Moving & Feeling

The modulation of tactile perception during goal-directed movements:

Evidence from reaching, grasping, catching, & throwing

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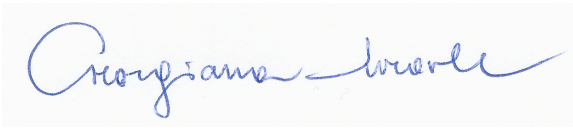
Trinity Term, 2012

To my parents, George and Elena

Declaration

The work contained in this thesis is entirely my own and has not been submitted, in part or in whole, in connection with another degree.

Signature



Georgiana Juravle

Date

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Publications and presentations

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Short abstract

This thesis focuses on tactile perception and aims at a comprehensive analysis of its characteristics over the time-course of various goal-directed movements. Tactile perception is assessed by means of discrimination and detection paradigms, as well as event-related potentials (ERPs). The main question investigated throughout the thesis is: '*What changes in tactile perception, if any, take place over the time course of a goal-directed movement?*' In **Chapter 2,** the mechanisms related to such identified changes are examined: a facilitatory one – *attention*, and an inhibitory one – *suppression*. The experiment in **Chapter 3** tests, at a brain level, amongst several explanations of the experimental results outlined in **Chapter 2**: timing-based, effector-based, and modality-based attentional/suppressive influences. In **Chapter 4,** other naturalistic movements are investigated (i.e., the movements involved in juggling and throwing/catching a basketball).

The results indicate a lack of facilitation in the processing of tactile information during the preparatory phase of the movement. Furthermore, differential changes are identified in tactile perception over the execution phase of the movement: At a behavioural level, tactile sensitivity significantly declines over the execution phase of the movement (though the detection of incoming tactile stimulation is enhanced), while at a neuronal level the same period exhibits significantly enhanced responses to somatosensory stimulation.

The experiments reported here thus bring evidence in favour of a dissociation between detecting and discriminating what is felt while moving. These results suggest that the quality of what is felt while moving may not be important for movement and, at the same time, that different pathways in the brain may be responsible for detecting

and discriminating what is felt over the time course of a goal-directed movement. Based on these findings, in **Chapter 5**, the implications of these results are discussed and directions for further research are outlined.

Long abstract

The importance of perception for the execution of a goal-directed action, as well as of action for the processing of perceptual inputs arriving at our sensory receptors has been intensely considered (e.g., see James, 1890; Jeannerod, 1994; Prinz, 1997; Sperry, 1952; see also Spence, 2011). This thesis is centered on the investigation of the modulation of tactile perception over the time course of goal-directed movements.

Chapter 1 provides an overview of research on tactile perception in a resting state of the body and upper limbs, together with modulations of tactile perception during the preparation and execution stages of a goal-directed movement. Two theories are highlighted with respect to what happens to tactile perception over the time-course of a goal-directed movement. The first one, known as the *premotor theory of attention*, states that shortly before initiating an eye-movement toward an object of interest, our visual spatial attention will first be deployed at the goal location (i.e., during the preparatory phase of the action), so that our perception, and consequently our action, can be facilitated (Rizzolatti, Riggio, & Sheliga, 1994). While the motor preparatory period is characterized by an enhancement in what it is felt, the period in-between – the motor execution period – brings with it a temporary decline in our perceptual prowess. This phenomenon is well-known in the visual domain: Almost two centuries ago, von Helmholtz (1867) identified saccadic suppression as the 'blind' period occurring while we move our eyes. The reafference principle (von Holst & Mittelstaedt, 1950) and corollary discharge (Sperry, 1950) have both been put forward to explain saccadic suppression and the significance of the phenomenon was attributed to the need to maintain a stable representation of the world while we move our eyes

(see Ross, Morrone, Goldberg, & Burr, 2001, for a review). Tactile suppression has often been compared to saccadic suppression. This decrease in tactile sensitivity, also known as tactile attenuation, or tactile gating, appears shortly before and during movement execution, with a peak decrease in tactile sensitivity at the moment of contact with the goal surface (Bays, Wolpert, & Flanagan, 2005). While the tactile attenuation occurring before movement has been attributed to the motor command (i.e., to the efference copy), the suppression occurring during movement execution is commonly attributed to a combination of the motor command and the sensory signals resulting from the self-generated movements themselves (Chapman & Beauchamp, 2006). In this context, the second theoretical approach identified in **Chapter 1** (i.e., *forward models of motor control*, Wolpert, Ghahramani, & Jordan, 1995) posits that the sensory information which can be taken as a consequence of the motor command (i.e., tactile information) will most likely be attenuated, such that the salience of external information can be enhanced (Bays & Wolpert, 2007).

The scope of this thesis was to investigate such attentional/suppressive influences predicted to affect tactile perception with respect to: the timing of stimulation delivery (preparation, execution, or post-movement phase), the location on the body (moving vs. resting effector), the nature (modality-based vs. supramodal), and the type of movement (reaching for an object vs. exploring a surface, as well as self- vs. externally-initiated movements).

In **Chapter 2**, participants performed reach-to-grasp movements for objects placed frontally in peripersonal space. Tactile perceptual performace was evaluated by means of discrimination (**Experiments 2.1-2.5** and **2.7-2.8**) and detection paradigms (**Experiment 2.6**) at various points in time during the movement: preparation, execution, and post-movement. The results of **Experiments 2.1** and **2.2** indicated that

tactile sensitivity was lowest (i.e., perceptual performance was poorest) over the execution phase of the movement. In a second step, the results of **Experiment 2.3** highlighted that attentional facilitation does not affect what is felt during the preparation and post-movement phases of the tested movement; The data suggest that these periods could instead be characterized by a natural non-disturbed state of tactile perception. **Experiment 2.4** further strengthened the decline in tactile sensitivity over the execution period of the movement and demonstrated that this decline was not due to an attentional capture effect from the moving hand. Since the attentional effects were expected particularly over the motor preparation period, **Experiments 2.5-2.7** further investigated attentional influences on tactile perception over this time period. Their results highlighted that the mere preparation to move does not result in a shift of spatial attention to the moving effector (i.e., tactile sensitivity in the preparatory phase of the movement was comparable to that of the execution phase in **Experiment 2.5**). Nevertheless, the results of **Experiment 2.6** indicated that endogenously directing attention to either the moving or resting effector of a reach-to-grasp movement resulted in faster reaction times (RTs) to tactile events presented there. Interestingly, the results of **Experiment 2.6** also highlighted that RTs decreased from the preparation phase to the execution, and then post-movement phase of the movement. **Experiment 2.7** excluded an inhibitory attentional influence (i.e., inhibition of return (IOR), Klein, 2000; Spence et al., 2000a) thought to reflect the poorer tactile sensitivity found in the preparatory phase of the movement in **Experiments 2.5-2.6**. Lastly, **Experiment 2.8** provided an insight into the relevance of goal-directed movements for what is felt, by comparing tactile performance in the reach-to-grasp movements utilized in **Experiments 2.1-2.7**, to the performance of tactile exploratory

movements. If tactile sensitivity declined over the execution phase of the former, tactile sensitivity was significantly enhanced for the same phase of the latter.

With these behavioural results in mind, in **Chapter 3** the modulations of tactile perception during reach-to-grasp movements were investigated by using the electrophysiological method of event-related potentials (ERPs). Participants performed goal-directed reaches for an object placed centrally on the table in front of them. In separate trials, somatosensory ERPs, as well as visual ERPs, were recorded in response to sensory stimulation delivered to participants moving/resting effectors, over the preparation, execution, or post-movement phases. In a control condition, the participants only performed the movement while this time omission (movement-only) ERPs were recorded. The results highlighted an overall attentional effect, as evidenced by enhanced ERPs negativities. The attentional influences were greatest over the execution phase of the goal-directed movement, they were effector-based (i.e., significantly higher at the moving hand) and supramodal (i.e., attention similarly affected the two tested modalities of touch and vision).

Lastly, the experiments reported in **Chapter 4** investigated tactile perception modulations in more naturalistic movements, such as the specific ball catching/throwing movements used in juggling (**Experiments 4.1-4.3**) and basketball (**Experiments 4.4-4.8**), by making use of signal detection theory measures (e.g., sensitivity and response bias, **Experiments 4.1-4.3**, and **4.8**), as well as RTs (**Experiments 4.4-4.7**).

In **Experiments 4.1-4.3**, tactile performance was assessed in a sustained juggling movement task, and at rest. The results indicated that tactile suppression most likely is the combination of the juggle movement itself, and the sensory feedback of the juggling balls touching the hands while juggling (**Experiments 4.1** and **4.3**).

Crucially, the decline in tactile sensitivity found in the juggling session of **Experiment 4.1** was accompanied by a significant conservative shift in participants' response bias. Such a result indicates a decisional component to tactile suppression and suggests that suppression could already be triggered in the brain ahead of the motor command. Lastly, another control experiment (**Experiment 4.2**) demonstrated that auditory sensitivity does not decline over the execution phase of the movement. The results of **Experiments 4.1-4.3** thus point toward a modality-based suppressive influence on tactile perception during movement.

The remaining experiments reported in **Chapter 4** investigated tactile perception during the execution of externally-generated movements (**Experiments 4.4-4.6**, and **4.8**), as well as self-initiated movements (**Experiments 4.7-4.8**). In a similar manner to the RT data reported in **Chapter 2**, **Experiments 4.4-4.7** highlighted faster RTs over the execution phase of ball-catching movements for both tactile (**Experiment 4.4**) and auditory events (**Experiment 4.5**), together with slower RTs for the preparatory phase of the movement. A control experiment (**Experiment 4.6**) demonstrated that the slowing of RTs over the preparatory phase of the ball-catching movement was not due to a dual-task effect, whereby movement acted as a distraction on the concomitant perceptual task. Moreover, **Experiment 4.7** further demonstrated that the preparatory phase of a ball-throwing movement exhibits the same slowing of tactile RTs, similarly to the ball-catching movements. Lastly, **Experiment 4.8** highlighted that the attenuation found to affect tactile perception during the preparatory phase of the movement has a genuinely perceptual cause for self-initiated movements, but only a decisional one for the reactive externally-generated movements.

Chapter 5 provides a general discussion of the experimental findings presented in this thesis. This last chapter puts forward the claim that the two mechanisms of attention and suppression tested throughout this thesis work *in parallel* over the execution phase of a goal-directed movement. Attention could be taken to account for detecting and promptly responding to the incoming sensory novelty, whereas suppression could be contributing to the filtering of those characteristics belonging to the novel stimulus that are not relevant for the current task. The preparatory phase of the movement does not receive attentional facilitatory influences. Instead, a truly perceptual decrement takes place in the preparatory phase of a self-initiated movement (i.e., reach-to-grasp movement, ball-throwing movement), but only a decisional decrement in the case of externally-generated movements. These results suggest that the cognitive system is readily responding to incoming stimulation while moving. However, the type of such stimulation (or its quality) is not relevant during this phase of the movement. Nevertheless, exploratory movements indicate that tactile perception is highly relevant for movement, when tactile feeling is the result of the active movement. Lastly, **Chapter 5** provides a discussion on the implications of these results and indicates directions for further movement-related research in the tactile domain.

List of abbreviations

The abbreviations used throughout the thesis are presented in the following, split into general abbreviations and abbreviations of (measurement) units.

General abbreviations:

Ag - silver

ANOVA – analysis of variance

BCI – brain computer interface

CBF – cerebral blood flow

Cl - chloride

CMA – cingulate motor area

CNS – central nervous system

CNV – contingent negative variation

dlPFC – dorso-lateral prefrontal cortex

DW – difference wave

EEG – electroencephalography

EMG – electromyography

EPSP – excitatory postsynaptic potential

ERP – event related potential

FA – fast adapting

FP – false positive

IOR – inhibition of return

IPSP – inhibitory postsynaptic potential

LED – light emitting diode

LH – left hand

LRP – lateralized readiness potential

M – mean

MI – primary motor cortex

PRP – psychological refractory period

PSC – postsynaptic current

PSE – point of subjective equality

PSP – postsynaptic potential

RF – receptive field

RH – right hand

RT – reaction time

SA – slow adapting

SD – surface discrimination

SDT – signal detection theory

SE – standard error

SI – primary somatosensory cortex

SII – second somatosensory cortex

SMA – supplementary motor area

SOA – stimulus onset asynchrony

TD – tactile discrimination

TMS – transcranial magnetic stimulation

TP – true positive

VET – visual enhancement of touch

VPL – ventral posterior lateral

VPM – ventral posterior medial

Units:

cm – centimeter

dB - decibels

EUR – euro

g - gram

Hz – Hertz

kΩ – kiloOhms

μV – microVolts

mm – millimeter

ms – millisecond

s – second

3D – three-dimensional

Chapter 1

The effect of goal-directed movements on tactile perception

1.0. Introduction

Perception reveals its importance to everyday life by means of goal-directed actions. As the name implies, goal-directed actions provide the means to achieve what we want from the surrounding environment. Although goal-directed actions/tasks include a broad spectrum of activities (e.g., everything from mental arithmetic to motor imagery, to name just a few; see Mele, 2000, for a commentary on teleological explanations of goal-directed action), this thesis is focused strictly on goal-directed *movements* of the upper limbs. As such, goal-directed movements are intrinsic to everyday life and most often involve the use of our upper limbs in order to manipulate objects, or the movement of our eyes, when searching for objects. (Even though not the focus of this thesis, it should, of course, be remembered that our lower limbs also perform a wide spectrum of actions, e.g., kicking balls when playing sports). In the context of human volition, goal-directed actions have been separated into several temporal phases, such as: identifying the reasons for performing an action, selecting the task and the specific action to be performed together with a final predictive check before the execution of the action takes place; in the last step, the effects of our action on the surrounding environment can be evaluated (see Haggard, 2008).

Such goal-directed movements of the upper limbs are performed in the space around our body, i.e., *in peripersonal space*. Peripersonal space has been defined as the space surrounding our body delimited by the distance in which we can reach for, grasp, and manipulate objects (Grüsser, 1982; Previc, 1998). Peripersonal space makes

use of two major motor systems: the first controls the movements of the hand(s), or arm(s), when reaching or grasping for objects and the second programs and controls the eye movements that complement such movements. Peripersonal space typically extends to a distance of approximately one metre from the body (depending on arm length), it is biased toward the lower visual field and the major sensory systems utilized within its realm are vision and touch (Previc, 1998). Evidence from primate studies point toward there being a body-centered coordinate system (Fogassi & Gallese, 2004; Rizzolatti et al., 1997). For example, neurons in the premotor cortex (F4) have – besides motor properties – spatially congruent receptive fields (RFs) for different modalities, pointing toward a common coding of space for motor and sensory functions. Studies of both healthy humans (Kitagawa & Spence, 2006), and of right-hemisphere brain-damaged patients (Làdavas, 2002) have provided evidence for crossmodal integration in the space surrounding our body (see Spence & Driver, 2004). Furthermore, crossmodal integration in peripersonal space has been obtained experimentally by means of tools or mirrors (Maravita, Spence, Sergent, & Driver, 2002; Maravita, Spence, Kennett, & Driver, 2002; see also Maravita, Spence, & Driver, 2003 as well as Spence, 2011, for a recent review). Moreover, extensive practice with certain tools (e.g., as in the case of blind persons, sportsmen, or lion tamers) leads to an enlargement of peripersonal space (e.g., Bassolino, Serino, Ubaldi, & Làdavas, 2010; Serino, Bassolino, Farnè, & Làdavas, 2007).

Furthermore, the 3D space surrounding our body also includes the more distant extrapersonal (focal, action and ambient) spaces, split according to their function, location, primary coordinate systems, and their characteristic sensory and motor systems (Previc, 1998; see Figure 1.1 for a depiction of the various spatial layers of the region surrounding our body). It has been argued that the main functions of the

extrapersonal focal and action spaces are visual search, face and object recognition, as well as navigation, scene memory and visual target orientation. Therefore, they extend more than two metres and are biased toward the upper visual field. The sensory systems utilized most are vision and audition, while the major motor systems are the oculomotor system (responsible for saccadic eye-movements) and the head-neck motor system (responsible for head movements).

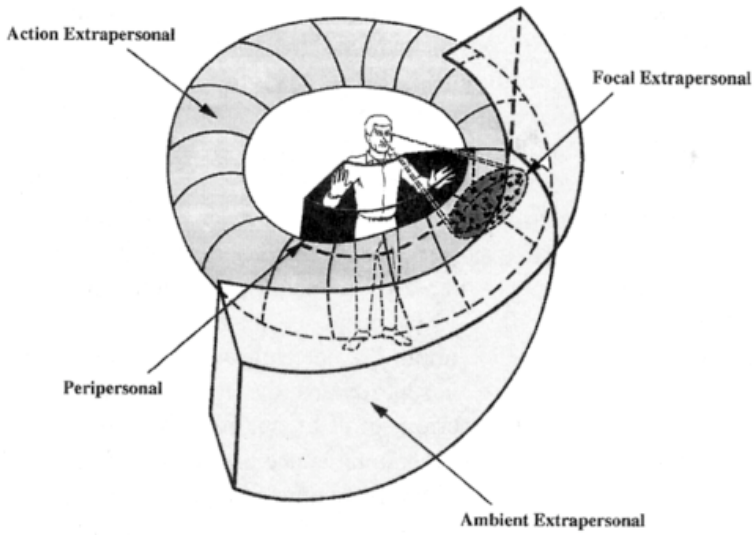


Figure 1.1. Schematic drawing illustrating the various realms of the space surrounding our body. Note that the space of interest to the purpose of this thesis (i.e., peripersonal space) is depicted in black. Figure taken from Previc, 1998.

In this thesis, goal-directed movements will refer to actions of our hands (i.e., reaching for, grasping, exploring, or throwing and catching a ball). By definition, they are always directed toward objects located in the space surrounding our body.[1] Since peripersonal space is constructed via the integration of information received from different sensory channels, these goal-directed actions provide an ideal means of testing perceptual functioning, in particular, tactile perception, the focus of this thesis.

With regards to its use, touch hasn't received anything like as much attention as vision (though see for example Field, 2001; Katz, 1925/1989; McGlone & Spence,

[1] Nevertheless, **Chapter 4** makes a parallel between self- and externally-generated actions, and thus differentiates between peripersonal and extrapersonal space in action execution together with the effects of action on the underlying perceptual characteristics.

2010, for comprehensive accounts on touch). Recently though, there has been an upsurge in the number of applications that have started to capitalize on the benefits of stimulating the tactile modality (e.g., touch is the perfect replacement when vision is impaired, as well as an additional excellent input modality for those cases when the eyes (vision) and the ears (audition) are occupied with other routines) in design and other industries, such as marketing or the design of multisensory displays (Gallace, Tan, & Spence, 2007; Spence & Gallace, 2011). As a matter of fact, the skin is our biggest sensory organ (16-18 % of our body mass, see Field, 2001; Montagu, 1971) and impairments in the tactual sense most often result in severe deficits or danger for the human body. For example, due to complete damage to sensory nerves carrying tactile information, as well to those nerves carrying information from the tendons, joints, and muscles below the neck, patient Ian Waterman lost all feeling below his neck, as well as his proprioceptive sense (Cole, 1995).

