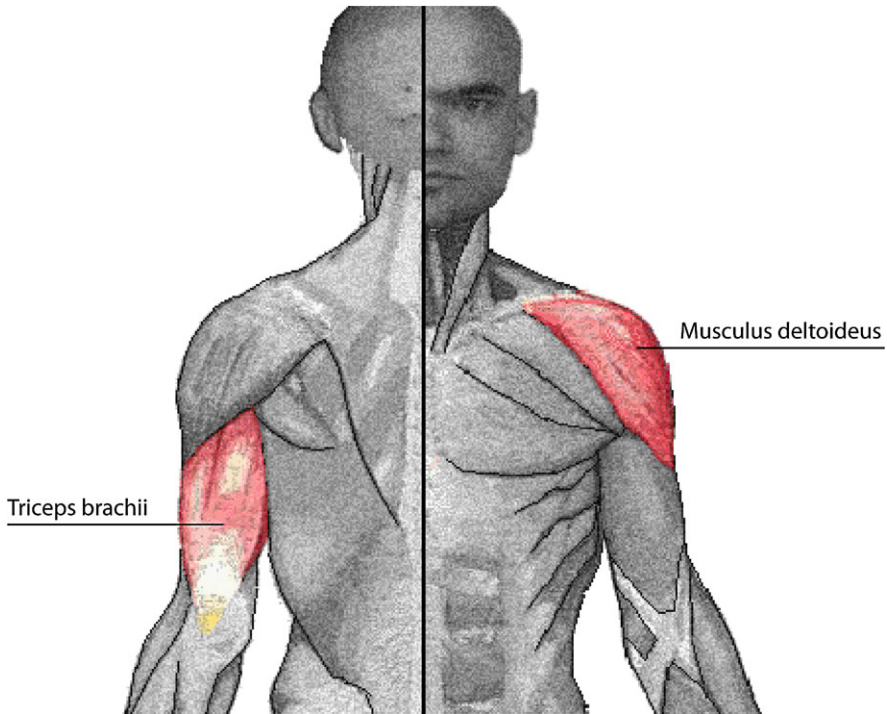


Fig. 2.11 Schematic diagram of muscles which electromyographic activity was measured. (Picture based on <http://upload.wikimedia.org/wikipedia/commons/9/93/Deltoideus.png> by Nikai, available under a Creative Commons Attribution-ShareAlike license)

the skin with alcohol, along a line parallel to the muscle fiber orientation. A ground electrode was attached to the subject's right upper arm. These electrodes were connected to an amplifier and afterwards via an AD-converter to a PC. The signal was band pass filtered from 3 Hz to 400 Hz by the amplifier.

A custom made MATLAB program (The MathWorks, Natick, Massachusetts, USA) was used to sample the potentials with a sample rate of 5 kHz in a time range of 300 ms before until 1000 ms after a trigger indicating muscle activity.

EMG data was pre-processed for each subject and each experimental condition (active and passive movement) separately. The AC component of the signal was rectified and then smoothed over 25 ms using the moving average. The baseline for thresholding was calculated for each trial independently: the data between the time point at which the velocity reached 1 cm/s and the trigger of the muscle activity was taken and the threshold for the trial was set to the mean of these data plus three standard deviations. The first time point at which the curve stayed over the threshold for at least 24 ms was taken as onset time of the response latency. Figure 2.12 shows a typical course of muscle activation in the "active" and "passive" condition. Muscle activation occurs 145 ms before the onset of arm movements in the active condition whereas in the passive condition it occurs 3 ms before (Fig. 2.13).