Indeed, the skin comprises a variety of receptors (and receptor types), distributed over the body, that provide information about what is felt. This is otherwise known as *somatosensation*. The somatic sensibility includes four major modalities: touch, nociception, itch, and the temperature sense (see Carlson, 2009; Kandel, Schwartz, & Jessell, 2000; McGlone & Spence, 2010). Since the experiments reported in the present thesis use vibratory stimulation to investigate what is felt, the focus of this thesis lies within the first of the somatic senses, *discriminative touch*, which is involved in recognizing the size, the shape, the texture of objects, and their movement across our skin.

The skin, the outer covering of our body is responsible for what we feel[2], is formed of three layers: epidermis, dermis, and subcutis. The greatest tactile sensitivity is found on the hairless (glabrous) skin of the fingers, the palms of the hands, the soles of the feet, and the lips (Klatzky & Lederman, 2002; McGlone & Spence, 2010; see also Weinstein, 1968), but also on the genitalia (see Farah, 1998) and inside the oral cavity (i.e., tip of the tongue and the hard palate, Ringel & Ewanowski, 1965; Trulsson & Essick, 1997). At a physiological level, feeling is made possible by means of four types of receptors that mediate the sense of touch. The receptors are usually classified according to the size of their receptive fields (RFs) and their adaptation to sustained stimulation (see Table 1.1).

Receptive field (RF)	*Adaptation response*	
	FAST; no response to sustained stimulation	SLOW; responds to sustained stimulation
Small, well defined	FA I (Meissner corpuscles)	SA I (Merkel's disks)
Large, diffuse	FA II (Pacinian corpuscles)	SA II (Ruffini endings)

Table 1.1. Mechanoreceptors found in the glaborous skin of the human hand; FA=fast adapting; SA=slow adapting. Table adapted from Klatzky & Lederman (2002).

The ability to sense vibration is the result of fine adjusting in receptor thresholds. Humans are most sensitive to vibrations at frequencies of 200-250 Hz; for lower and higher frequencies we need proportionately larger amplitude vibrations (Kandel et al., 2000; see also Verillo, 1963). According to their classification, the slowly adapting mechanoreceptors, such as Merkel's disks and Ruffini endings, are most sensitive to low vibration frequencies (i.e., usually lower than 8-16 Hz,

[2] Though, we feel not only through our skin, the sensory organ that this thesis is concerned with, but also from within our body (i.e., sense termed interoception), by means of the movements of our internal organs. This feeling of our body influences our mood and sense of well-being (Cameron, 2002; see also Craig, 2002, for a review).

Johnsson, 1978; Lundström & Johnsson, 1986). In turn, the fast adapting Meissner's corpuscles are most sensitive to midrange stimulation (i.e., the flutter sensation range of approximately 40 Hz), whereas Pacinian corpuscles are tuned to vibration frequencies above 40 Hz, with their strongest response in the range of 200-300 Hz (Johansson & Valbo, 1983; McGlone et al., 2007; Valbo & Johansson, 1984). Our normal everyday tactile experience typically involves the combined neural activity of all of the mechanoreceptors (Greenspan & Bolanowski, 1996; Johansen-Berg & Lloyd, 2000; see Figure 1.2 for a depiction of the different layers of the skin).

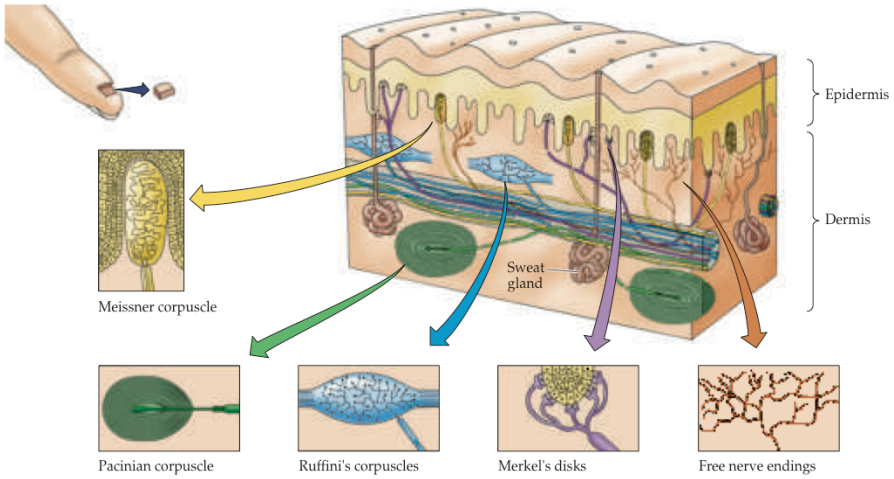


Figure 1.2. Depiction of the different layers of the skin at the human index fingertip with insets of the various mechanoreceptors described in text. Figure taken from Purves et al. (2004).

How do we come to *feel* a tactile sensation on our body? The dorsal column-medial lemniscus pathway controls the transmission of mechanosensory information from our body by means of three neuron relays (Purves et al., 2004). That is, the mechanosensory information first reaches the dorsal root ganglion cells at the level of the vertebral column and then ascends ipsilaterally to the brainstem, where it synapses at the level of the nucleus cuneatus (for tactile information from the upper body regions) and nucleus gracilis (for somatic information from the lower body parts) in the caudal medulla. At this point, it then crosses to the contralateral side and ascends to the ventral posterior lateral (VPL) nucleus of the thalamus, an important region that

relays somatosensory information from the whole body, aside from the face (the somatic information carried by the trigeminal system of the face is relayed by another important thalamic nucleus – the ventral posterior medial one, VPM). VPL further transmits the somatic information to the appropriate region in the primary somatosensory cortex (Kahle & Frotscher, 2002; see also Netter, Craig, & Perkins, 2004, for detailed illustrations).

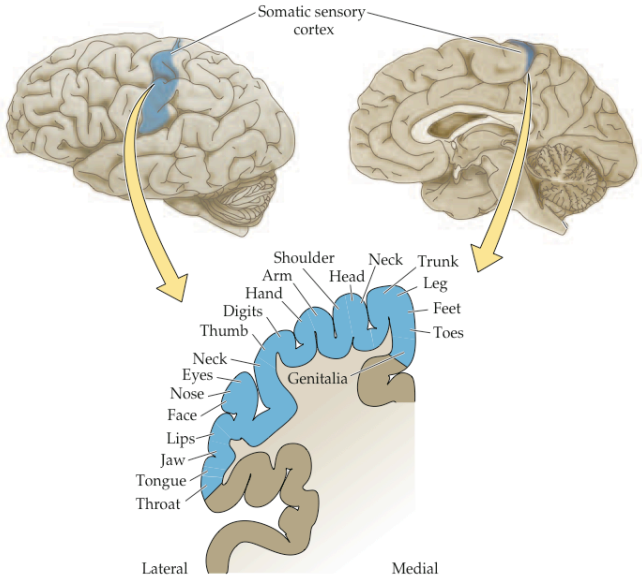


Figure 1.3. The somatotopic organization of tactile information in the brain: The figure depicts lateral views (top panels) of the brain with the somatosensory cortices highlighted in blue. The lower part of the figure illustrates how the different regions of the skin are represented in the brain. Figure taken from Purves et al. (2004).

The primary somatosensory cortex is located in the brain just posterior to the central sulcus and is composed of Brodmann's regions 3a, 3b, 1, and 2, with regions 3b and 1 specialized in processing tactile information, whereas region 3a and 2 process proprioceptive information (Carlson, 2009; Purves et al., 2004). The primary somatosensory cortex has a somatotopic organization, with each of the body regions being represented according to its importance/innervation density, such that the hands, the face, and the lips have an exaggerated representation with respect to their size, as compared to the other regions of the body (i.e., the somatosensory homunculus,

Penfield & Boldrey, 1937; see also Nakamura et al., 1998; and Koch et al., 2010, for recent neuroimaging evidence, and Figure 1.3).

The sensory information that reaches the primary somatosensory cortex is finally projected onto the association cortices, located within the parietal lobe (these are responsible for attention and awareness of our body in space), as well as the frontal lobe (responsible for planning our actions and adapting them to the current changes in stimulation), and is thus ultimately 'translated' into behaviour (Purves et al., 2004).

The working hypothesis underlying this thesis is that temporal changes occur in what is felt over the time-course of a goal-directed movement. Having introduced tactile perception and goal-directed actions in the context of this thesis, here the focus is on the existing evidence on the characteristics of tactile perception, as they unfold in the presence or absence of movement.

1.0.1. Tactile perception in the absence of movement

The classical psychological accounts of tactile perception have typically investigated it in a resting passive state of the body (Katz, 1925/1989), and hence, of the upper limbs, the focus of this thesis. In this respect, *attention* is perhaps the most important psychological construct in cognitive psychology that investigates basic functions, such as sensory processes, or perception.

More than a century ago, William James argued that:

> *Everyone knows what attention is: It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others, and is a condition which has a real opposite in the confused, dazed, scatterbrained state. (William James, 1890, pp. 403-404).*

In this context, selective attention could be defined as a cognitive brain

mechanism that enables us to process relevant inputs, thoughts, or actions and ignore irrelevant or distracting ones (Gazzaniga, Ivry, & Mangun, 2002; Spence, 2011). Attention, and, in particular, spatial attention, calls for a few major distinctions that will be used in this chapter and throughout the remainder of this thesis. These distinctions are based on the sensory receptors (overt vs. covert orienting), or on the particular sensory stimulus, as well as the goals of the participants (exogenous vs. endogenous orienting). To begin with, a first distinction is drawn between overt and covert shifts of attention.

Overt shifts of attention refer to a redirection in the receptors (i.e., the eyes, head, or hand movements) toward a region of interest (i.e., a stimulus in psychological experiments). On the other hand, *covert shifts of attention* typically result from an experimenter's verbal instructions. In such situations, a redirection in the physical receptors is prevented (i.e., the participant is normally required to fixate on a central fixation spot); nevertheless, even though the saccade does not occur, the oculomotor program is still programmed (Rizzolatti et al., 1994). Covert shifts of attention are most often studied by means of the *spatial cuing paradigm* introduced by Posner in the 1970s (Posner, Snyder, & Davidson, 1980; Spence, 2010b; Spence & Driver, 2004). As such, the experimenter usually directs the participant's attention to a certain location before the appearance of the target, by means of a cue. In this respect, trials in which the target appears at the cued location are referred to as valid, whereas the opposite cases, in which the target appears at a different location from the cue, are referred to as invalidly cued trials; the other cases in which all locations are cued are referred to as neutrally-cued trials. Therefore, when manipulating **spatial attention**, one does so by using *valid*, *invalid*, or *neutral cues* (though see Jonides & Mack, 1984, for a discussion on the spatial attention preparatory processes present when

using valid versus neutral cues).

One final important distinction with regard to attention concerns endogenous versus exogenous attention. *Endogenous spatial attention* is an active process of orienting attention and depends on the participant, who is motivated to put effort in order to enhance the clarity of external stimulation. This process is defined in terms of voluntary shifts of attention and has traditionally been studied by means of 'central' or 'cognitive' cues (see Müller & Rabbitt, 1989; Posner et al., 1980). On the other hand, exogenous spatial attention is a passive process of orienting attention and depends on the intrinsic characteristics of the stimulus. This process implies an automatic shift of attention and has been traditionally studied by means of 'peripheral' cues (Müller & Rabbitt, 1989; Posner et al., 1980; Spence & Driver, 2004; see also Gibson & Kingstone, 2006, for a discussion of central, but nevertheless exogenous-like gaze and arrow cues).

Everyday life situations are typically multisensory in nature, meaning that we are confronted with several stimuli at the same time and, in order to pick up the relevant information to control the current behaviour, we need to utilize mechanisms of *selective attention* (see Spence & Driver, 2004). In this respect, one research question aims at investigating whether people can selectively attend to touch. Improvements in tactile performance are therefore studied in such situations, as compared to situations in which participants have to divide their attention between modalities or to attend to a different sensory modality. To this end, tactile attention has been investigated by means of spatial cuing paradigms that involved the discrimination of tactile stimuli preceded by visual cues, but also auditory cues, in both exogenous (Spence, Nicholls, Gillespie, & Driver, 1998), as well as endogenous

attentional manipulations (Spence, Pavani, & Driver, 2000b). The results of such studies have highlighted the faster discrimination of tactile targets presented at the valid spatial location of the cue as compared to other irrelevant locations, thus suggesting a tendency for common shifts of spatial attention for both vision and touch (see Driver & Spence, 2004, for a review).

Similarly, in another study that used tactile cues to direct attention, a genuine exogenous facilitatory effect on tactile attention was found: Participants were overall faster and more accurate at discriminating the tactile targets in the validly cued trials, as compared to the invalidly cued trials (Spence & McGlone, 2001). Studies such as these required covert shifts of attention from participants (i.e., eye movements were not permitted). However, overt, non-informative vision of one's own hand(s) has also been shown to improve both the detection (Tipper et al., 1998) and discrimination (Kennett, Taylor-Clarke, & Haggard, 2001) of tactile targets. Nevertheless, such improvements in what is felt under conditions of overt orienting are present only for spatial tactile tasks (i.e., discrimination between two tactile stimuli delivered to the hand and separated by a certain distance, which allows one to derive a spatial relationship between the two), as well as when tactile discrimination performance is tested well above the perceptual discrimination threshold (see Press, Taylor-Clarke, Kennett, & Haggard, 2004; see also Michael et al., 2012; Mirams, Poliakoff, Brown, & Lloyd, 2010).

To summarize, it has been shown that tactile performance is enhanced in classical behavioural psychological tasks based on spatial attention. An important characteristic of the experiments reported so far is that they have been carried out under conditions of a passive resting state of the body and consequently, of the upper

limbs. In real life, though, we are constantly interacting with the environment and thus most of the time we are in a constant state of movement in order to achieve our goals. The importance of perceptual input for the appropriate execution of a goal-directed action (i.e., perception to action link), as well as conversely, of action preparation and execution for the processing of perceptual inputs (i.e., action to perception link), has been considered intensely over the years (James, 1890; Jeannerod, 1994; Prinz, 1997; see also Spence, 2011). For example, in one of the early works on perception it was clearly underlined that:

> *... perception is basically an implicit preparation to respond. Its function is to prepare the organism for adaptive action. The problem of what occurs in the brain during perception can be attacked more effectively once this principle is recognized (Sperry, 1952, p. 302).*

Convincing evidence for the link from perception to action comes from lesion and inactivation studies. For example, by inactivating the primary somatosensory finger areas of a monkey that had been trained to grasp and lift an object, a deteriorated coordination of the fingers, as well as a disturbance in the prehensile and lifting forces was observed (Brochier, Boudreau, Pare, & Smith, 1999). Results such as these underline the importance of sensory feedback in reach-to grasp movements. In a similar manner, human digital anaesthesia during grasping has revealed the importance of cutaneous information in object manipulation tasks (Augurelle, Smith, Lejeunne, & Thonnard, 2003; Monzée, Lamarre, & Smith, 2003; Nowak et al., 2001). Furthermore, studies of severe sensory loss (e.g., sensory neuropathies, deafferented patients) provide further evidence on the importance of tactile information to our daily actions. Patients with a complete lack of cutaneous sensation exhibit a disturbed control of the grip forces required in manipulating objects (Nowak, Glasauer, & Hermsdörfer, 2003; Thonnard, Detrembleur, & Van den Bergh, 1997), as well as a

deficit in interpreting other people's estimations of weights when lifting objects (Bosbach, Cole, Prinz, & Knoblich, 2005).

On the other hand, the second link (i.e., from action to perception) underlines the need to closely consider perception during movement. In the following, the characteristics of tactile perception during the preparatory phase of goal-directed movements are analysed.

1.0.2. Tactile perception during movement preparation

When we engage in purposeful actions, the visual system is the dominant motor system. An abundance of research has investigated eye-movements and their effect on (visual mostly, but also auditory and tactile) perception. Studies involving the preparation of saccadic eye-movements (e.g., Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995; Rorden & Driver, 1999) clearly show enhanced perceptual performance at the target location or '*facilitation'* prior to eye movements. Along similar lines, facilitation in discriminating visual targets at the goal location has been reported following manual reaching movements (Deubel, Schneider, & Paprotta, 1998), as well as following grasping movements (Schiegg, Deubel, & Schneider, 2003). In the tactile domain, facilitation has been observed when participants have to discriminate tactile stimuli presented at the location of an upcoming saccade (Rorden, Greene, Sasine, & Baylis, 2002). In a dual-task paradigm requiring the preparation and execution of a goal-directed saccade or a simple finger-lifting movement on every trial, Juravle and Deubel (2009) demonstrated that tactile detection was enhanced for stimuli delivered in the preparation period both at the finger toward which the saccade was directed – goal-location, as well as the finger that executed the action – movement effector.

These studies, highlighting a facilitation of participants' behavioral performance in response to tactile stimuli delivered in the motor preparation period, have been complemented by the results of event-related potential (ERP) studies that have revealed enhanced somatosensory ERPs (P90, N140) in response to tactile stimuli presented during the preparation of both eye-movements (Gherri & Eimer, 2008) and finger/arm movements (Eimer, Forster, Van Velzen, & Prabhu, 2005; Forster & Eimer, 2007).

Results such as those presented above are consistent with the premotor theory of spatial attention (Rizzolatti et al., 1994; see also Rizzolatti & Craighero, 2009). This influential theory posits a unified view of spatial attention and sensorimotor processing. As such, according to the theory, the mechanisms responsible for spatial attention are located in pragmatic spatial maps (i.e., cortical maps that perform the transformation of spatial information into movements, or those brain regions that are responsible for sensorimotor integration, see Rizzolatti et al., 1994). *Facilitation* in neurons in the spatial pragmatic maps brings in spatial attention and this facilitation is dependent on the preparation to perform goal-directed movements. Different pragmatic maps become active depending on the current task requirements. The theory therefore claims that the preparation of goal-directed movements and shifts of spatial attention are closely linked, since they are controlled by shared sensorimotor mechanisms (i.e., the same frontal-parietal brain circuits control both motor behaviour and spatial attention)[3]. Thus, this theory underlines the importance of motor planning in the allocation of attention (see Rizzolatti & Craighero, 2009, for a discussion).

[3] In this context, another famous theory that could be of theoretical relevance to the present thesis needs to be mentioned: the two visual systems theory ('vision for action' vs. 'vision for perception', Milner & Goodale, 1995, 2008). This elegant theory has seeded an impressive amount of valuable experimental work; However, its focus lies in visual perception and its implications are broader than the aims of this thesis – tactile perceptual modulations in the context of movement.

1.0.3. Tactile perception during movement execution

Another influential theoretical stand regarding what happens in the perceptual domain in the context of movement is provided by forward models of motor control (see Desmurget & Grafton, 2000; Wolpert, 1997; Wolpert, Diedrichsen, & Flanagan, 2011; Wolpert & Flanagan, 2009, for reviews). These models imply an internal representation of the body and the environmental signals (i.e., a neural forward model, internal to the central nervous system) that is used to predict the sensory consequences of the outgoing motor command (Miall & Wolpert, 1996; Wolpert et al., 1995). As such, the forward model describes the causal link between action and its sensory consequences (Wolpert & Flanagan, 2009), based on the current state of the body and a copy of the motor command (i.e., efference copy).