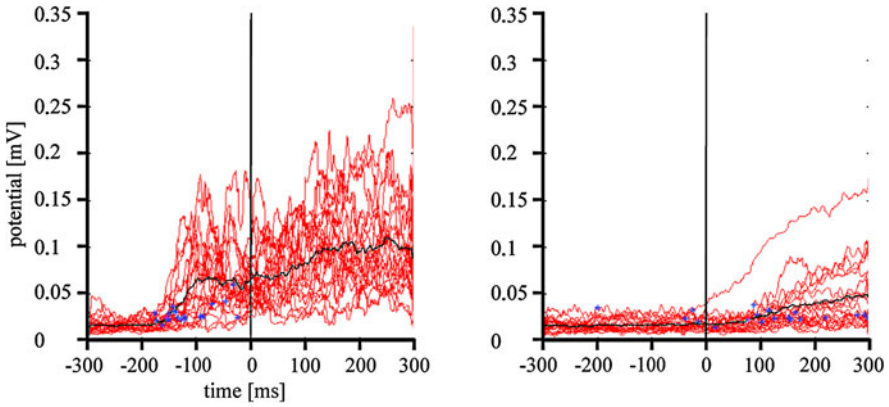
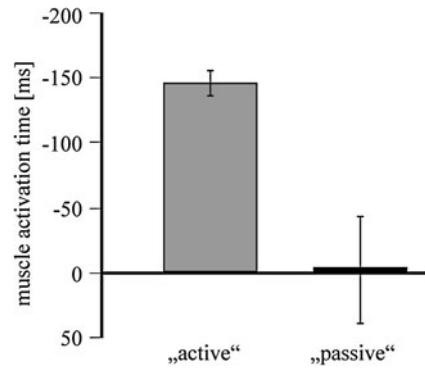


Fig. 2.12 An example of EMG recordings from the Triceps brachii of one subject for active (*left*) and passive (*right*) condition. *Light curves (red)* depict muscle activities of each trial. *Black curve* depicts the average activity potential across 20 trials. *Stars (blue)* depict the first supra-threshold activities. *Vertical black line* marks the onset of the arm movement

Fig. 2.13 EMG data depicts the average time of muscle activation onset across 4 subjects. Negative values on the y-axis indicate muscle activation before onset of arm movement. Error bars are standard errors



2.5.2 Results

2.5.3 Discussion

This experiment was conducted to define the origin of tactile suppression in the “passive” arm movement condition after the onset of arm movement. The results show that in the “active” condition there is steady muscle activation well before the onset of the actual arm movement. The mean activation time for both groups is 145 ms prior to the arm movement. In the “passive” condition, on the other hand, no muscle activity occurred prior to the arm movement. These results indicate that the decrease in tactile sensitivity in the “passive” condition after onset of an arm movement derives from sensory noise, since no muscle activation could be detected.

2.6 Conclusion

Tactile suppression is a phenomenon which describes a dampening of tactile sensitivity during active body movements. Today, the underlying mechanisms and the perceptual effects are still not satisfyingly understood. In this study it is shown that active arm movements clearly modulate tactile perception. An actively performed arm movement elicits a statistically significant drop in tactile discrimination performance compared to holding the arm still. Passive movements also lead to tactile performance decrease but to a lesser extent. Taken together, the results suggest an involvement of a descending motor command that is present during active arm movements but not in mere passive movement. Further proof for the involvement of a motor command in tactile suppression is given by a control experiment where tactile and kinesthetic task was split up to different body sides. No significant difference between the arm movement conditions was observed. Additionally, the investigation of the time course of tactile suppression shows that two major differences occur between the active and the passive arm movement condition. First, the discrimination threshold increases in the passive condition only as of the onset of the arm movement, suggesting that the sensory noise of the arm movement per se leads to the observed decrease in tactile sensitivity. Secondly, in the active condition an increase in tactile discrimination threshold is already measurable prior to the movement, which speaks for the involvement of a descending motor command that then causes a neural blockade that reduces tactile information transfer to the CNS.