One main role of internal models in movement control is to regulate performance by comparing, in real time (i.e., optimal feedback control, Todorov, 2004), the predicted sensory states with the actual sensory states. At the same time, forward models are used *to attenuate* movement-irrelevant sensory information or *to enhance* the sensory information that is essential for movement control. A good demonstration of the existence of such a predictive mechanism comes from the fact that a tactile event, such as a tickle, is felt as less ticklish when applied to oneself. However, when a time delay is introduced between the motor command and the felt tickle, the tickle is perceived as being more intense, as compared to the synchronous self-applied tickle (Blakemore, Frith, & Wolpert, 1999; Weiskrantz, Elliott, & Darlington, 1997). It has thus been suggested that by attenuating the sensory signals resulting from the movement, such a predictive mechanism serves to enhance the salience of external events, or those that cannot be predicted from the motor command (Bays & Wolpert, 2007).

A clear demonstration of sensory suppression comes from the work of Voss and colleagues (Voss, Ingram, Haggard, & Wolpert, 2006). They measured the point of subjective equality (PSE) between a pulse delivered to a finger on the left hand which was kept at rest throughout the trial and a second pulse delivered to a finger on the right hand which, depending on the condition, participants had to lift following an auditory cue or else keep still. The results showed that the stimulation of the moving finger had to be 2.69 times stronger in order to be perceived as similar to the stimulus delivered to the finger that was at rest.

In another study, the participants initiated each trial by pressing a force sensor with their right index finger; the left index finger was always kept at rest beneath another force sensor (Bays et al., 2005). At the presentation of the go signal, the participants had to make a speeded (reaching) movement toward a third force sensor placed on top of the left force sensor. Therefore, at the end of the trial, participants actively tapped their left finger with their right finger. At variable time delays before or after the active tap (with a maximum of $\pm$300 ms), they also received a test tap on the right finger and the participants had to rate which of the taps they perceived as being more intense. The results highlighted the existence of sensory suppression, starting in the execution phase of the speeded movement (-300 ms), with a peak *at the contact* with the force sensor (active tap) and ending 100 ms after contact has been made.

By using a controlled paradigm that allowed tactile stimulation delivery relative to muscle activity onset prior to the movement of the index finger, tactile suppression effects were found up to 120 ms prior the onset of the movement and to be localized on the moving limb or adjacent locations to this as compared to more distant body stimulation sites (Williams, Shenasa, & Chapman, 1998). Subsequent

studies have indicated that the intensity of the tactile stimulation does not interfere with either the temporal or spatial pattern of sensory suppression manifested during movement (Williams & Chapman, 2000).

In this context, one important point to note concerning the sensory suppression studies that have been discussed thus far is that such attenuating effects on tactile perception were found in either active or passive movements executed by independent digits of the hand, and not during more complex goal-directed movements, such as, for example, reach-to-grasp movements.

Before presenting experimental evidence related to tactile suppression during goal-directed hand/arm movements, a study that looked at reach-to-grasp movements under conditions of anaesthesia of the tactile receptors on the index finger and thumb will be highlighted first (Gentilucci, Toni, Daprati, & Gangitano, 1997). The participants in this study were instructed to reach and grasp for either a small or large object, following a go signal. (Note that this movement task is very similar to that utilized in **Chapter 2** of this thesis). When no tactile input was available to the fingers of the reaching hand, the control of grasping was affected. More specifically, the finger-opening phase that preshapes the hand for grasping during the reaching movement was significantly delayed, as compared to the normal unanaesthesized condition. These results therefore suggest that we use the tactile input from our hands in order to compute and adjust the temporal parameters of grasping, as well as to extract and rely on proprioceptive feedback during movement.

The evidence regarding the modulation of tactile perception during the execution of goal-directed movements is not as ample as the one found for the preparatory phases of such movements, or it is even offered by studies that have not considered the phenomenon as a potential explanatory factor for the data. For

example, Brozzoli and his colleagues (2009) had their participants reach for, and grasp, targets positioned in different orientations. They delivered vibrotactile stimuli either in the motor preparation period, at the start of the movement, or during the execution phase of the movement. The participants had to indicate the elevation of the tactile target presented at either the index finger (up) or thumb (down), while trying to ignore a simultaneously-presented visual distractor presented at either the same or different elevation on the to-be-grasped target object. The results indicated that, prior to the start of the movement, the interference from the visual distractor was minimal. This finding relates to the previous behavioral studies presented above (see Juravle & Deubel, 2009; Rorden et al., 2002) and argues in favor of enhanced tactile discrimination performance in the motor preparation period, as predicted by the premotor theory of spatial attention (Rizzolatti et al., 1994; Rizzolatti & Craighero, 2009). However, as soon as the movement started (*movement initiation*), interference from the visual distractor impaired participants' discrimination performance significantly. Furthermore, the decline in performance continued over the course of the *execution* period. Brozzoli and his colleagues' (2009) explanation of these findings involved an on-line remapping of peripersonal space as action unfolds over time (the integration of different sensory information at different spatial locations within peripersonal space). Alternatively, however, it may also be that tactile perception was suppressed during the execution of the goal-directed reach-to-grasp action and, in that case, vision 'took advantage', and significantly interfered with participants' tactile discrimination performance. This study is very important in that it *hints* at the suppression of tactile information during the execution of goal-directed *hand and arm* movements. Note that earlier experimental work has demonstrated sensory suppression for simple (not goal-directed) arm flexions (Chapman et al., 1987, see

also **Experiment 2.4** in this thesis for similar results with a goal-directed movement).

Another study focused on the phenomenon of tactile change blindness (see Gallace, Tan, & Spence, 2006) during reaching movements and also more naturalistic movements, such as turning a steering wheel (Gallace, Zeeden, Röder, & Spence, 2010). In Gallace et al.'s Experiment 1, participants wore eight tactors, four on either side of the body, with two tactors attached to the arm and two tactors attached to the leg. On each trial, one display (composed of two tactors on a side and another on the opposite side) was turned on, followed by a go signal and at three different stimulus onset asynchronies (SOAs) of 100, 300, and 600 ms, the second display was activated. Depending on the condition, the participants either had to execute a speeded reaching response toward the left or right side, a vocal response, or else no response. At the end of the trial, participants had to decide whether the second display was the same as the first or not. The results of the motor response condition indicated that participants were significantly less sensitive to detect a change between the two tactile displays when this occurred at the longer SOAs after the go signal. Presumably, 100 ms after the go signal, participants were still preparing their movement, as documented by their high sensitivity; the 300 ms period after the delivery of the go signal could still be motor preparation or already the start of the movement, whereas the 600 ms SOA was definitely movement execution. The authors listed sensory suppression as one of the possible causes of the decrease in sensitivity at the longer SOAs, but, considering the chances of either display activation, it turns out that when the change occurred, it could be located in only 50% of the trials on the movement effector (the right hand). Therefore, the data indeed successfully support secondary-task interference on a tactile change detection task. Nevertheless, as the change in this study could take place both in the moving effector of the action, as well as in the same-side non-moving

limb, it cannot account for a pure suppression explanation. Possibly, if one were to consider suppression as an explanation of Gallace and colleagues' (2010) data, sensory suppression could then be viewed as a 'whole-side-of-the-body suppression', as documented by Williams et al. (1998), with attenuation affecting not only the moving limb, but also, to a lesser extent, the more distal parts of the body which are not involved in the movement.

It is important at this stage to acknowledge earlier studies on sensory suppression in humans. For example, it has been elegantly demonstrated that tactile thresholds measured in a moving limb are increased starting around 200 ms before the execution of simple finger flexion movements (Dyhre-Poulsen, 1975), as well as of ballistic movements, and finger tracking movements (Dyhre-Poulsen, 1978). Such suppressive modulations of what is felt have been conducted in order to explain electrophysiological animal findings of decreased/attenuated evoked potentials in the medial lemniscus over the same movement preparatory period (Coulter, 1974; Ghez & Pisa, 1972). Thus, as an explanation for tactile suppression, it has been suggested that the motor command may generate inhibition in the first relay of the lemniscal pathway and then may potentially generate facilitation in the thalamic relay; At the same time the afferent information may generate inhibition in the transmission of the tactile percept, with the direct result of perceptual masking (Coquery, 1978).

To summarize the motor-execution-related gating studies, tactile suppression has been demonstrated for various active and passive movements of the independent digits of the hand or forearm (Chapman & Beauchamp, 2006; Coquery, 1978; Dyre-Poulsen, 1975, 1978; Voss et al., 2006, 2008; Walsh & Haggard, 2008; Williams & Chapman, 2002; Williams et al., 1998), as well as for goal-directed arm movements (Brozzoli et al., 2009; Gallace et al., 2009; see also Buckingham et al., 2010). While

the tactile attenuation observed before movement onset has been attributed to the motor command (i.e., the efference copy), the suppression occurring during movement execution is commonly attributed to a combination of the motor command and the sensory signals resulting from the self-generated movements themselves (Chapman & Beauchamp, 2006; see also Chapman, 2009).

The aim of the experiments reported in this thesis is to investigate the temporal changes affecting tactile perception over the time-course of *goal-directed hand movements*. Having reviewed the characteristics of tactile perception during the passive, resting state of the upper limbs, as well as during the movement preparation and execution phases, several open questions have surfaced.

1.1. Open questions

As outlined above, a differential pattern of changes in tactile perception was reported in the literature, with enhancement in what is felt by participants during the preparatory phase, and a decrement in tactile sensation over the execution phase of the movement. However, evidence is sparse on goal-directed movements (i.e., the reach-to-grasp movement in the present thesis).

One first open question treated in this thesis relates to the **timing** of tactile stimulation delivery: during the preparation, execution, or post-movement phase of the movement. The first experimental prediction of this thesis is that a differential pattern of tactile sensitivity would be observed over the different temporal phases of goal-directed movements: Tactile sensitivity is expected to be higher during the preparatory and post-movement phases (i.e., both benefiting from the facilitatory effects of tactile, but also visual attention), and it is expected to decline during the execution period of the movement (i.e., as predicted by the forward models of motor control). Beneficial

effects of movement on tactile sensitivity are predicted for the grasping phase, as well as the post-movement phase of the movement.

The second open question relates to the **location** (on the body) where an enhancement or decrement in what is felt is more likely to appear: the moving versus resting effector of a goal-directed reach-to-grasp movement. The two theories outlined above (i.e., the premotor theory of attention and forward models of motor control) predict a differential pattern of sensitivity in the moving upper limb. As such, an attentional-based explanation would posit an enhancement in what is felt for the moving effector, whereas the forward models of motor control would predict a decrement in what is felt for the same effector.

The third open question concerns the **nature** of the attentional versus attenuating mechanisms that evidently affects tactile perception during the various temporal phases of goal-directed movements. As such, this thesis investigates whether enhancement or attenuation in what is felt affects touch and stimuli presented in the other spatial modalities (i.e., audition, vision) in a similar manner.

A final open question relates to the **type of movement** utilized. This thesis aims at investigating whether a similar distribution of attentional versus suppressive influences on tactile perception generalizes to more naturalistic everyday movements (i.e., catching and throwing a ball, as well as tactile exploratory movements).

1.2. Summary and outline of the individual chapters

Chapter 2 addresses the question '*Does tactile sensitivity change during the various phases of a goal-directed movement?*' and aims at identifying and testing possible causes of the mechanisms related to such identified changes (tactile attention vs. suppression). In **Chapter 3**, this question is addressed at a neural level by contrasting

the various explanations of the experimental results outlined in **Chapter 2**. In **Chapter 4**, tactile perception is analyzed during the execution of other naturalistic movements (i.e., the movements involved in juggling and throwing/catching a basketball). Lastly, in **Chapter 5,** a general discussion of the experimental results of this thesis together with their implications and directions for future research is provided.

Chapter 2

Behavioural investigation of tactile perception during goal-directed movement

2.0. Introduction

In **Chapter 1,** evidence was presented regarding the characteristics of tactile perception that are connected to movement, as well as to tactile perception, while the upper limbs are in a passive, resting state. In this respect, previous studies have demonstrated a facilitation in tactile perception in the motor preparation period, as well as sensory suppression starting shortly before movement initiation and continuing until shortly after the termination of the movement. Facilitation has been explained primarily in terms of shifts of (presumably visual) attention (but also combined visual and tactile attention). These shifts of attention are directed to either the goal location of the movement (Deubel & Schneider, 1996; Diederich, Colonius, Brockhorst, & Tabeling, 2003; Gherri & Eimer, 2008; Hoffman & Subramaniam, 1995; Kowler et al., 1995; Rorden et al., 2002; Schiegg et al., 2003), or to the movement effector (Eimer et al., 2005; Forster & Eimer, 2007; Juravle & Deubel, 2009).

Prior to the start of movement, studies of tactile suppression have highlighted efferent or afferent processes of the central nervous system that may be responsible for the existence of such an attenuating effect. According to the first 'tactile sensory suppression' account, when voluntarily preparing to move, feed-forward motor signals influence the activity elicited by the incoming sensory information. Therefore, the sensory suppression that is experienced in advance of the voluntary movement has a

central origin and should arise upstream from the primary motor cortex. Evidence in support of this account has been provided by Voss and colleagues (Voss et al., 2006): Tactile stimulation in a moving finger needs to be more than twice as intense as that presented to a resting finger, in order for the two to be perceived as having a similar intensity. Moreover, this account can also accommodate 'top-down' influences on sensory suppression, such as allowing the motor system to modify the available sensory inputs as a function of expectation (Voss et al., 2008).

The second account of 'tactile sensory suppression', which is more physiologically based, states that sensory suppression arises from the afferent sensation resulting from bodily movements and could backward mask the new sensory stimulus (see Coquery & Amblard, 1973; Chapman et al., 1987); Evidence supporting this latter account comes from the equal sensory suppression that has been observed during both passive and active movements (Chapman & Beauchamp, 2006; Williams & Chapman, 2002). It is currently accepted that the tactile attenuation that occurs during movement execution results from a combination of the motor command and the sensory signals resulting from the self-generated movements themselves (Coquery, 1978; Chapman, 2009; Chapman & Beauchamp, 2006).

Crucially, previous studies of the characteristics of tactile perception used simple flexions of the fingers or forearms, and not purposeful, goal-directed action, such as a reach-to-grasp movement. As such, the importance of the goal-directed movement to the underlying perceptual characteristics may have been overlooked. Indeed, the current view of perception considers it not as a purely passive process, but rather as a dynamic process that is tightly intertwined with action (Engel & Fries,

2010; Engel, Fries, & Singer, 2001; Fries, 2005; Siegel, Engel, & Donner, 2011).

Experiments 2.1-2.3 of this thesis examine the distribution of temporal changes in tactile perception over the time course of a goal-directed movement. The effects of motor preparation on tactile perception may have already been well-documented in the literature, as well as there being some robust evidence regarding the start of the movement and the period before the actual contact with the goal-surface. However, there is a gap in the literature regarding what happens to tactile perception during the execution, grasp, as well as the post-movement phases of a goal-directed movement.

In **Experiment 2.1**, the participants had to prepare and execute a speeded reach-to-grasp movement following a go signal. At the beginning of the trial, a standard vibratory tactile pulse was delivered to the participant's left hand that was kept at rest throughout each block of trials. The participant's right hand received a comparison pulse that could be delivered, depending on the experimental condition, at one of five different points in time: motor preparation, start of the movement, execution, grasp, and post-movement. Participants rated the intensity of the right hand pulse as being either stronger or weaker than that delivered to the left hand.

Given the two theoretical accounts introduced in **Chapter 1** (predicting attentional or suppressive influences on tactile perception at different time points during the execution of a goal-directed movement), the hypothesis was that increased tactile sensitivity (i.e., better performance when comparing the tactile stimuli presented to the two hands) would be observed during the motor preparation period, as compared to an expected decline in performance during the execution of the

movement. Moreover, no difference in tactile sensitivity was expected between the motor preparation and post-movement periods.

2.1. Experiment 2.1: Tactile sensitivity declines during movement execution

2.1.1. Methods

2.1.1.1. Participants

Nineteen participants (9 male, one left-handed) took part in this experiment. The mean age of the participants was 27 years (age range 20-39 years). All of the participants in this experiment (and in all the other experiments reported in this chapter) reported normal touch, as well as normal or corrected to normal vision. The participants gave their informed consent prior to their participation and the experiment was conducted in accordance with the Declaration of Helsinki (2008). The experimental session lasted for approximately 75 minutes and participants received a £10 (British pounds) gift voucher in return for taking part in the study.

2.1.1.2. Apparatus

The participants were seated at a table in a darkened room with illumination provided centrally across the table surface by a single lamp positioned to their upper right side. Two computer mice were affixed to the surface of the table, to the right of the participant, with the mouse closest to the participant (the *start mouse*) positioned at a comfortable distance for the participant to interact with, and the second mouse (the *goal mouse*; see Figure 2.1a) placed 25 cm in front of the start mouse.

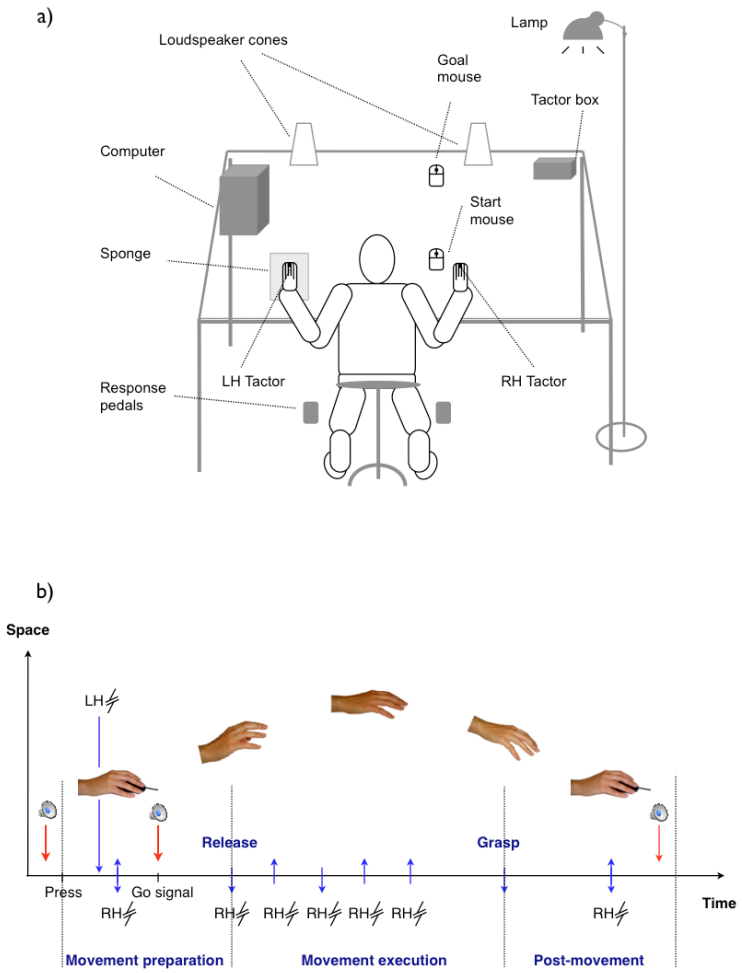


Figure 2.1. *a)* Bird's-eye view of the experimental set-up used in **Experiments 2.1-2.3**. *b)* Timeline of a single trial in **Experiments 2.1** and **2.2**. Upward arrows indicate the timing of the comparison pulse delivered to the right hand at various points during the goal-directed movement in **Experiment 2.1**, whereas downward arrows indicate the timing of the comparison pulse delivered to the participants' right hand in **Experiment 2.2**.

Tactors (VBW32 skin stimulators, 1.6 x 2.4 cm vibrating surface, Audiological Engineering Corp., Somerville, MA, USA) were attached with tape to the ventral part of the middle fingers of each of the participant's hands. The tactors were covered in several layers of thin sponge in order to reduce the possibility that the participants would be able to hear their operation. The participants also wore disposable earplugs (3M 1100), as well as over-the-head earmuffs (Peltor H7A) for the duration of the experiment for the same reason. The tactors were driven by means of a custom-built tactor box connected to the main computer (Dell Technologies) and interfaced through

Matlab (Psychophysics Toolbox 3, Brainard, 1997; Pelli, 1997) on Windows XP. The participants rested their left hand on an additional piece of soft sponge for the duration of the experiment; they placed their right hand to the right of the start mouse at the beginning of each trial. The auditory stimuli were delivered from two loudspeaker cones, one placed on either side of the table. Participants responded by means of two footpedals connected to the computer.

2.1.1.3. Procedure

The dual-task experiment consisted of a speeded movement task paired with an unspeeded perceptual task. In each trial of the *movement task*, the participants were instructed to listen out for three auditory beeps (450 Hz, 100 ms) presented from the two loudspeaker cones placed on the table. The participants were instructed, following the first beep, to grasp the start mouse with their right hand and to keep the left mouse button depressed. They had to prepare and execute a goal-directed movement toward the goal mouse as soon as they heard the second beep (which acted as the *go signal*). The participants executed the speeded movement, grasped the goal mouse, and kept the left button on the goal mouse depressed until they heard the third beep. At that time, they had to release the mouse and return their right hand to the starting position, to the right of the start mouse.

For the *perceptual task*, a *standard* tactile pulse (250 Hz, 12 dB sensation level, 660 ms) was presented to the participant's left middle finger (200-300 ms) after the first beep on each and every trial. This pulse was followed by another random time interval (300-400 ms) before the delivery of the go signal. The *comparison* tactile

pulse (250 Hz, 660 ms) was delivered to the participant's right middle finger. For each trial, depending on the experimental condition, the comparison pulse was presented at a different point in time. In particular, right hand stimulation could be delivered either during the *movement preparation period* (0 ms after the standard left hand pulse), at the *start* of the movement following the go signal (0 ms after the release of the start mouse), or during the *movement execution* period (100 ms after the release of the start mouse). Right hand tactile stimulation could also be delivered at *the grasp* of the goal mouse (0 ms after the grasp), or in the *post-movement* period (100 ms after the grasp of the goal mouse; see Figure 2.1b for a depiction of the timeline in a typical trial).

The perceptual task involved participants having to make a tactile intensity discrimination response: That is, they had to compare the right hand pulse to the left hand pulse and decide whether the intensity of right hand stimulation was stronger or weaker than that of the comparison pulse once they had completed the movement task and returned to the starting position. The participants were instructed to press one footpedal whenever a stronger pulse was presented to the right hand and the other footpedal whenever the right hand pulse was weaker. Response assignments for the left and right footpedals were counterbalanced across participants. Once the participants had made their response, the experiment progressed on to the next trial following a random intertrial interval (1500-2500 ms).

2.1.1.4. Design

The experiment involved an adaptive procedure comprising five different interleaved staircases for each of the five conditions of the experimental factor of Timing of the

right hand tactile stimulation – (motor preparation, movement start, movement execution, grasp, and post-movement). Each of the five staircases consisted of a three-interval one-up three-down adaptive procedure (Leek, 2001; Treutwein, 1995), designed to keep performance at a level of 79.4% correct (Levitt, 1970).

The standard pulse delivered to the left hand in the first trial was kept constant for all trials and all staircases throughout the experiment. The comparison pulse delivered to the right hand was calculated by either subtracting or adding one step from the standard pulse delivered to the left hand. For all staircases, the first comparison pulse delivered to the right hand was stronger than the standard pulse delivered to the left hand, hence all staircases converged on the upper thresholds. After one incorrect response, or a sequence of three correct responses, the staircase changed direction: 'UP' (increasing the right hand pulse by one step for an incorrect response) or 'DOWN' (decreasing the right hand pulse by one step following three consecutive correct responses), respectively. Changes in the direction of the staircase are referred to as 'reversals'. The step-size was doubled for the first five reversals in order to approach the threshold more rapidly (e.g., see Tan et al., 2006). The first five reversals were excluded from the final threshold calculations (the average value of upward and downward reversals). The staircase for each condition terminated once the total number of reversals (17) or the total number of trials (120) had been reached.

The presentation of trials from each of the staircases was randomized throughout the experiment. After the completion of every 60 trials, the participants were informed by three consecutive beeps that the block has finished and that they could take a break, if they so desired. A progress bar was presented on the screen

behind their chair. This provided an estimate of the number of trials remaining, calculated on the basis of the total number of possible reversals (85). The participants pressed a key on the keyboard in order to continue on to the next block. The experiment required the participants to complete a maximum of 600 trials. The experiment finished when all five staircases had terminated. The participants performed a short block of 10 practice trials at the beginning of the experiment. These practice data did not constitute part of the final analysis.

2.1.1.5. Data analysis

Three participants were excluded from the final data analysis as they did not wait for the go signal before initiating their movement in the majority of trials, or else they failed to keep the start mouse button depressed following the first beep. Due to the fact that the stimulation delivered during movement execution was triggered by the release of the start mouse, failure to keep the mouse depressed resulted in the delivery of the right hand tactile comparison pulse while the participant's hand was still at rest. The remaining 16 participants were included in the final data analysis.

For the *perceptual task*, a one-way repeated measures analysis of variance (ANOVA) was conducted on the threshold data with the factor Timing of tactile stimulation delivery comprising the five different timings of tactile right hand stimulation: movement preparation, start, execution, grasp, and post-movement. Mauchly's test of sphericity was used to ensure that the data did not violate the sphericity assumption. If the assumption was violated, then the Greenhouse-Geisser[4]

[4] Unless stated otherwise, the Greenhouse-Geisser correction for multiple comparisons was used for all of the experiments reported in this thesis.

correction was applied to correct the degrees of freedom; corrected p values are reported. Repeated contrasts were utilized in order to flag significant differences between the different levels of the experimental factor Timing of tactile stimulation delivery.

2.1.2. Results

On average, the participants needed 380 trials in order to complete the experiment (approximately 78 per staircase). The average time to grasp (the time between the tactile stimulation of the right hand and the grasp of the goal mouse), the average time difference between the stimulation of the right hand relative to the left hand, and the timing of right hand stimulation relative to the start of the different movement phases (note that for the preparation period, the timing is provided relative to the left hand and not the beginning of the preparation period which coincides with the beginning of the trial) are highlighted in Table 2.1. Mean thresholds and individual data from all participants are presented in Figure 2.2a. Numerical values of the thresholds in the five conditions are presented in Table 2.2. The results revealed that the timing of tactile stimulation to the participant's right hand significantly influenced the threshold data [$F(4,60)=7.23$; $p<.001$]. Repeated contrasts showed thresholds to be significantly higher (i.e., poorer performance was observed) in the execution period as compared to the preparation period [$F(1,15)=9.36$; $p=.008$], the start period [$F(1,15)=5.97$; $p=.027$], the grasp period [$F(1,15)=18.67$; $p=.001$], and the post-movement period [$F(1,15)=35.54$; $p<.001$]. The thresholds were significantly lower (i.e., better performance was observed) in the post-movement period as compared to the preparation [$F(1,15)=5.07$; $p=.04$] and grasp periods [$F(1,15)=5.99$; $p=.027$].

	Experiment 2.1			Experiment 2.2a			Experiment 2.2b			Experiment 2.3		
	RH	LH/RH	TTG	RH	LH/RH	TTG	LH	RH/LH	TTG	RH	LH/RH	TTG
Preparation	0	0	993	100	100	928	100	100	1043	200	100	n.a.
Early	0	266	859	50	600	488	50	590	459	n.a.	n.a.	n.a.
Mid	100	692	634	150	699	434	150	692	382	998	699	n.a.
Late	0	1004	0	250	775	338	250	784	299	n.a.	n.a.	n.a.
Post-move	100	1142	-100	100	1145	-100	100	1188	-100	1442	1145	n.a.

Table 2.1. Experimental timings (in ms) for **Experiments 2.1-2.3**. For each of the experiments, the first column (right hand, RH) represents the timing (in ms) of the RH pulse delivery relative to the start of the experimental conditions listed on the left side of the table. The second column (LH-RH) indicates the average time difference between the delivery of the pulses to the two hands. The third column (TTG) highlights the average time to grasp the goal mouse following the delivery of the RH pulse; negative values indicate that the grasp occurred first. Note that the RH is switched with the LH for**Experiment 2.2b**. In **Experiment 2.1**, Early stands for Start, Mid for Execution and Late for Grasp. In **Experiment 2.3**, Preparation stands for Short, Mid for Medium, and Post-move stands for Long.

	Experiment 2.1		Experiment 2.2a		Experiment 2.2b		Experiment 2.3	
	Mean threshold	SE	Mean threshold	SE	Mean threshold	SE	Mean threshold	SE
Preparation	2.49	0.18	2.75	0.19	3.22	0.26	3.11	0.19
Early	2.56	0.23	3.56	0.29	4.12	0.27	n.a.	n.a.
Mid	3.20	0.15	3.53	0.34	3.79	0.26	2.49	0.27
Late	2.36	0.20	3.83	0.28	3.94	0.26	n.a.	n.a.
Post-move	2.04	0.14	2.70	0.25	3.33	0.27	2.19	0.16

Table 2.2. Mean thresholds (dB) and SEs for **Experiments 2.1-2.3**, split according to the different experimental conditions. In **Experiment 2.1**, Early stands for Start, Mid for Execution, and Late for Grasp. In **Experiment 2.3**, Preparation stands for Short, Mid for Medium, and Post-move stands for Long.

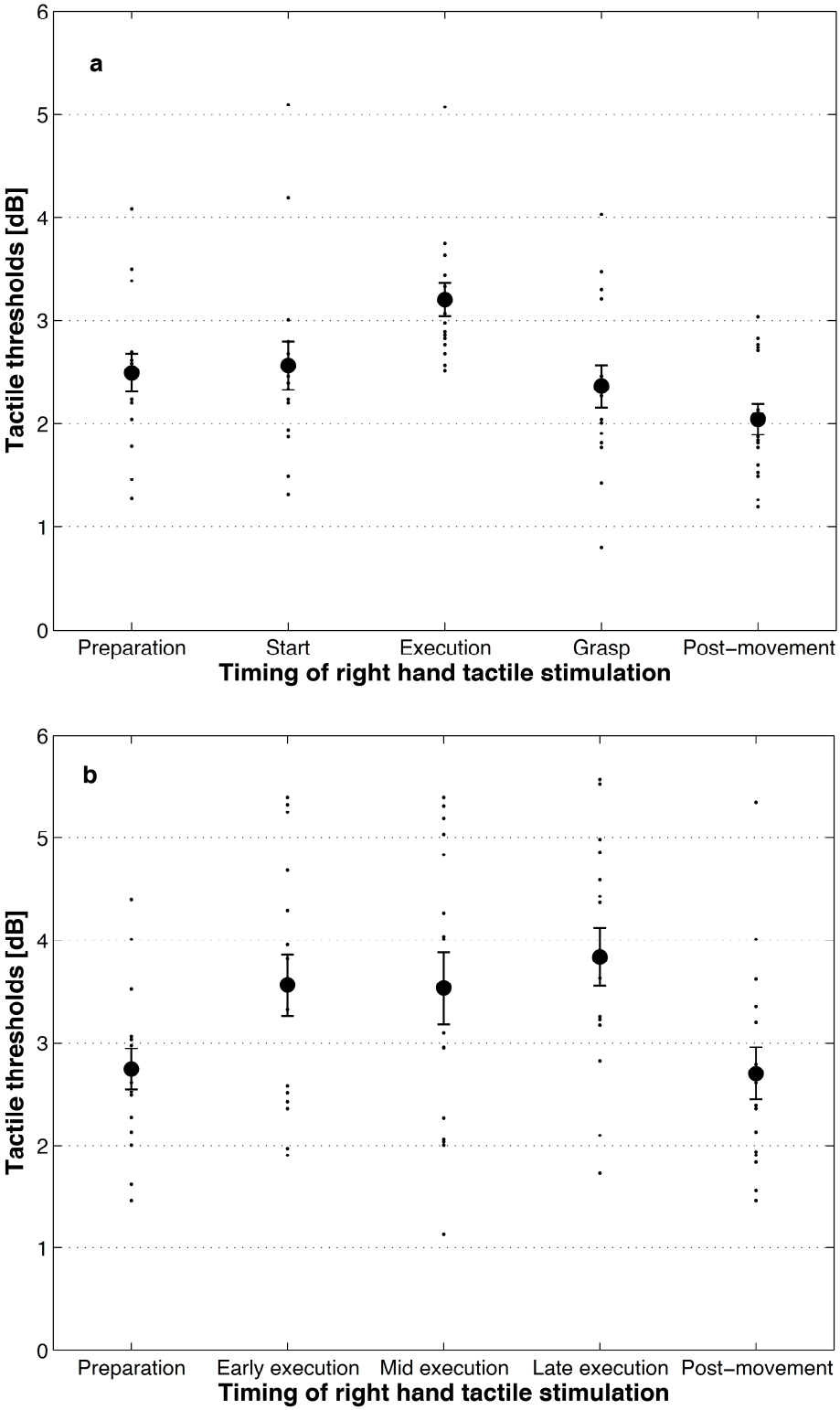


Figure 2.2. Scatter-plots of the individual threshold data together with the means for the various timings of the right hand pulse delivery for **Experiment 2.1** (**a**) and **Experiment 2.2a** (**b**). Vertical error bars represent the standard errors of the means.

2.1.3. Discussion

The prediction for **Experiment 2.1** was that the tactile thresholds would be significantly higher in the execution period of the movement, as compared to when the participant's hand was at rest. Consistent with this prediction, the results did indeed highlight a significant increase in participants' perceptual thresholds in this active period as compared to the other phases of the movement. This finding could be taken to support the facilitation of tactile perception thought to occur during the motor preparation period (Juravle & Deubel, 2009; Rorden et al., 2002). Nevertheless, changes in tactile performance have been shown to occur at the start of the movement (Brozzoli et al., 2009), during movement execution (Gallace et al., 2010; Voss et al., 2006; 2008), and at the point of contact with the goal-object (Bays et al., 2005). Such results, in turn, support the tactile suppression account of what happens during movement execution (Bays et al., 2005; Voss et al., 2006, 2008).

The results of **Experiment 2.1** also suggest that a potential facilitation (most probably resulting from overt orienting, see Kennett et al., 2001; Tipper et al., 1998), of tactile performance could be experienced once the movement has been terminated, since the performance in the post-movement period was significantly better, as compared to the preparatory and grasp phases. It should, however, be noted here that the duration of tactile stimulation might have had an effect on the sensitivity data. More specifically, it has been shown that the longer the stimulation, the more cues for discrimination would have been available to participants, and therefore, the better their performance (Verrillo & Gescheider, 1992).

In order to determine whether the duration of stimulation could exhibit a significant effect on tactile sensitivity, the duration of tactile stimulation was

shortened to 100 ms in **Experiment 2.2** (for the stimulation presented to both hands). Right hand tactile stimulation was delivered at one of five different time points referenced to the left hand stimulation and the different movement phases: movement preparation, early execution, mid execution, late execution, as well as post movement. It was hypothesized that tactile sensitivity would decrease during the execution period (Bays et al., 2005; Voss et al., 2006, 2008), and that it should be enhanced during the preparation (Juravle & Deubel, 2009; Rorden et al., 2002) and post-movement periods.

By using three different timings to test the attenuation of tactile perception during movement, **Experiment 2.2** was designed to investigate whether this phenomenon is uniformly distributed over the execution period of the movement. An alternative outcome would instead be that the movement-related tactile attenuation is dependent on the exact spatial location of the hand, and consequently, on the exact timing of tactile stimulation delivery. Following on from this, with regard to the actual grasping of the goal object, an initial hypothesis concentrated on the importance of tactile perception for movement[5]: If the fine kinematic adjustments made prior to the grasp of the goal object are dependent on the tactile information from the fingertips (Augurelle et al., 2003; Brochier et al., 1999; Gentilucci et al., 1997; Monzée et al., 2003; Nowak et al., 2001), then tactile sensitivity in the moving limb should be enhanced when tested in this late execution period. However, if tactile information is not relevant throughout the entire movement phase, as suggested by forward models of motor control (see Bays & Wolpert, 1997; Miall & Wolpert, 1996; Wolpert et al.,

[5] See also **Experiment 2.8** on this.

1995), then no difference in tactile sensitivity should be found between the different execution phases (early, mid, and late execution).

Furthermore, another aim was to investigate whether this phenomenon of sensory suppression observed during reaching movements executed by the right hand would be present during left hand reaching as well. It has been argued by some researchers, primarily on the basis of the literature on spatial neglect and extinction, that spatial judgments might primarily involve the right hemisphere (Làdavas, Di Pellegrino, Farnè, & Zeloni, 1998; Marshall & Fink, 2001; Mattingley, Driver, Beschin, & Robertson, 1997), the same hemisphere that controls the movements, as well as the somatosensory processing, of the left hand. Therefore, in **Experiment 2.2b**, participants had to perform the same reach-to-grasp movement as in **Experiment 2.2a**, this time using their left hand. The goal of **Experiment 2.2b** was to investigate, by comparing the performance of the two hands, whether the observed differences in tactile sensitivity were influenced by the active hand that performs the movement or the static hand that receives the 'standard' comparison stimulation.

2.2. Experiment 2.2: The decrement in tactile sensitivity is uniformly distributed over the execution phase of movement

Experiment 2.2 was composed of two parts: **Experiment 2.2a** and **2.2b**. The only methodological difference between the two parts was in terms of the hand that performed the movement: If, in **Experiment 2.2a**, the right hand reached between the two computer mice, in **Experiment 2.2b**, it was the left hand that performed the movement (with the computer mice affixed now on the left side of the table). For this reason, the methods for the two experiments are presented together.

2.2.1. Methods

2.2.1.1. Participants

Nineteen participants (11 male, one left handed) took part in **Experiment 2.2a**. They had a mean age of 28 years old (age range 21-36 years). Six of the participants had already taken part in **Experiment 2.1**. Sixteen participants (7 male, one left-handed) participated in **Experiment 2.2b**. They had a mean age of 26 years old (age range 20-34 years). Six of the participants had already taken part in **Experiment 2.2a**.