Interpreting the results of this chapter supports the hypothesis of a descending motor command that blocks the neural afferent pathway and thereby limits the tactile information available to the CNS. Our results are in line with the results of [23] who found evidence for presynaptic inhibition via neurophysiologic experiments, which suppresses cutaneous input to the spinal cord during voluntary movements in primates. The two major sources of this inhibition are thought to come from descending central commands and peripheral inputs from afferent fibers, that is, sensory feedback from other cutaneous areas, muscle spindle and tendon organ afferents [41–44].

Suppression of tactile sensation may play an important functional role, namely filtering out task irrelevant tactile information during self-movement. Blakemore [17] claim that self-produced (actively) tactile stimuli are perceived less intensely than tactile stimuli that are generated by an unpredictable source, which agrees with our results. In other words one can say that tactile stimuli are less salient when they are accompanied by an active limb movement as when they are applied without self-movement. Blakemore, however, proposes predictions of the sensory consequences of self-induced movements to be compared to the actual sensory inputs. Subsequently, predictable sensory consequences will be cancelled out and only the differential signal of the prediction and the afferent signal will be processed.

The results of Blakemore suggest the involvement of the reafference principle in tactile suppression. Moreover, velocity, intensity and motion direction of tactile stimuli have to be predicted in order to explain Blakemore's results. The reafference principle, however, does not seem to have a major impact in our study, because the

discrimination threshold on the finger tip is equally worse with respect of the standard direction of the stimulus motion. Here, stimulus motion which is orthogonal to the arm movements should be accentuated since during a forward arm movement only stimulus motions along the same axis should be expected. Hence, a perceptual anisotropy for the discrimination threshold would be expected to occur. But this did not happen, the reduction in sensitivity turned out to be not selective for the direction of stimulation. This difference between the two studies (Blakemore's and mine) may be explained by differences in the setup, the task and the experimental paradigm. That is, Blakemore used self- and externally generated tactile stimuli while the stimulated hand was unmoved. In our experiment the stimulus was always externally generated while the arm was moved actively, passively or was kept still.

We argue that tactile suppression during active exploration of, for example surfaces, is not desirable since (relevant) tactile features would be blurred out. However, tactile suppression may reduce uninformative tactile information from task irrelevant skin stretch and muscle contraction. Filtering out these task irrelevant information can help to optimize the signal to noise ratio and, thus, to highlight tactile features of an actively explored object.

Experiment 2 was conducted to control whether tactile suppression could be explained by an increased workload during arm movement compared to the "static" condition. By separating the tactile and motor tasks between the left and right hand, respectively, we were able to corroborate the results in Experiment 1. The results rule out an explanation in terms of changes in workload since the workload was similar to that in Experiment 1. The results show only a small but non-significant increase of the discrimination threshold in the "passive" and "active" condition compared to the "static" condition. A modest decrease in tactile sensitivity by splitting the tactile and motor task is also reported by [28] and supports our finding even if the decrease does not reach significance.

Experiment 3 provides insight in the time course of tactile suppression and identifies the main components of tactile suppression. Both the active and passive movement conditions show a significant decrease of tactile sensitivity around the time of the arm movement onset (Fig. 2.10). The main difference between these movement conditions is the beginning of the sensitivity drop. In the "active" condition the sensitivity drops 70 to 120 ms prior to the arm movement. In the "passive" condition, on the other hand, it does not start until the onset of the actual arm movement. The timing of this gating effect varies between studies. It was reported to occur 60 to 100 ms before movement onset [33, 34] whereas others found gating only after movement onset [35–37]. In agreement with our results Williams et al. [28] found a decrease in detection performance of weak electrical stimuli applied to a moving finger prior to its abduction which is reported to become significant at 120 ms before the movement onset.

The inconsistencies between the various studies can be partly explained by differences in the setup and protocol design, including such factors as the type of stimulus that was used, whether near-threshold or supra-threshold stimuli were applied, whether magnitude estimation or detection tasks were conducted, and whether limb movement was purposeful or spontaneous. Seki et al. [23] gained evidence that tac-

tile afferent input to spinal cord interneurons is blocked during active wrist movement in awake monkeys. They claim that a presynaptic inhibition is effectively produced by descending motor commands. Their findings are congruent with our results showing that a descending motor command, which is present only in the “active” condition, is supposed to be responsible for a significant drop in tactile discrimination performance prior to the movement onset (Fig. 2.10).