2.2.1.2. Apparatus, design, and procedure

The apparatus, design, and procedure were similar to those used in **Experiment 2.1** with the following exceptions: 1) The duration of tactile stimulation was shortened to 100 ms for both the left hand and right hand pulses; 2) The auditory beeps in **Experiment 2.2** were shortened and had a higher pitch (800 Hz, 50 ms); 3) The third difference relates to *the timing* of the tactile stimuli. For **Experiment 2.2a**, just as for **Experiment 2.1**, the *standard* tactile pulse presented to the middle finger of the left hand was followed by a random time interval (of 300 to 400 ms), after which time, the go signal was presented. The *comparison* tactile pulse was delivered to the right hand either in the *movement preparation period* (100 ms after the standard left hand pulse), at one of three points in time during the *movement execution* period (50, 150, or 250 ms after the release of the start mouse), or in the *post-movement* period (100 ms after the grasp of the goal mouse). These different timings will be referred to as: motor preparation, early execution, mid execution, late execution, and post-movement (see

Figure 2.1b for a depiction of the timeline of a typical trial). All these timings apply to **Experiment 2.2b** as well; note that for this experiment the right hand received the standard pulse, whereas the left hand performed the movement and received the comparison pulse.

2.2.1.3. Data analysis

Three participants were excluded from the final data analysis of **Experiment 2.2a** as they either did not wait for the go signal before initiating their movement or else they did not keep the start mouse button depressed following the first beep. The remaining 16 participants were included in the final data analysis.

For the *movement task* of both **Experiment 2.2a** and **2.2b**, a one-way repeated measures ANOVA was conducted on the reaction times (RTs) data with the factor Timing of tactile stimulation delivery comprising five levels of right hand/left hand tactile pulse delivery: movement preparation, early execution, mid execution, late execution, and post-movement. A further one-way repeated measures ANOVA was conducted on the movement duration data. For the *perceptual task*, a one-way repeated measures ANOVA was conducted on the threshold data with the same factor Timing of tactile stimulation delivery comprising the five different timings of tactile right hand/left hand stimulation.

Further repeated measures ANOVAs were then conducted on the RT data, the movement duration data, and the threshold data with the within-participants factor Timing of tactile stimulation delivery (preparation, early execution, mid execution, late execution, and post-movement) and the between-participants factor Experiment (2.2a

vs. 2.2b). Levene's test was used in order to test the homogeneity of variance of the experimental data from **Experiments 2.2a** and **2.2b**.

2.2.2. Results

For each of **Experiments 2.2a** and **2.2b**, the participants needed an average of 403 and 402 trials, respectively, in order to complete the experiment (i.e., approximately 80 per staircase). The experimental timings are highlighted in Table 2.1. Mean threshold data from both **Experiments 2.2a** and **2.2b** are presented in Figure 2.3a.

2.2.2.1. Movement task: RTs results

2.2.2.1.1. Experiment 2.2a

The analysis of the results revealed the timing of delivery of tactile stimulation to the participants' right hand had a significant effect on RTs [$F(4,60)=9.76$; $p=.004$; $\varepsilon=.312$]. Pairwise post-hoc comparisons revealed that the effect was due to RTs in the preparation period being significantly faster than RTs in the early execution period ($p=.002$) and in the post-movement period ($p=.008$).

2.2.2.1.2. Experiment 2.2b

The results revealed that the timing of delivery of tactile stimulation to the participants' left hand had no significant effect on RTs [$F(4,60)=3.08$; $p=.094$; $\varepsilon=.283$].

2.2.2.2. Movement task: Movement duration results

2.2.2.2.1. Experiment 2.2a

The results showed that the timing of the right hand tactile stimulation did not have a significant influence on movement duration [$F(4,60)=1.46$; $p=.25$; $\varepsilon=.465$].

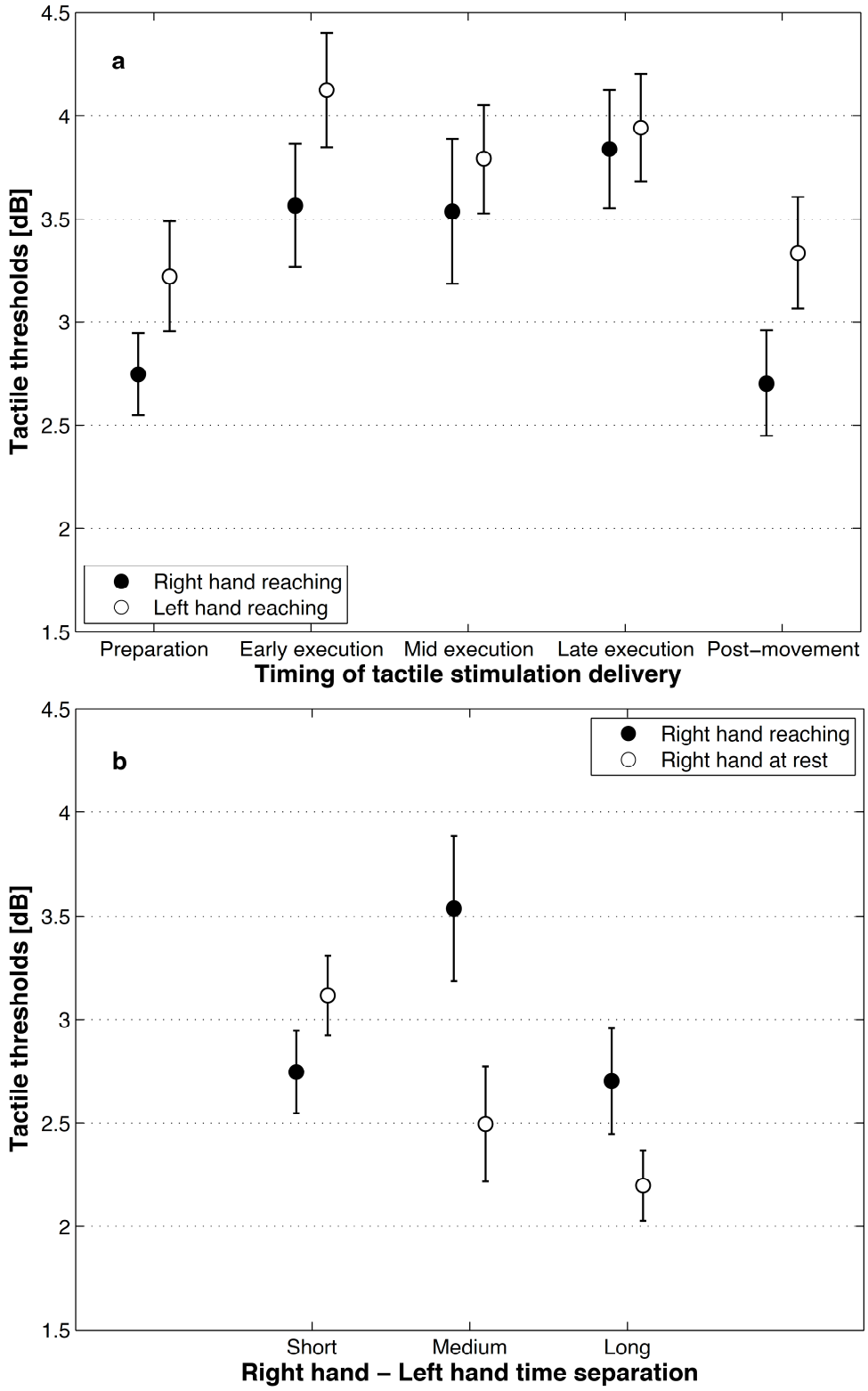


Figure 2.3. Mean threshold data for the various timings of the right hand pulse delivery for **Experiment 2.2a** vs. mean threshold data for the various timings of the left hand pulse delivery for **Experiment 2.2b** (**a**); Mean threshold data for the short, medium, and long Left hand-Right hand time separation in **Experiments 2.2a** vs. **2.3** (**b**). Vertical error bars represent the standard errors of the means.

2.2.2.2.2. Experiment 2.2b

The results indicated that the timing of the left hand tactile stimulation did not have a significant influence on movement duration [$F(4,60)<1$; p=n.s.; $\varepsilon=.574$].

2.2.2.3. Perceptual task results

2.2.2.3.1. Experiment 2.2a

Mean thresholds and individual data from all participants are presented in Figure 2.2b. Numerical values of the thresholds in the five conditions are presented in Table 2.2.

The results indicated that the timing of tactile stimulation to the right hand significantly influenced the threshold data [$F(4,60)=10.87$; $p<.001$]. Repeated contrasts revealed that the thresholds were significantly lower (i.e., better performance was observed) in the movement preparation period as compared to the early execution period [$F(1,15)=13.37$; $p=.002$], the mid execution period [$F(1,15)=8.69$; $p=.010$], and the late execution periods [$F(1,15)=27.28$; $p<.001$]. Thresholds were significantly lower in the post-movement period as compared to the early execution period [$F(1,15)=12.87$; $p=.003$], the mid execution period [$F(1,15)=9.07$; $p=.009$], and the late execution period [$F(1,15)=22.72$; $p<.001$]. These results therefore demonstrate that participants were significantly worse at comparing the two tactile pulses when one of them was delivered at any stage during the execution of the movement between the two mice.

2.2.2.3.2. Experiment 2.2b

Numerical values of the thresholds in the five conditions are presented in Table 2.2. The results indicate that the timing of tactile stimulation to the left hand significantly influenced the threshold data [$F(4,60)=4.55$; $p=.003$]. Repeated contrasts indicated the

thresholds to be significantly lower (i.e., better performance was observed) in the preparation period than in the early-execution [F(1,15)=13.35; p=.002], mid execution [F(1,15)=5.03; p=.040], or late execution periods [F(1,15)=5.45; p=.034]. Thresholds were significantly lower in the post-movement period as compared to the early-execution period [F(1,15)=7.89; p=.013], and marginally, the late-execution period [F(1,15)=4.69; p=.05]. Participants were therefore significantly worse at comparing the two tactile pulses when one of them was delivered early during the execution of the movement between the two mice, as compared to the 'no movement' conditions.

2.2.2.4. Experiment 2.2a vs. 2.2b

2.2.2.4.1. Movement task: RTs results

Independent-samples t-tests indicated that there was no significant difference in the mean RTs for either the preparation [t(30)=.14; p=.890, r=.02], early execution [t(30)=.28; p=.777; r=.05], mid execution [t(30)=.22; p=.826; r=.04], late execution [t(30)=-.25; p=.806; r=.04], or post-movement periods [t(30)=-.16; p=.872; r=.03].

2.2.2.4.2. Movement duration results

Independent-samples t-tests revealed that there was no significant difference in the mean movement duration of the two hands for either the preparation [t(17.862)=-.56; p=.578; r=.13], early execution [t(30)=.65; p=.519; r=.12], mid execution [t(30)=.13; p=.899; r=.02], late execution [t(30)=-1.01; p=.815; r=.18], or post-movement periods [t(30)=-.24; p=.815; r=.04].

2.2.2.4.3. Perceptual task results

Lastly, independent samples t-tests highlighted no significant differences in the mean tactile thresholds for the two hands for either the preparation [t(30)=-1.42; p=.166; r=.25], early execution [t(30)=-1.37; p=.181; r=.24], mid execution [t(30)=-.58;

p=.565; r=.10], late execution [t(30)=-.27; p=.789; r=.05], or post-movement periods [t(30)=-1.69; p=.100; r=.29].

2.2.3. Discussion

The movement task in **Experiment 2.2a** revealed faster RTs to release the start mouse following the go signal for comparison pulses delivered during the movement preparation period (i.e., with a SOA of 100 ms between the left hand and the right hand), as compared to the early-execution and post-movement periods. One explanation for this result is an alerting effect resulting from the presentation of the right hand vibrotactile pulse, which may have speeded the already prepared goal-directed movement (Diederich et al., 2003). From this view-point, the beeps used in **Experiments 2.1-2.2**, as well as in the rest of the experiments of this thesis, could be regarded as alerting and thus potentially contributing to the early inception of a facilitatory substrate for the forth-coming perceptual task[6].

When considering the tactile sensitivity results, **Experiment 2.1** highlighted a significant improvement in performance in the post-movement period as compared to the preparation period. Nevertheless, the same pattern of results was not observed in **Experiment 2.2a**. Tactile thresholds for the movement execution periods were significantly increased as compared to motor preparation and post-movement, thus indicating poorer performance for the moving right hand as compared to rest conditions. Just as for the right hand, the results of **Experiment 2.2b** indicated a sensory suppression-like pattern of results for the left hand. Moreover, when the

[6] Though see **Experiment 2.7** that investigated different lengths of the go signal to initiate movement. See also **Appendix A3** for an outline of the beeps sequence used in every experiment reported in this thesis.

pattern of performance for the two hands was compared, the RTs, the total movement duration, as well as the thresholds of the left hand were not statistically different from those reported for the right hand. It could therefore be concluded that sensory suppression is a robust empirical phenomenon, one that affects both moving hands equally.

One explanation for the significantly decreased thresholds found in the preparation and post-movement periods of both **Experiments 2.2a** and **2.2b** involves the notion of attentional facilitation (Deubel & Schneider, 1996; Deubel et al., 1998; Hoffman & Subramaniam, 1995; Juravle & Deubel, 2009; Kowler et al., 1995; Rorden et al., 2002; Schiegg et al., 2003). When we are about to move, we attend to the hand that we are preparing to move, as well as to the hand that grasps the goal object. More specifically, one can argue that this post-movement period is of particular importance for grasping, since the tactile feedback from the object conveys information to us regarding whether we should be making adjustments in our grip force in case, for example, the object slips. On the other hand, it may be that tactile sensitivity was indeed suppressed during movement execution in both **Experiments 2.2a** and **2.2b**, but that it returned to a normal state in the post-movement period.

In order to test this hypothesis, a third experiment was performed (**Experiment 2.3**) in which the participants sat still and received the standard and comparison tactile pulses separated by a short, medium, or long time interval. If facilitation were to be observed in the post-movement period, then one would expect tactile thresholds to be significantly higher in **Experiment 2.3** (i.e., poorer performance in the absence of movement) as compared to **Experiment 2.2a**. However,

if the decreased thresholds in **Experiment 2.2a** were indicators of the normal tactile perception once a movement has terminated, then one would not expect to find any significant difference between the two **Experiments 2.2a** and **2.3**.

2.3. Experiment 2.3: No attentional facilitation during the preparatory and post-movement phases of a reach-to-grasp movement

2.3.1. Methods

Sixteen participants (5 male, one left handed) took part in this experiment. They had a mean age of 25 years old (age range 20-34 years). Eleven of the participants had already taken part in **Experiment 2.2b**. The experiment lasted for approximately 20 minutes.

The apparatus, design, and procedure were similar to those used in **Experiment 2.2a**. However, the participants now only performed the *perceptual task*. For this, they were instructed to take a comfortable position on the chair, with their hands on either side of the armrests. Moreover, they were asked to keep their hands still, to not look at their hands, or touch the arm rests with their hands.

Each trial started with an auditory signal (800 Hz, 50 ms) that was followed after a random time interval (200-300 ms) by the delivery of a *standard* tactile pulse (250 Hz, 100 ms) to the participants' left hand. Following a short (100 ms), medium (699 ms), or long (1145 ms) time interval, a second *comparison* tactile pulse (250 Hz, 100 ms) was delivered to the participants' right hand. The three time intervals correspond to the average left hand-right hand time difference from **Experiment 2.2a**

(see Table 2.1). The left hand-right hand time difference for the three movement periods (short, medium, and long) in **Experiment 2.2a** were very close together in time as well as not statistically different in terms of their tactile thresholds. For this reason, the mid execution phase was used as the medium time interval in the present experiment. The comparison pulse was followed by another random time interval (300-400 ms) and the trial finished with an auditory signal (800 Hz, 50 ms) that indicated to the participants that they should make a response. The rest of the procedure, as well as the design, were identical to **Experiment 2.2a**.

A one-way repeated measures ANOVA was conducted on the threshold data with the factor Timing of tactile stimulation delivery comprising the three levels of left hand-right hand time difference in stimulation: short, medium, and long. In a second step, a repeated measures ANOVA was then conducted on the threshold data, with a within-participants factor Timing of tactile stimulation delivery (short, medium, and long), and a between-participants factor of Experiment (2.2a vs. 2.3). For this analysis, the mid execution period of **Experiment 2.2a** was considered in the analysis as the mid level of factor Timing of tactile stimulation delivery.

2.3.2. Results

Mean threshold data for the short, medium, and long time periods of **Experiment 2.3** are plotted together with the corresponding time periods of **Experiment 2.2a** in Figure 2.3b.

2.3.2.1. Results of Experiment 2.3

The results show that the left hand-right hand time difference in tactile stimulation

significantly influenced the threshold data [F(2,30)=12.93; p=.001; ε=.670]. Repeated contrasts showed thresholds to be significantly higher (i.e., worse performance was observed) in the short time difference period as compared to the medium [F(1,15)=8.85; p=.009] and long periods [F(1,15)=82.04; p<.001]. There was no significant difference between the medium and long periods [F(1,15)=1.85; p=.194]. Participants were therefore significantly worse at comparing the two tactile pulses for a time difference between the two of them of as little as 100 ms.

2.3.2.2. Comparison of the results of **Experiments 2.2a** and **2.3**

Independent-samples t-tests indicated there was no significant difference in the mean tactile thresholds for the two hands for the short [t(30)=-1.33; p=.192; r=.24] and long [t(30)=1.65; p=.109; r=.23] periods of the two experiments. A significant difference was observed between the mean thresholds of the medium period of the two experiments [t(30)=2.33; p=.027; r=.39], with significantly decreased thresholds in the medium period of **Experiment 2.3**, as compared to the same period of **Experiment 2.2a**.

2.3.3. Discussion

Tactile performance in **Experiment 2.3** was worse when the time difference between the two pulses presented to the left and right hands was as short as 100 ms. It has been demonstrated that for very short durations of up to 150 ms, a contralateral comparison stimulus will most likely be perceived as having a decreased intensity with respect to the standard stimulus. This 'sensory suppression' in the absence of

movement appears when two vibratory stimuli are delivered to different skin locations with a very short time separating them (Verrillo & Gescheider, 1992). Moreover, tactile performance was comparable in the early and late time periods of both **Experiments 2.2a** and **2.3**, suggesting, contrary to the predictions of the premotor theory (see Rizzolatti & Craighero, 2009; Rizzolatti et al., 1994; see also **Chapter 1**) that tactile perception is in a normal (non-facilitated) state shortly before starting, as well as immediately after finishing, a goal-directed reaching movement.

2.4. General discussion of Experiments 2.1-2.3

The first three experiments reported in **Chapter 2** were designed to measure any changes in participants' tactile sensitivity over the course of a goal-directed reach-to-grasp movement. It was hypothesized that participants' tactile discrimination performance would be facilitated in the motor preparation period, decrease at the start of the movement, over the reach phase, and at the time of grasping the goal object. Furthermore, performance in the post-movement period was expected to be comparable with that observed in the preparation period. Lastly, no difference in performance between the preparation and post-movement periods was expected.