It is remarkable that tactile sensitivity seems to recover some time after the onset of the arm movement. The increase is evident in both arm movement conditions although it does not reach significance and assumptions about the origin are speculative. According to Williams et al.’s [39] model of detection threshold over time, tactile sensitivity is supposed to decrease after the movement onset. Recovering is not supposed to happen. The rate at which sensitivity is expected to decrease depends on the intensity of the tactile stimulus. The higher the intensity of tactile stimulation is, the longer it takes to lower the sensitivity. However, interpreting the observed sensitivity increase, one can speculate on the behavioral relevance. During tactile exploration, for example, one intuitively assumes that tactile sensitivity is supposed to be as high as possible in order to detect as many tactile features as possible. Tactile suppression, however, antagonizes an exploration task by gating out tactile stimuli with low intensities. Presumably, re-sensitizing occurs after the movement onset, that is, after the transition from rest to movement, which might be relevant for masking unwanted sensory signals but provide a lower discrimination threshold during movement. However, the results of Experiment 1 do not support this speculation. There, tactile stimuli were applied 300 ms after the onset of arm movements and a high level of tactile suppression was measured. According to the time course of Experiment 3, an almost full recovery of tactile sensitivity would be expected by then. This contradiction speaks for a random effect which is observed in the time course in Experiment 3.

Furthermore, the drop in tactile sensitivity after the onset of an arm movement can be attributed to sensory noise masking the tactile target stimulus. This assumption is supported by previous studies [42–44] claiming that tactile performance becomes worse *during* movement because of sensory feedback evoked by skin and muscle deformation. Thus, peripheral sensory feedback increases which creates a drop of tactile sensitivity.

The final control experiment allowed for the observation that EMG activity precedes the arm movement by the same time as a drop in tactile discrimination performance was observed to drop. Previous studies have shown that a suppression of afferent information during active movement precedes EMG onset, providing a hint for the dominant role of descending motor commands in generating presynaptic inhibition of afferent input [23]. Unfortunately, the participation of different subjects in our experiments did not allow us to correlate the time of EMG onset and the drop in discrimination performance.

In conclusion, the results strongly suggest the involvement of motor commands, generated during voluntary movements, in tactile suppression. This main conclusion is supported by the fact that voluntary movements on different limbs do not affect the tactile discrimination performance. Thus, this is the first evidence that active

movement does not only affect the detection threshold but also the discrimination threshold. Another finding that supports the involvement of a motor command in tactile suppression is that tactile sensitivity decreases before the arm movement and that the electromyographic signal was detected before the muscle contraction. This indicates the presence of the motor command prior to the muscle activity which is known to induce a gating effect of the afferent pathway leading to reduced tactile information in the CNS and, thus, to a poorer representation of tactile stimuli and to poorer discrimination abilities.

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References

1. Kastner, S., De Weerd, P., Desimone, R., Ungerleider, L.G.: Mechanisms of directed attention in the human extrastriate cortex as revealed by functional mri. *Science* **282**(5386), 108–111 (1998)
2. Burr, D.C., Holt, J., Johnstone, J.R., Ross, J.: Selective depression of motion sensitivity during saccades. *J. Physiol.* **333**, 1–15 (1982)
3. Burr, D.C., Morrone, M.C., Ross, J.: Selective suppression of the magnocellular visual pathway during saccadic eye movements. *Nature* **371**(6497), 511–513 (1994)
4. Richards, W.A.: Saccadic suppression. *J. Opt. Soc. Am.* **59**, 617–623 (1969)
5. Helmholtz, H.: *Handbuch der physiologischen Optik*. Voss, Leipzig (1867)
6. von Holst, E., Mittelstaedt, H.: Das Reafferenzprinzip. *Naturwissenschaften* **20**, 464–475 (1950)
7. Ilg, U.J., Hoffmann, K.P.: Motion perception during saccades. *Vis. Res.* **33**(2), 211–220 (1993)
8. Matin, E.: Saccadic suppression: a review and an analysis. *Psychol. Bull.* **81**(12), 899–917 (1974)
9. Sperry, R.W.: Neural basis of the spontaneous optokinetic response produced by visual inversion. *J. Comp. Physiol. Psychol.* **43**(6), 482–489 (1950)
10. Holt, E.: Eye movement and central anesthesia. *Harv. Psychol. Stud.* **1**, 3–45 (1903)
11. Mackay, D.M.: Elevation of visual threshold by displacement of retinal image. *Nature* **225**(5227), 90–92 (1970)
12. Burr, D.C., Morgan, M.J., Morrone, M.C.: Saccadic suppression precedes visual motion analysis. *Curr. Biol.* **9**(20), 1207–1209 (1999)
13. Bridgeman, B., Hendry, D., Stark, L.: Failure to detect displacement of the visual world during saccadic eye movements. *Vis. Res.* **15**(6), 719–722 (1975)
14. Shioiri, S., Cavanagh, P.: Saccadic suppression of low-level motion. *Vis. Res.* **29**(8), 915–928 (1989)
15. Diamond, M.R., Ross, J., Morrone, M.C.: Extraretinal control of saccadic suppression. *J. Neurosci.* **20**(9), 3449–3455 (2000)
16. Blakemore, S.J., Frith, C.D., Wolpert, D.M.: Spatio-temporal prediction modulates the perception of self-produced stimuli. *J. Cogn. Neurosci.* **11**(5), 551–559 (1999)
17. Blakemore, S.J., Goodbody, S.J., Wolpert, D.M.: Predicting the consequences of our own actions: the role of sensorimotor context estimation. *J. Neurosci.* **18**(18), 7511–7518 (1998)