The results reported in **Experiments 2.1-2.3** demonstrate that *the timing* of the delivery of tactile stimulation constituted a decisive factor that differentially affected tactile sensitivity in the various phases of a goal-directed movement. Depending on the paradigm used, motor preparation has been characterized by *facilitation* in either tactile detection (Juravle & Deubel, 2009) or tactile discrimination (Rorden et al., 2002). At the start of the movement, *interference* from visual distractors (Brozzoli et al., 2009),

interference from the performance of a secondary task (Gallace et al., 2010), as well as *suppression* of tactile stimuli applied to the moving limb (Bays et al., 2005; Chapman & Beauchamp, 2006; Voss et al., 2006, 2008) have all been documented. Such suppressive effects on tactile perception are present throughout the reach phase and peak at the hand's contact with the goal object (see, for example, Bays et al., 2005; Chapman & Beauchamp, 2006). Shortly after contact – i.e., during the post-movement period – suppression diminishes and gives way to a return to the baseline state of tactile perception.

With regard to the present study, tactile thresholds were significantly increased over the start, execution, and grasp periods (**Experiment 2.1**), or the early, mid, and late execution phases of the movement (**Experiment 2.2a**) indicating a suppression mechanism acting on tactile perception as soon as the hand began its reach-to-grasp toward the goal location. Interestingly, the results of **Experiment 2.2b** demonstrated that the right hand is not special: That is, the tactile sensitivity of right hand reaching was no different from left hand reaching. Lastly, when comparing the right hand reaching between the two computer mice and the right hand at rest receiving passive stimulation (**Experiments 2.2a** vs. **2.3**), the suppression thesis was reinforced; however, no attentional facilitation (Juravle & Deubel, 2009; Rorden et al., 2002) was observed.

Interestingly, tactile sensitivity in the movement preparation period of **Experiment 2.1** was significantly lower than in the post-movement period. Such a result could be explained by the fact that visual attention may have interfered with participants' tactile performance during the course of the movement. For example,

viewing one's hand has been shown *to improve* the detection (Tipper et al., 1998) as well as the discrimination (Kennett et al., 2001) of tactile targets, even though vision of the hand was itself non-informative with regard to the task at hand in these studies.

In the first two experiments reported in this chapter, the movement task involved a speeded reach-to-grasp movement from the 'start mouse' to the 'goal mouse'. As such, the task instructions given to our participants did not specify any constraints on visual fixation, since it was intended to achieve the execution of the movement under the most naturalistic conditions possible (that one can achieve in a constrained laboratory setting). Therefore, it may be that following the instruction to execute the speeded movement from the start mouse to the goal mouse, the participants in **Experiment 2.1** first moved their eyes to the goal location and, at the delivery of the go signal, the hand 'followed' the eyes to the goal mouse. From this point of view, performance in the post-movement period would clearly be facilitated by visual attention with the eyes already 'waiting' at the goal location (Paillard, 1982). Indeed, when participants are asked to execute a hand movement to a peripheral target, it has been shown that their eyes first land at the goal location within 250 ms of the initiation of the saccade and the hand follows approximately 100 ms later (Prablanc, Echallier, Komilis, & Jeannerod, 1979), suggesting that the latency of the goal-directed movement was affected by the vision of the hand. More importantly, studies that have actively manipulated the time period in which vision is available during the course of a goal-directed movement (Binsted, Chua, Helsen, & Elliott, 2001; Fukui & Inui, 2006; Winges, Weber, & Santello, 2003) have demonstrated that early vision, especially at the beginning of the movement, is decisive in the control of prehensile movements.

With this consideration in mind, as observed in **Experiments 2.2a** and **2.2b**, shortening the duration of tactile stimulation resulted in steadier performance and no significant difference between the preparation and post-movement periods. This result implies that vision could indeed have played a role when the hand was at rest. However, it stemmed from the time given to the eyes 'to linger' over the goal location and consequently, to extract discrimination cues (Kennett et al., 2001; Tipper et al., 1998). It can therefore be concluded that the preparation and post-movement periods have comparable tactile sensitivity and the role of vision when comparing the two is, if anything, of little importance.

Some further considerations with regard to the timing of the tactile stimulation have to be taken into account though. First, tactile stimulation in the first three experiments of **Chapter 2** involved the delivery of a standard pulse to the left hand at the beginning of each trial, which was followed at various intervals (see Table 2.1) by the delivery of the comparison pulse to the right hand. Gallace and Spence (2009) refer to a 'memory for touch', pointing to the fact that the tactile memory trace should decay rapidly as the temporal interval between sequential stimuli increases, especially when distractors from the same modality are presented. However, this was not the case for **Experiments 2.1-2.3**; tactile sensitivity was highest at the longest interval[7]. Evidence supporting the lack of impact of tactile working memory on the performance of the task reported here comes from another study in which the participants had to compare vibrotactile stimuli separated by various time intervals ranging from 300 to 1200 ms (Harris, Miniussi, Harris, & Diamond, 2002). The results of this study

[7] See also **Experiment 2.7** that investigated a possible role for IOR in the processing of tactile sensory information during the preparation period of a goal-directed movement.

revealed that during this period there was no effect of SOA on participants' discrimination performance.

Furthermore, an interesting unexpected effect in **Experiment 2.3** was to find better tactile discrimination performance for the right hand at rest in the medium period as compared to the short time period. If one considers people's memory for tactile stimulation (Gallace & Spence, 2009), then performance should have shown the opposite: namely, higher sensitivity at the shorter time interval to deliver stimulation to the two hands. However, in this case, it may be that an attentional mechanism acts on tactile perception, facilitating performance at the longer time intervals. Indeed, traditional studies of spatial attentional cuing have shown costs of a little over 30 ms, on average, for contralaterally-cued trials (Spence & McGlone, 2001). Moreover, it has been shown that it takes around 250 ms, on average, to direct tactile attention from the right arm to the left (Lakatos & Shepard, 1997), which argues in favour of either an attention-directing process (Lakatos & Shepard, 1997; Spence & McGlone, 2001), or a possible contralateral sensory masking process (Verrillo & Gescheider, 1992), already taking place at the shortest time difference between the delivery of tactile stimulation at the two hands in **Experiment 2.3**.

To continue with other possible interfering factors, even if, as traditionally thought, we tend to rely on vision when performing goal-directed movements in peripersonal space (Cardinali, Brozzoli, & Farnè, 2009; Rizzolatti et al., 1997; Spence, Pavani, Maravita, & Holmes, 2004, 2008), information from the other senses is combined with vision in a statistically optimal fashion in the process of sensorimotor control (Ernst & Banks, 2002; Körding & Wolpert, 2006). Another factor contributing

to the present data may therefore be proprioception. For example, it has been shown that when moving in depth, hand positions closer to the shoulder are localized in a more precise manner, as compared to more distant positions (see Van Beers, Sitting, & Denier van der Gon, 1998). Moreover, studies that involved the introduction of a perturbation to the visual feedback of the moving hand have pointed toward an important role for proprioception, as well as motion feedback and hand position signals to the on-line control of hand reaching movements (Saunders & Knill, 2004; Van Beers, Wolpert, & Haggard, 2002). In this context, returning briefly to the importance of vision, it is interesting to note that other studies have reported the visual capture of proprioception when the right hand performs reaching movements behind an occluding panel with visual feedback provided only from the static left hand (Holmes, Crozier, & Spence, 2004; Holmes & Spence, 2005a).

Therefore, tactile performance as reported in **Experiments 2.1-2.3**, may indeed have been influenced primarily by vision, and, to a lesser extent, by proprioception. **Experiments 2.1-2.3** bring clear behavioral evidence for a different temporal distribution of tactile sensitivity over the various phases of reach-to-grasp movements. If tactile suppression is present throughout the movement execution phase, tactile perception most likely returns to a normal non-enhanced state while preparing and after the movement has terminated.

Lastly, even though attentional facilitation was expected to occur during the preparation, as well as the post-movement phases, this was not the case for the data reported in the first two experiments of the present chapter. Attention could nevertheless act as an explanatory factor for the results of **Experiments 2.1** and **2.2**.

In this respect, an alternative explanation for the sensory suppression effect present during the execution phase of the goal-directed movement regards movement *per se* as a distraction, that captures attention. As such, in order to exclude an attentional capture effect resulting from movement, one needs to test tactile sensitivity under conditions of goal-directed movement and rest. For this, in **Experiment 2.4** participants performed right hand goal-directed reaches, or else, they kept both their hands at rest. Tactile stimulation was provided to the left hand only during the execution period of the movement, where tactile attenuation effects were found in **Experiments 2.1-2.3**.

If an attentional capture from the movement itself were responsible for the previously found attenuating effects on tactile perception, then tactile perceptual sensitivity should be significantly better for stimulation received when both hands are at rest, as compared to the moving right hand condition. Alternatively, if suppression were to be regarded as a result of both movement and peripheral interference, then no difference should be found between conditions of rest and movement.

2.5. Experiment 2.4: Attention capture does not explain the tactile suppression observed during the movement execution phase

2.5.1. Methods

2.5.1.1. Participants

Ten participants (one male, all right-handed) took part in this experiment. The mean age of the participants was 27 years (age range 23-29 years). The experimental session

lasted for approximately 30 minutes and participants received a £5 gift voucher in return for taking part in the study.

2.5.1.2. Apparatus

Participants were seated at a table in a large well-lit room. A metallic box (goal object, 5 cm diameter, 6 cm height) was placed centrally on the table surface, at a distance of 30 cm from the participant's chest. Participants wore two tactors attached to the ventral part of their left forearm, one at their wrist and the second placed at a distance of 15 cm toward their elbow. The tactors were covered in several layers of thin sponge, in order to reduce the possibility that the participants could hear their operation. Participants responded by means of two footpedals, one placed on the floor in front and the other behind their left foot, at a comfortable distance.

2.5.1.3. Procedure

The participants performed two blocks of trials (movement and rest) with a short break in-between. In the *rest* condition, the participants kept both their hands at rest on top of sponge-like supports placed on the table. A first auditory signal (400 Hz, 50 ms) that announced the start of the trial was followed after a variable time interval (800 to 1200 ms) by a second higher-pitched auditory signal ('*go signal*', 800 Hz, 50 ms). 500 ms after this second auditory beep, both of the tactors that the participants wore on their left hand started vibrating (250 Hz, 150 ms).

The *movement* condition had the same trial definition as the rest condition. However, at the beginning of each trial, participants now placed their right palm at the edge of the table. At the delivery of the auditory go signal, they were instructed to reach forward and rapidly grasp the goal object. After making the grasping action, the

participants returned to the start position.

At the end of the trial, participants responded to indicate which tactor vibration they felt as being weaker or stronger, by pressing one or the other pedal with their left foot. Response assignments and the order of the two conditions were counterbalanced across participants.

2.5.1.4. Design

The design of **Experiment 2.4** was very similar to that of **Experiments 2.1-2.3** in this chapter. In the following, only the methodological differences are highlighted. Each of the experimental conditions utilized one staircase consisting of a three-interval one-up three-down adaptive procedure. The major difference was that in this experiment (as well as in the rest of the experiments presented in this chapter), both tactors that the participants wore on their left hand vibrated at the same time, thus possible interference effects from participants' memory for tactile stimulation (Gallace & Spence, 2009), or contralateral masking (Verrillo & Gescheider, 1992) were excluded. Furthermore, participants were given a break at the end of the block, once the perceptual threshold was reached for either the rest, or the movement condition. The rest of the design is the same as that of **Experiments 2.1-2.3**.

2.5.1.5. Data analysis

A paired-samples t-test was conducted on the mean threshold data from the two experimental conditions (rest vs. movement).

2.5.2. Results

On average, the participants needed 88 trials in order to complete the rest condition and 79 trials for the movement condition. The mean number of trials needed in order to

finish was not significantly different between the two conditions [t(9)=1.30, p=.227; r=-.37].

Mean thresholds and individual data from all participants are presented in Figure 2.4. The results indicated that movement of the hand did not affect sensitivity on the resting hand [t(9)=-1.18; p=.268; r=.42].

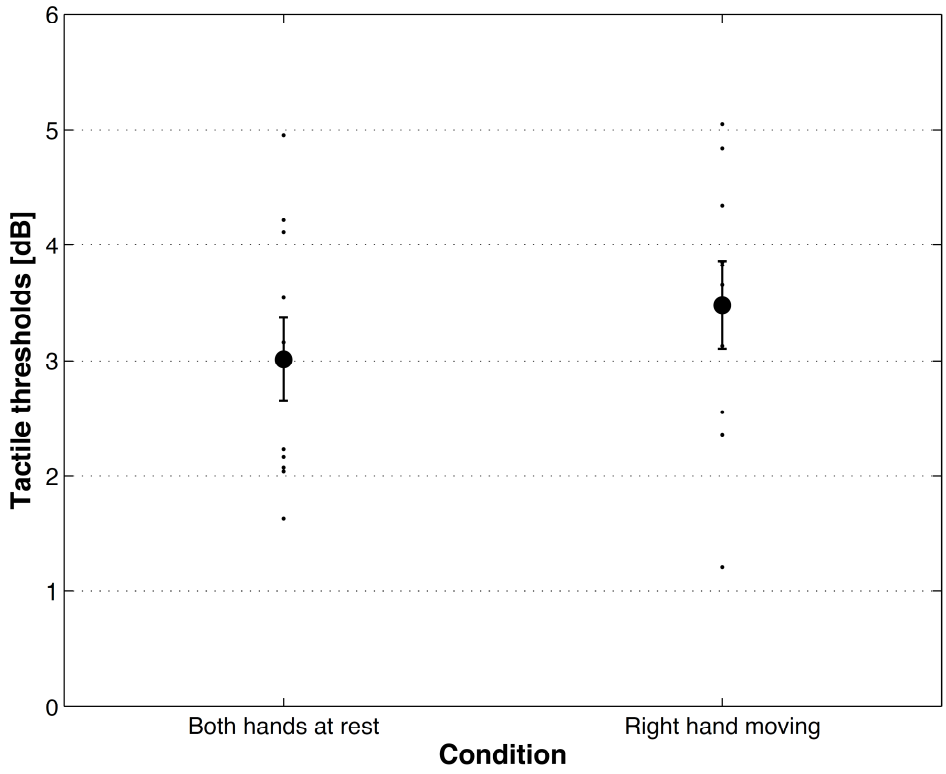


Figure 2.4. Scatter-plots of the individual threshold data together with the means for the two conditions (rest vs. movement) tested in **Experiment 2.4**. Vertical error bars represent the standard errors of the means.

2.5.3. Discussion

Experiments 2.1-2.2 highlighted a significant decrease in what is felt during the execution phase of a goal-directed reach-to-grasp movement. **Experiment 2.4** was conducted in order to investigate whether this decrement in tactile sensitivity could be explained by an attentional capture effect (i.e., the moving hand 'capturing' visual attention and hence, the increased thresholds/poorer performance). As highlighted by the present results, participants exhibited comparable tactile sensitivity in a resting

hand between conditions of rest (i.e., both hands are immobile), and movement (the hand receiving tactile stimulation is at rest, and the other is moving). Such results indicate that visual attentional capture cannot explain the attenuation in tactile sensitivity documented in **Experiments 2.1-2.2** in the present chapter. Most likely, as argued before, this attenuation in tactile perception during movement execution results from the combination of the motor command and peripheral interference from the movement (Chapman & Beauchamp, 2006).

If the movement-related attenuation in tactile sensation was expected during movement execution (see the predictions of the forward models of motor control in **Chapter 1** and the Introduction to this chapter), the finding of a normal non-facilitated state in the preparatory period of the movement period (as suggested by **Experiments 2.1** and **2.2)** was not expected**.** Indeed, according to the premotor theory of attention (Rizzolatti & Craighero, 2009; Rizzolatti et al., 1994), the preparation to move should facilitate perception. As such, the next goal of the experiments in this chapter is to further investigate the preparatory phase of the movement.

Therefore, in a first step, in order to test for the presence of an attentional effect during the preparation of goal-directed movements, another experiment was designed that discriminated between two preparatory phases: a *general preparatory phase* (i.e., participants prepared to move but they didn't know which effector would be used for the movement) and a specific *attentionally-invested phase* (i.e., participants had selected the effector for the goal-directed movement, but had not started the movement yet). As such, the participants in **Experiment 2.5** executed reach-to-grasp movements for an object placed centrally in front of them on the table. Tactile

sensitivity was tested at several points in time during the goal-directed movement: movement preparation (with and without the selection of the movement effector) and movement execution. In a control condition, tactile sensitivity was tested in the time window for movement execution. However, movement of the hand was restrained.

It was hypothesized that the preparation to move would shift tactile attention to the effector of the movement (Rizzolatti & Craighero, 2009; Rizzolatti et al., 1994). Therefore, improved performance (i.e., a lower threshold) was predicted when attention was allocated to the selected movement effector (preparation period – known hand), as compared to the general preparatory phase, where participants prepared to move, but had not selected the movement effector yet (preparation period – unknown hand). Moreover, in line with previous research (Chapman & Beauchamp, 2006, see also **Experiments 2.1-2.3** in this chapter), it was hypothesized that performance would be worse (i.e., thresholds would be higher) during the *execution* of the goal-directed reach-to-grasp movement because of sensory suppression.

2.6. Experiment 2.5: The mere preparation to move does not result in an enhancement in tactile sensitivity at the moving hand

2.6.1. Methods

2.6.1.1. Participants

Twelve participants (5 male, two left-handed, one ambidextrous) recruited from the student population of the University of Hamburg took part in this experiment. The mean age of participants was 24 years (age range 19-32 years). The experimental

session lasted for approximately 150 minutes and participants were paid 8 EUR/hour or they were given course credit for taking part in the study.

2.6.1.2. Apparatus

The participants were seated at a table in a well-lit room. A rectangular foam block (15.5 cm long, 4 cm wide, and 4 cm high) was attached centrally on the table at a distance of approximately 30 cm directly in front of the participant. Tactors were attached with tape to the ventral part of the index fingertips of each of the participant's hands. White noise was played continuously from loudspeakers positioned to the left of the participant. The auditory stimuli were delivered from two loudspeaker cones, one placed on either side at the back of participants. The movements of both hands were monitored on-line using an Optotrack Certus motion tracking system with a sampling rate of 150 Hz (Northern Digital Inc., Waterloo, Canada). The Optotrack marker was attached to the nail of the index finger of the moving hand by means of adhesive pastels (UHU-patafix, UHU Gmbh, Bühl, Germany) and medical tape. The participants responded by means of a two-button custom-built response box, placed on the table in front of the start position. See Figure 2.5 for a depiction of the experimental set-up.

2.6.1.3. Procedure

The dual-task experiment consisted of a speeded movement task paired with a non-speeded discrimination task. In each trial of the *movement task*, the participants had to listen out for three auditory signals presented from the two loudspeaker cones placed behind them. The participants were told that each trial would start with a short beep

(600 Hz, 50 ms), followed, after a random time interval (750-1000 ms), by a second beep. They were instructed to prepare the goal-directed reaching movement for the duration of the second beep in the trial (*prepare signal*, 800 Hz (high-pitched) or 400 Hz (low-pitched), 1000 ms).