18. Blakemore, S.J., Wolpert, D., Frith, C.: Why can't you tickle yourself? *NeuroReport* **11**(11), 11–16 (2000)
19. Blakemore, S.J., Wolpert, D.M., Frith, C.D.: Central cancellation of self-produced tickle sensation. *Nat. Neurosci.* **1**(7), 635–640 (1998)
20. Blakemore, S.J., Wolpert, D.M., Frith, C.D.: The cerebellum contributes to somatosensory cortical activity during self-produced tactile stimulation. *NeuroImage* **10**(4), 448–459 (1999)
21. Rushton, D.N., Rothwell, J.C., Craggs, M.D.: Gating of somatosensory evoked potentials during different kinds of movement in man. *Brain* **104**(3), 465–491 (1981)
22. Chapman, C.E., Beauchamp, E.: Differential controls over tactile detection in humans by motor commands and peripheral reafference. *J. Neurophysiol.* **96**(3), 1664–1675 (2006)
23. Seki, K., Perlmutter, S.I., Fetz, E.E.: Sensory input to primate spinal cord is presynaptically inhibited during voluntary movement. *Nat. Neurosci.* **6**(12), 1309–1316 (2003)
24. Chapman, C.E., Bushnell, M.C., Miron, D., Duncan, G.H., Lund, J.P.: Sensory perception during movement in man. *Exp. Brain Res.* **68**(3), 516–524 (1987)
25. Post, L.J., Zompa, I.C., Chapman, C.E.: Perception of vibrotactile stimuli during motor activity in human subjects. *Exp. Brain Res.* **100**(1), 107–120 (1994)
26. Schmidt, R.F., Schady, W.J., Torebjork, H.E.: Gating of tactile input from the hand. I. Effects of finger movement. *Exp. Brain Res.* **79**(1), 97–102 (1990)
27. Schmidt, R.F., Torebjork, H.E., Schady, W.J.: Gating of tactile input from the hand. II. Effects of remote movements and anaesthesia. *Exp. Brain Res.* **79**(1), 103–108 (1990)
28. Williams, S.R., Shenasa, J., Chapman, C.E.: Time course and magnitude of movement-related gating of tactile detection in humans. I. Importance of stimulus location. *J. Neurophysiol.* **79**(2), 947–963 (1998)
29. Lamb, G.D.: Tactile discrimination of textured surfaces: psychophysical performance measurements in humans. *J. Physiol.* **338**, 551–565 (1983)
30. Ueberle, M., Mock, N., Buss, M.: Vishard10, a novel hyper-redundant haptic interface. In: 12th International Symposium on Haptic Interfaces for Virtual Environment and Teleoperator Systems (HAPTICS'04) (2004)
31. Drewing, K., Fritschi, M., Zopf, R., Ernst, M.O., Buss, M.: Tactile display exerting shear force via lateral displacement. *ACM Trans. Appl. Percept.* **2**(2), 118–131 (2005)
32. Faisal, A.A., Selen, L.P., Wolpert, D.M.: Noise in the nervous system. *Nat. Rev., Neurosci.* **9**, 292–303 (2008)
33. Chapman, C.E., Jiang, W., Lamarre, Y.: Modulation of lemniscal input during conditioned arm movements in the monkey. *Exp. Brain Res.* **72**(2), 316–334 (1988)
34. Cohen, L.G., Starr, A.: Localization, timing and specificity of gating of somatosensory evoked potentials during active movement in man. *Brain* **110**(Pt 2), 451–467 (1987)
35. Dyhre-Poulsen, P.: Perception of tactile stimuli before ballistic and during the following manner tracking movements. In: Gordon, G. (ed.) *Active Touch*, pp. 171–176. Pergamon, Oxford (1978)
36. Ghez, C., Pisa, M.: Inhibition of afferent transmission in cuneate nucleus during voluntary movement in the cat. *Brain Res.* **40**(1), 145–155 (1972)
37. Jiang, W., Lamarre, Y., Chapman, C.E.: Modulation of cutaneous cortical evoked potentials during isometric and isotonic contractions in the monkey. *Brain Res.* **536**(1–2), 69–78 (1990)
38. Kron, A., Schmidt, G.: Haptic telepresent control technology applied to disposal of explosive ordnances: Principles and experimental results. In: *Proceedings of the IEEE International Symposium on Industrial Electronics (ISIE)*, pp. 1505–1510 (2005)
39. Williams, S.R., Chapman, C.E.: Time course and magnitude of movement-related gating of tactile detection in humans. II. Effects of stimulus intensity. *J. Neurophysiol.* **84**(2), 863–875 (2000)
40. Williams, S.R., Chapman, C.E.: Time course and magnitude of movement-related gating of tactile detection in humans. III. Effect of motor tasks. *J. Neurophysiol.* **88**(4), 1968–1979 (2002)
41. Eccles, J.C., Schmidt, R.F., Willis, W.D.: Depolarization of the central terminals of cutaneous afferent fibers. *J. Neurophysiol.* **26**(4), 646–661 (1963)

42. Janig, W., Schmidt, R.F., Zimmermann, M.: Two specific feedback pathways to the central afferent terminals of phasic and tonic mechanoreceptors. *Exp. Brain Res.* **6**(2), 116–129 (1968)
43. Jankowska, E., Slawinska, U., Hammar, I.: Differential presynaptic inhibition of actions of group II afferents in di- and polysynaptic pathways to feline motoneurons. *J. Physiol.* **542**(Pt 1), 287–299 (2002)
44. Rudomin, P., Schmidt, R.F.: Presynaptic inhibition in the vertebrate spinal cord revisited. *Exp. Brain Res.* **129**(1), 1–37 (1999)



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