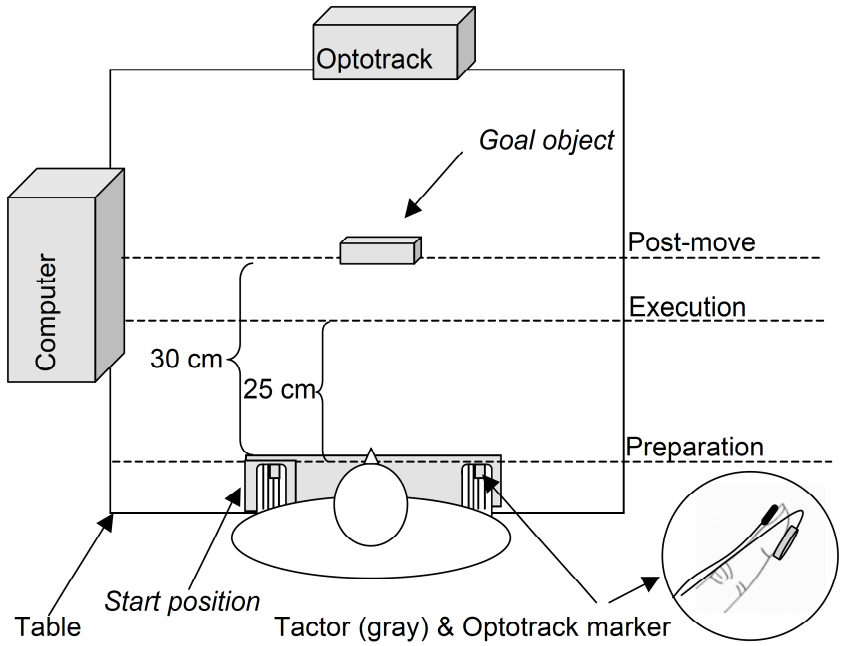


Figure 2.5. Experimental set-up used in **Experiment 2.5**

Half of the participants executed a left hand movement following the low-pitched prepare signal and a right hand movement following the high-pitched signal, and the other half of the participants had the reverse mapping. They then had to reach toward the goal object placed in front of them on the table at the offset of the preparation beep. When their hand was detected at the goal position, a double beep signal (600 Hz, 50 ms) was played following a random time interval (100-300 ms), indicating the end of the movement task and requiring a return to the start position. In a special condition (stopped execution), immediately after the preparation signal, when the movement of the hand was expected to start, a low-pitched tone was played (200 Hz, 200 ms). The participants were instructed not to execute the prepared movement

and ‘freeze’ at the start position until the double beep signal was delivered, signaling the end of the trial.

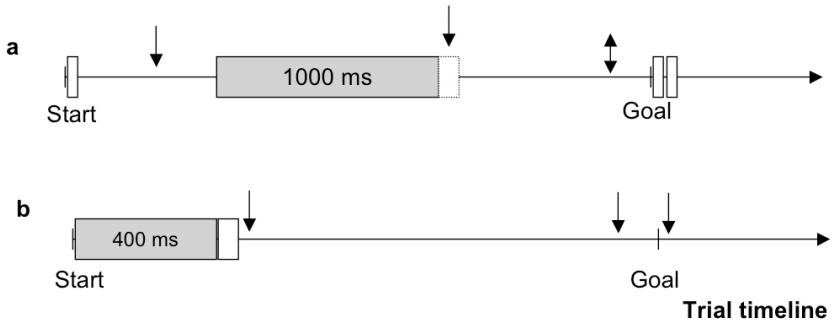


Figure 2.6. Trial timeline for **Experiment 2.5** (**a**) and **Experiment 2.6** (**b**). In **Experiment 2.5**, every trial started with a neutrally pitched beep (white bar), which was followed after a random time interval by either a low or high-pitched prepare beep (grey bar) requiring either a left hand/right hand, or a right hand/left hand movement at its offset. Tactile stimulation was delivered concomitantly to both index fingers, at different points in time during the trial, as highlighted by the downward arrows. The upper arrow indicates that the stimulation was delivered during the execution period, however, no movement was executed. Once the moving hand was detected at the goal location, two neutrally-pitched beeps were played (white bars), indicating the end of the movement task and requiring a response with regard to the tactile stimulation quality (**a**). In **Experiment 2.6**, the participants prepared the goal-directed movement for the entire duration of the prepare signal (grey bar) and initiated the movement following the go signal (white bar). Downward arrows represent the timing of the tactile stimulation delivery (**b**).

For the secondary task, the *non-speeded discrimination task*, tactile pulses (250 Hz, 100 ms) were presented concomitantly to the participant’s index fingers at different points in time during the trial, depending on the spatial location of the hand executing the movement. In particular, tactile stimulation could be delivered either during the *movement preparation period – ‘unknown hand’* (i.e., between the first beep (start of trial) and the second (prepare) beep, when the hands were at rest, but when it was not yet known which hand would have to be moved during the trial). Tactile stimulation could also be delivered during the *movement preparation period – ‘known hand’* (50 ms after the second (prepare) beep, when the hands were still at rest and it was known which hand was to be moved during the trial). Finally, tactile stimulation could be delivered during the *movement execution* period (when the moving hand crossed the intermediate coordinates on the table, 25 cm from the start

point), or during the *stopped execution* period (600-800 ms after the 'freeze' beep, when the participants prepared the movement, but did not execute it).

Participants used a power palmar grasp (Feix et al., 2009) to grasp the goal object; the index finger on which the tactor was mounted therefore being used in performing the action. At the end of the trial, the participants were instructed to press one of the two buttons of the response box on their way back to the start position, depending on which pulse they felt as being stronger or weaker (left vs. right hand). Once the participants had made their response, the experiment progressed to the next trial following an intertrial interval of 2000 ms (see Figure 2.6a for a depiction of the trial timeline in **Experiment 2.5)**.

2.6.1.4. Design

The design of Experiment **2.5** was very similar to that of **Experiments 2.1-2.3**. In the following, only the differences in the psychophysical design are highlighted. **Experiment 2.5** involved an adaptive procedure comprising eight different interleaved staircases for each of the 8 conditions at the intersection of the two experimental variables: 4 Timings of tactile stimulation delivery (motor preparation – unknown hand, motor preparation – known hand, motor execution, and stopped execution) x 2 Movement Hand (left hand vs. right hand). For each staircase, the pulse delivered to the resting hand was kept constant (standard pulse) throughout the trials/experiment; the moving hand pulse was calculated by either subtracting or adding one step from the standard pulse delivered to the resting hand. Therefore, the resulting thresholds were comparison thresholds for the moving hand, with the resting hand as a standard.

The presentation of trials from each of the staircases was randomized throughout the course of the experiment. The experiment required the participants to complete a maximum of 960 trials. It finished when all eight staircases had terminated. The participants performed a short block of 40 movement-only practice trials at the beginning of the experiment. These practice data did not constitute part of the final analysis.

2.6.1.5. Data analysis

The data were analyzed using a repeated-measures ANOVA with the following factors: Timing of the tactile stimulus (delivered during movement preparation – unknown hand, movement preparation – known hand, execution, or stopped execution) Movement hand (left vs. right hand).

2.6.2. Results

On average, the participants needed 617 trials in order to complete the experiment (approximately 79 per staircase). There was no statistical difference between the average number of trials needed to finish the staircase per tested condition.

Mean thresholds and individual data from all participants are presented in Figure 2.7. Numerical values of the thresholds in the eight conditions are presented in Table 2.3.

The results indicated that the timing of tactile stimulation significantly influenced the threshold data [$F(3,33)=9.09$; $p<.001$]. Pairwise comparisons revealed the thresholds to be significantly lower (i.e., better performance was observed) in the

stopped execution period as compared to the preparation – known hand period (p=.003) and the execution period (p=.002).

	Left hand		Right hand	
	Mean	SE	Mean	SE
Preparation-unknown hand	2.83	0.29	3.00	0.27
Preparation-known hand	2.92	0.29	3.86	0.42
Execution	3.47	0.31	3.52	0.30
Stopped execution	2.39	0.35	2.26	0.25

Table 2.3. Mean tactile thresholds (in dB) from **Experiment 2.5** together with their standard errors (SE) for the two hands, split according to the four different timings of tactile stimulation delivery (stimulation delivered during movement preparation when the moving hand was unknown, during movement preparation at the known movement hand, during movement execution, and in the hand that prepared the movement, but did not execute it, during the movement execution period).

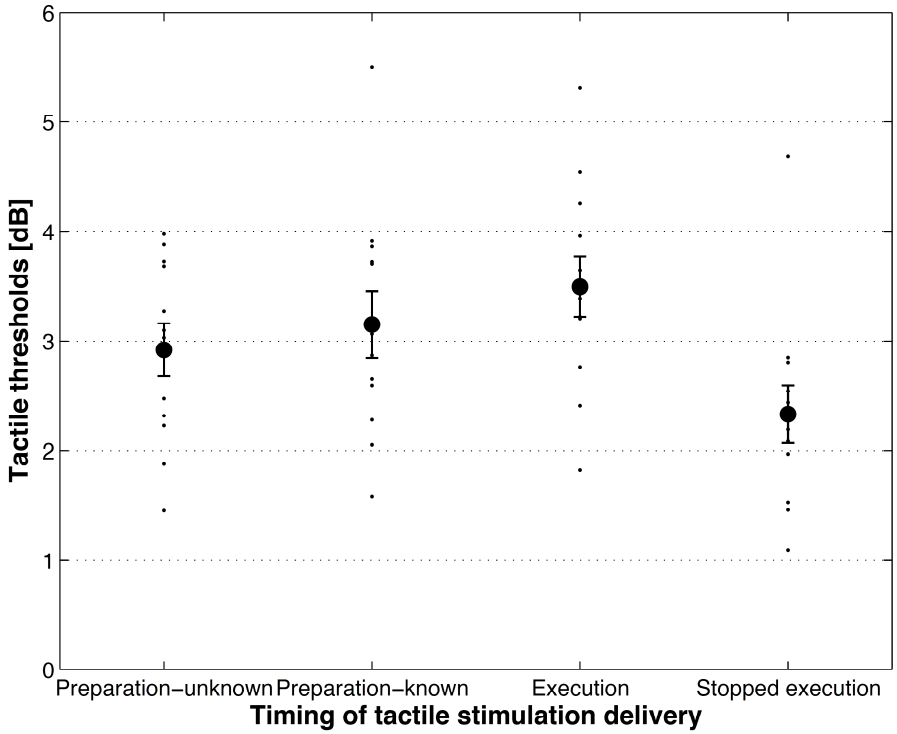


Figure 2.7. Scatter-plots of the individual threshold data together with the means for the various timings of tactile stimulation delivery in **Experiment 2.5**. Vertical error bars represent the standard errors of the means.

None of the other comparisons reached statistical significance. The threshold data revealed no significant difference between the tactile thresholds computed for the left and right hand [$F(1,11)<1$; n.s.]. Moreover, there was no interaction between the Movement hand and Timing of the delivery of the tactile stimulus [$F(3,33)<1$; p=n.s.].

2.6.3. Discussion

The goal of **Experiment 2.5** was to investigate whether any attentional prioritization was present at the moving effector during the preparation period of a goal-directed reach-to-grasp movement, prioritization elicited by the mere act of selecting the effector and preparing to move (Rizzolatti & Craighero, 2009; Rizzolatti et al., 1994). At the same time, given previous accounts of sensory suppression (Chapman & Beauchamp, 2006), it was hypothesized that perceptual performance would be significantly impaired for tactile stimuli delivered during the movement of the hand toward the goal object.

The results of **Experiment 2.5** are intriguing: While, as expected, a decline in the performance of the perceptual task for the motor execution period was indeed found (asserting the suppression mechanism acting on tactile perception previously found during the execution of the movement), the attentional manipulation utilized in **Experiment 2.5** (the selection of the effector to be moved) didn't have the expected outcome: Tactile thresholds measured during the preparation period at the moving hand (when the participants 'invested' their attentional resources in the movement effector) were not significantly different from those recorded during the motor execution period.

Moreover, the thresholds recorded in this same 'attention' condition were also not significantly different from those recorded in the preparation period, when the participants did not yet know which hand was to be moved during the trial. These results indicate that the preparation to move does not induce a shift of tactile attention to the movement effector. Rather, the present results advocate in favour of an inhibitory mechanism resulting from the movement itself (i.e., the motor command),

which builds up well in advance of the start of the movement, after the selection of the movement effector has taken place. Indeed, electrophysiological investigations have long-established the *Bereitschaftpotential* – a particular EEG modulation triggered by the activity that starts building up in the motor cortex long before movement onset, as well as the conscious decision to move (Kornhuber & Deecke, 1964; see also Haggard, 2008).

In contrast, thresholds measured in the stopped execution period, when participants prepared the goal-directed movement, but nevertheless, did not execute it, were significantly lower than both the execution period, as well as the preparation period, when the movement effector was known to the participants.

Therefore, taken together, the results of **Experiment 2.5** indicate that the movement effector does not benefit from the 'default' attentional prioritization (i.e., as given by the selection for the movement) in the preparatory period of goal-directed movements. Instead, it appears that at least at a *behavioural* level, movement (encompassing both preparation and execution periods) most likely brings only a deterioration in what it is felt for the effector of the goal-directed movement.

Experiment 2.6 was designed as a final attempt to investigate whether *endogenous* attention results in facilitation for what is felt during the various phases of a goal-directed movement. This hypothesis was tested by asking participants to perform a dual-task with a speeded reach-to-grasp movement task together with a speeded tactile response as a perceptual task. Endogenous spatial attention was manipulated by increasing the probability that the tactile stimulus would be delivered to either the moving or resting hand; the probability of stimulation was known in

advance by the participants (Spence et al., 2000b). In a control condition, the probability that stimulation would be delivered to either the moving or resting hand was matched. Given the probability-based attentional manipulation, faster RTs were expected in those conditions in which it was more probable that the tactile stimulus would be delivered to one or other hand (either moving or resting), as compared to the equal probability condition.

2.7. Experiment 2.6: Endogenous attention results in an enhanced speed of reaction to tactile events during movement execution

2.7.1. Methods

The methods of this experiment are very similar to those of **Experiment 2.5**. Therefore, in the following only the methodological differences will be highlighted.

2.7.1.1. Participants

Twelve participants (7 male, one left-handed; mean age of 27 years, age range 25-37 years) recruited among the student population of the University of Munich took part in this experiment. The experimental session lasted for approximately 45-60 minutes. Participants were given 8 EUR for taking part in the study.

2.7.1.2. Apparatus

The participants were seated at a table in a well-lit room, with their chin on a chinrest. A cylindrical wooden object (5.5 cm diameter, 5.5 cm height) was placed centrally on

the table at a distance of approximately 30 cm, directly in front of the participant. The tactors that the participants wore on the ventral part of their index fingers were covered in several layers of thin sponge in order to reduce the possibility that participants would be able to hear the sound of their operation. The participants also wore over-the-ear earmuffs (3M 1345) for the duration of the experiment for the same reason. At the start of every trial, the participants rested their hands on two pieces of soft sponge, placed symmetrically on the table, to the left and right of the chinrest. The auditory stimuli were delivered from two loudspeaker cones, one placed on either side of the table. The loudness was adjusted to guarantee that the participants were able to hear the stimuli, despite wearing earmuffs. The motion of the participant's hands was monitored on-line using a Polhemus Liberty electromagnetic motion tracking system with a sampling rate of 240 Hz (Polhemus Inc., Colchester, VT, USA). The participants responded by means of a footpedal placed on the floor below the table under their right foot and connected to the computer.

2.7.1.3. Procedure

The dual-task experiment consisted of a speeded movement task paired with a speeded detection task. In each trial of the *movement task*, the participants had to listen out for two auditory signals presented from the two loudspeaker cones placed on the table in front of them. They were instructed to prepare the goal-directed reaching movement for the duration of the first auditory signal of the trial (*prepare signal*, 600 Hz, 400 ms). They then had to reach toward the cylindrical wooden object placed in front of them on the table as soon as they heard the second beep (which acted as the *go signal*,

400 Hz, 100 ms). The participants reached for and grasped the goal object, after which they returned to the start position.

For the *speeded detection task*, a tactile pulse (250 Hz, 50 ms) was presented to the participant's index finger at a different point in time, depending on the spatial location of the hand executing the movement. In particular, tactile stimulation could be delivered either during the *movement preparation period* (immediately after the go signal, when both hands were located at the start position), during the *movement execution* period (when the moving hand crossed the intermediate coordinates on the table, 25 cm from the start point), or in the *post-movement* period (100 ms after the grasp of the goal object). The participants were instructed to press the footpedal in response to the tactile pulse as soon as possible, while still executing their goal-directed reaching movement. Once the participants had responded, the experiment progressed to the next trial following an intertrial interval of 2000 ms. See Figure 2.6b for a depiction of the trial timeline in **Experiment 2.6**.

2.7.1.4. Design

The experiment comprised 6 blocks of 48 trials each, with a short break between each block. The Movement Hand (either left hand or right hand) was blocked, so that participants performed 3 blocks of trials with the right hand moving and the left hand resting, and another 3 blocks with the left hand moving and the right hand resting. Within each block of trials, the manipulated variables consisted of the Timing of the delivery of the tactile stimulus (during motor preparation, execution, or post-movement), and the Hand that received stimulation (moving vs. resting).

The Probability of stimulation as an attentional manipulation (either higher (75%) at the resting hand, equal probability (50% at each hand), or higher (75%) at the moving hand) was blocked and the order in which the experimental blocks were presented was randomized for each participant, as well as across participants. The experimenter, present in the room for the duration of the experiment, informed the participant prior to each block of trials where the tactile stimulus would likely be delivered from in the upcoming block (more likely at the moving hand, with equal probability to either hand, or more likely at the resting hand). The participants were also instructed which hand (either left hand or right hand) to move throughout the block of trials. The participants performed a short block of six practice trials at the beginning of the experiment; the practice data were not included in the final analysis.

2.7.1.5. Data analysis

Trials with RTs to initiate the goal-directed reach-to-grasp movements, as well as trials with total movement duration (between the start point and the to-be-grasped object) greater than two seconds, were excluded from the final data analysis. In total, 4% of the trials were excluded from the analysis. For the remaining trials, an RT analysis was carried out. RT was defined as the time required to press the foot-pedal in response to the tactile stimulus delivered on the index finger. The data were analyzed with a repeated-measures ANOVA with the following factors: Probability of tactile stimulus (higher at the resting hand, equal, or higher at the moving hand), Stimulated hand (moving vs. resting), the Timing of the tactile stimulus (delivered during preparation, execution, or post-movement), and the Movement hand (left vs. right hand).

	Left hand												Right hand											
	High probability at rest				Equal probability				High probability while moving				High probability at rest				Equal probability				High probability while moving			
	Moving hand		Resting hand		Moving hand		Resting hand		Moving hand		Resting hand		Moving hand		Resting hand		Moving hand		Resting hand		Moving hand		Resting hand	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Preparation	496	52	429	40	522	39	470	44	452	34	457	43	501	48	452	37	580	67	561	54	477	39	501	57
Execution	319	19	319	22	358	23	346	23	327	17	313	20	307	28	300	23	362	29	366	32	329	28	308	25
Post-move	287	32	291	19	331	30	325	31	316	22	268	18	286	33	287	28	340	40	336	34	324	29	283	30

Table 2.4. Mean RTs (in ms) in **Experiment 2.6** together with their standard errors (SE) for the two hands, split according to the moving and resting hand and the timing of tactile stimulus, for the three different conditions (stimulus usually delivered to the resting hand, equal probability to either hand, and stimulus usually delivered to the moving hand).

2.7.2. Results

The mean RTs together with standard errors for tactile stimuli delivered at the various different points in time during the goal-directed reach-to-grasp movement, split according to the Probability of tactile stimulation and the Stimulated hand factors are shown in Table 2.4.

These results highlight a main effect of Probability of tactile stimulation delivery [$F(2,22)=10.68$; $p=.001$] with participants responding significantly more slowly to the tactile stimulus under conditions of equal probability of tactile stimulation delivery, as compared to high probability of delivery at either the resting ($p=.001$), or moving hand ($p=.021$; see Figure 2.8). There was no significant difference between conditions of higher probability of stimulation delivery at the resting or moving hand.

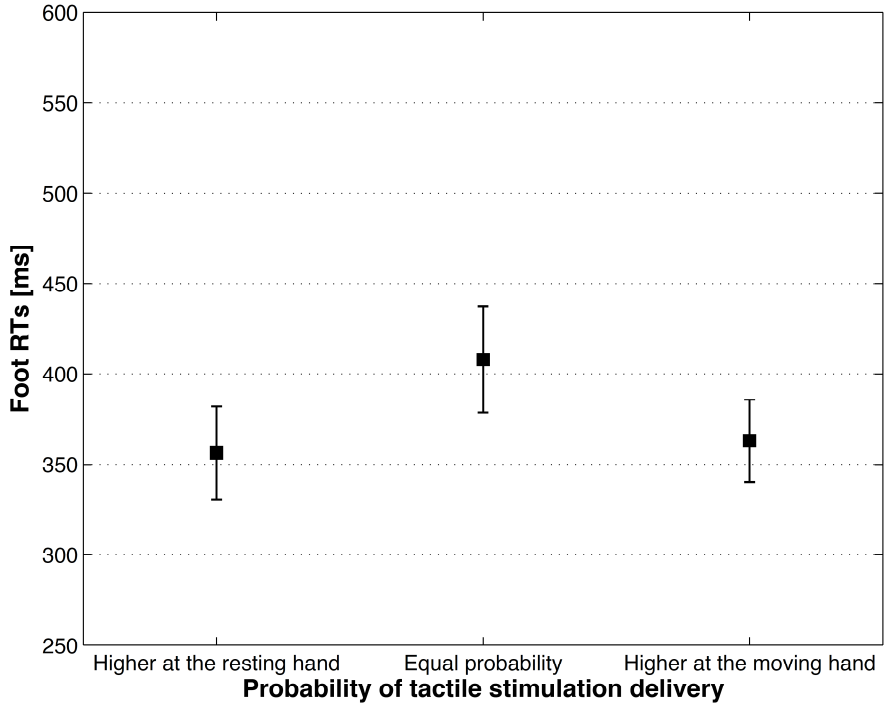


Figure 2.8. Mean tactile RTs for the different probabilities of tactile stimulation delivery in **Experiment 2.6**. Vertical error bars represent the standard errors of the means.

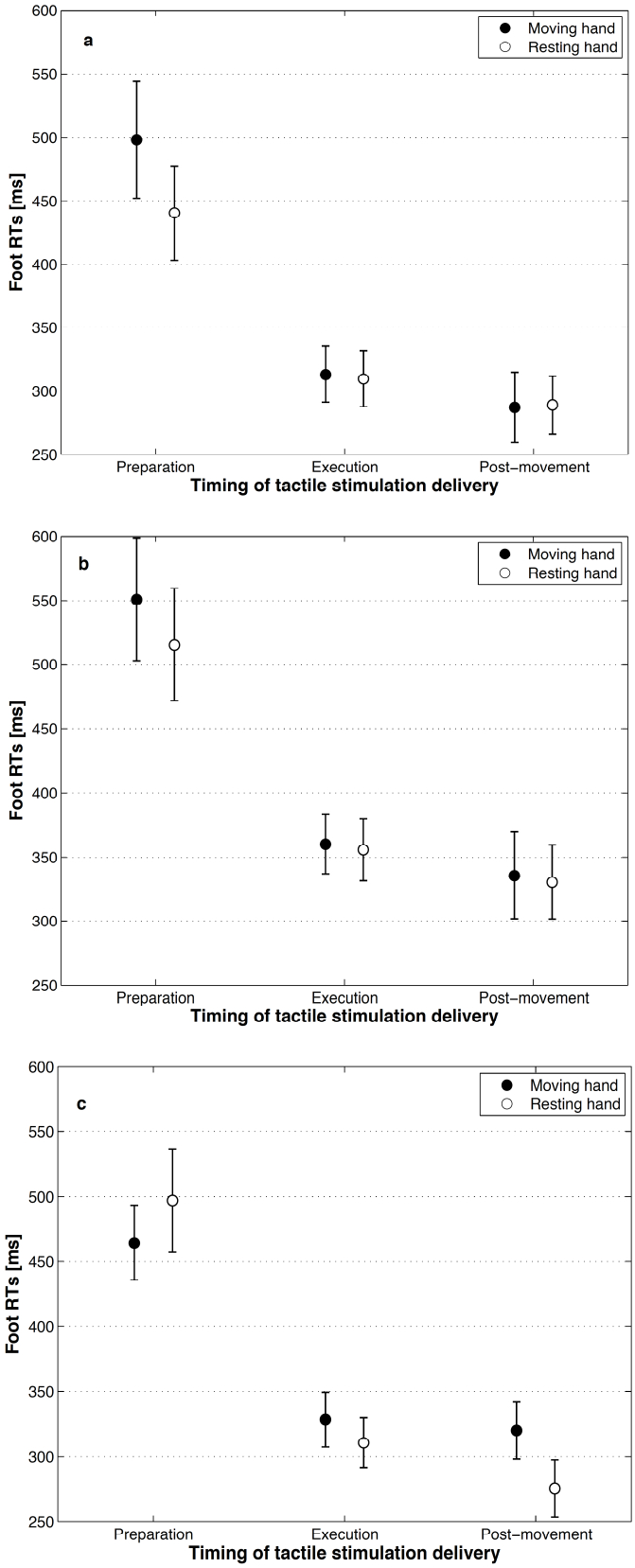


Figure 2.9. Mean RTs for the moving (filled circles) and resting hand (empty circles) split according to the timing of tactile stimulus for the different probabilities of tactile stimulation in **Experiment 2.6**: (**a**) Higher at the resting hand, (**b**) Equal probability, and (**c**) Higher at the moving hand. Vertical error bars represent the standard errors of the means.

The participants also responded significantly more slowly to tactile stimuli delivered to the moving hand, as compared to stimuli delivered to the resting hand [$F(1,11)=10.35$; $p=.008$]. Moreover, the analysis also revealed a main effect of the Timing of tactile stimulation [$F(2,22)=41.13$; $p<.001$; $\varepsilon=.571$]. Participants responded significantly more slowly to tactile stimulation while preparing to move, as compared to when executing the goal-directed movement ($p<.001$), or during the post-grasp period ($p<.001$); RTs in the execution period were also significantly slower than in the post-movement period ($p=.045$). There was no difference in RT as a function of which hand executed the reach (left vs. right hand) [$F(1,11) <1$; n.s.]. Finally, a 3 (Probability) x 2 (Stimulated hand) x 3 (Timing of tactile stimulus) interaction was observed [$F(4,44)=4.51$; $p=.004$]. Pairwise comparisons revealed that RTs to the tactile stimulus were significantly slower in the movement preparation period for the moving hand as compared to the resting hand when the probability that stimulation would be delivered to the resting hand was high ($p=.039$). RTs for tactile stimuli delivered to the moving hand were also significantly slower in the post-grasp period when the probability of the moving hand being stimulated was high ($p=.002$). See Figure 2.9 for a schematic depiction of this effect.

2.7.3. Discussion

It was hypothesized that by endogenously directing a participant's spatial attention to either the moving or resting hand, a reduction in tactile RTs would be observed. As expected, participants responded significantly more rapidly to tactile stimulation under conditions of high probability stimulation to both the moving and resting hand,

as compared to their responses in the control equal probability condition. There was no significant difference between the conditions of higher probability and lower probability of stimulation. This pattern of results suggests that a top-down attentional modulation of tactile perception may be present during both the preparation and execution of simple goal-directed reach-to-grasp movements.

However, one needs to consider the distribution of RTs over the course of the goal-directed movements that were executed by participants in **Experiment 2.6**: The participants responded significantly more slowly to tactile stimulation during the motor preparation period, as compared to the execution and post-movement periods. This result could be indicative of a dual-task limitation. It was in the preparation period that the participants were instructed to prepare the goal-directed reach-to-grasp movement and at the same time to make a speeded response to the tactile stimulus delivered at about the same time. Therefore, while they prepared the grasp, their reaction to the delivery of the tactile stimulus was slowed. This psychological refractory period (PRP; Welford, 1952) is common in dual-task situations, where the delay in RTs for the second task is due to a bottleneck in the response selection of the first task (Pashler, 1992; Spence, 2008). The response selection for the second stimulus (in this case, the footpedal response to a tactile stimulus) can only occur once the response selection of the first stimulus (the reach-to-grasp movement) has been completed. In this light, a purely attentional explanation cannot fully account for the effects reported above, as the response selection bottleneck has been commonly explained as a cognitive capacity limitation, one that is most often unaffected by attentional manipulations (e.g., Pashler, 1991; though see also Schumacher et al., 2001,

for examples of how the bottleneck can be over-ridden).

As such, so far **Experiments 2.5** and **2.6** presented evidence of a lack of attentional facilitation at the moving hand during the preparatory phase of reach-to-grasp movements. This outcome was demonstrated by attentional manipulations such as the mere preparation to move (**Experiment 2.5**), as well as the endogenous expectation-based manipulation of attention (**Experiment 2.6**). The starting premise for **Experiment 2.7** was that the shorter the *attentionally-invested prepare* auditory signal (1000 ms in **Experiment 2.5** and 400 ms in **Experiment 2.6**), the more likely attention is to influence the perception of tactile stimuli delivered to the moving hand (see Deubel & Schneider, 2003, 2004). Therefore, in **Experiment 2.7,** tactile thresholds were recorded during the motor preparation period of simple reach-to-grasp movements of the right hand. The attention allocation time was manipulated by means of different lengths of the auditory signal instructing the movement preparation/initialization (i.e., the attentionally-invested phase of the goal-directed movement was targeted).

Participants executed reach-to-grasp movements with their right hand at the offset of a short (100 ms), medium (400 ms), or long auditory signal (1000 ms). If attention does indeed influence the moving hand, then it would be expected to manifest itself at the shortest attentional allocation time, being potentially followed by an inhibitory mechanism, such as inhibition of return (IOR, see Spence et al., 2000a, and Klein, 2000, for a review). For example, in typical cuing paradigms, it has been demonstrated that attention is deployed at the cued location within the first 300 ms after the presentation of the cue; after longer periods of time, the inhibitory IOR effect

takes hold (McGlone, Lloyd, Newton, & Bowtell, 1999; Röder, Spence, & Rösler, 2002; Tassinari & Campara, 1996).

It was thus hypothesized that if IOR were responsible for the lack of attentional effects found in the preparatory phase of **Experiments 2.5** and **2.6**, then a differential pattern of tactile sensitivity should be found for the different timings of tactile stimulation delivery: short, medium, and long. However, a comparable pattern of tactile sensitivity found in **Experiment 2.7** would instead argue against IOR as a possible contaminating factor underlying the lack of attentional facilitation in the preparation period of **Experiments 2.5** and **2.6**, and thus accepting the hypothesis that the preparation phase of a reach-to-grasp movement is not prone to attentional facilitation.

2.8. Experiment 2.7: IOR does not account for the lack in attentional facilitation during the movement preparation period

The apparatus and procedure of **Experiment 2.7** closely follow those of **Experiments 2.1-2.2**. Furthermore, the design and data analysis are very similar to those of **Experiment 2.5**. In the following, differences in methodological aspects will be highlighted.

2.8.1. Methods

Ten participants (all female, all right-handed, mean age 26 years, age range 23-29 years) took part in this experiment. The experimental session lasted for approximately 30 minutes and participants were given a £5 gift voucher in return for their

participation.

The participants were seated at a table in a well-lit room. Two computer mice were affixed to the surface of the table, to the right of the participant, with the mouse closest to the participant (the *start mouse*) positioned at a comfortable distance for the participant to interact with and the second mouse placed 30 cm in front of the start mouse (*goal mouse*; see methods in **Experiments 2.1-2.2**). The participants wore headphones for the delivery of auditory stimulation. They responded by means of two footpedals connected to the computer.

The dual-task experiment consisted of a speeded movement task paired with a non-speeded perceptual task. In each trial of the *movement task*, the participants had to listen out for three auditory signals presented over the headphones. The participants were instructed to start each trial by keeping the start mouse button depressed. This ensured that they were at the start position at the beginning of the trial. As soon as their hand was detected at the start, each trial started with a neutrally pitched short beep (400 Hz, 50 ms), followed, after a random short time interval (100 to 200 ms), by a second beep. The participants were instructed to prepare the goal-directed reaching movement for the duration of the second beep of the trial (*prepare signal*: short (800 Hz, 100 ms), medium (800 Hz, 400ms), or long (800 Hz, 1000 ms). They then had to reach toward the goal mouse placed in front of them on the table at the *offset* of the preparation beep. As soon as their hand reached the goal position, another neutrally pitched beep signal (400 Hz, 50 ms) was presented, indicating the end of the trial.

For the *perceptual task*, participants received two concomitant vibratory

stimuli (250 Hz, 100 ms) at both their middle fingers after a random time interval (5-200 ms) from the offset of the prepare beep. They had to make a non-speeded response by comparing the two stimuli and deciding which one was stronger or weaker, once the movement was finished. The experiment progressed on to the next trial after an inter-trial interval of 1000 ms. The design and data analysis were identical to those of **Experiment 2.5**.

2.8.2. Results and Discussion

The results demonstrated that participants had comparable thresholds for all the three tested 'attention allocation times' (short (M=2.97 dB, SE=.40), medium (M=3.06 dB; SE=.37), and long (M=3.15 dB, SE=.45)) [$F(2, 18)<1$; n.s.], thus excluding IOR as a possible explanation for the attenuation results found in **Experiment 2.5** during the motor preparation period – known hand.

2.9. General discussion of Experiments 2.4-2.7

Experiments 2.1-2.3 presented evidence of tactile suppression during the execution of goal-directed movements. **Experiments 2.4-2.7** were designed to investigate attentional contributions during both the execution phase of the movement (**Experiment 2.4**), as well as the preparation period of the tested goal-directed reach-to-grasp movements (**Experiments 2.5-2.7**).

Having documented clear evidence of the lack of attentional contributions to the sensory suppression experienced during the execution phase of the movement (**Experiment 2.4**), the remaining experiments investigated attention during the

preparatory phase of the movement. As such, **Experiments 2.5-2.6** were designed to investigate whether attentional orienting toward the movement effector of a goal-directed reach-to-grasp movement would result in enhanced tactile perceptual performance. This question was investigated by measuring tactile thresholds in **Experiment 2.5** and tactile RTs in **Experiment 2.6**, and while using experimental movement paradigms that were almost identical. At the same time, attention was manipulated by the selection of the effector to be moved in the preparatory phase of the reach-to-grasp movement (**Experiment 2.5**) and by higher probabilities of stimulation at either the moving or resting effector (**Experiment 2.6**). Depending on the timing of delivery of tactile stimulation, a differential pattern of results was predicted: enhanced tactile performance at the movement effector during the motor preparation period, and a decline in performance during the motor execution period.

The results of **Experiment 2.5** highlighted that tactile performance was comparable in the two preparation periods ('known hand' and 'unknown hand'). This result indicates that the act of selecting the effector for action does not result in an enhancement in what is felt there. In this respect, if one were to 'apply' the premotor theory of attention (Rizzolatti & Craighero, 2009; Rizzolatti et al., 1994) to the tactile modality, then one would predict tactile attention shifts to the movement effector before the initiation of the planned movement. However, it should be noted that the premotor theory might not be the best candidate for explaining attention for goal-directed hand movements in the tactile domain. As mentioned in **Chapter 1**, the premotor theory was pioneered in the visual modality, and is dependent upon the highly spatial characteristics of the visual modality. In contrast, the tactile modality is

more finely temporally tuned (Geldard, 1960; Kandel et al., 2000; Occelli, Spence, & Zampini, 2011; von Bekesy, 1963), and research should consider touch during movement from the perspective of the different timings of the movement itself (i.e., goal-directed hand movement), each with its own characteristics.

Another important result concerns the fact that the thresholds recorded in **Experiment 2.5** for the motor preparation period (when stimulation was delivered to the 'unknown', as well as the 'known' hand to be moved during the trial) are comparable with those recorded in the motor execution period. Therefore, these results can be taken as indicative of an attenuation mechanism acting on perception shortly prior to, and during, the execution of the movement (Chapman & Beauchamp, 2006; Walsh & Haggard, 2008; Williams & Chapman, 2002; Williams et al., 1998). Note that the inhibitory IOR mechanism is not responsible for such attenuating effects, as highlighted by the results of **Experiment 2.7**; Nevertheless, IOR effects have previously been reported for speeded measures of perceptual functioning (McGlone, et al., 1999; Röder et al., 2002; Tassinari & Campara, 1996). Moreover, if one considers the 'stopped execution' condition in **Experiment 2.5**, the thresholds measured in this condition were significantly lower (indicating better performance) as compared to those measured in the motor execution condition. In both conditions, participants prepare the goal-directed movement, it is only that in one condition they actually do execute the movement, while in the other they inhibit their movement. Tactile stimulation is delivered at roughly the same point in time for both conditions. Performance is also significantly worse in the preparation period when the movement effector has already been selected, as compared to the control stopped execution

period. This significant difference in thresholds recorded for movement conditions as compared to the non-movement control condition could be taken as a clear indicator of an inhibitory effect on tactile perception occurring shortly prior to and during movement execution, movement itself being the trigger. Such results are in line with previous results on sensory attenuation.

The goal-directed movement could be regarded as a dual-task distraction (Pashler, 1991). For example, significant decreases in cerebral blood flow (CBF) in the primary somatosensory cortex were found when participants concentrated on the quality of the vibratory stimulation they received and at the same time performed a mental arithmetic task, as compared to the perceptual-only task; no differences were nevertheless observed though between the CBF responses under conditions of passive stimulation only and passive stimulation plus attention directed to its quality (Meyer et al., 1991). Thus, although such effects are taken as an indicator of attention, the attentional facilitation results from a dual-task situation, and not from a pure baseline of tactile perception. It appears then that even at a neural-level the facilitatory attentional effects appear only when having a distracting activity (e.g., mental arithmetic), not simply when passive stimulation is delivered plus attention directed to its quality.

Nevertheless, when considering the speed of reaction to tactile events, the results of **Experiment 2.6** highlighted the fact that participants responded more rapidly to tactile stimulation under conditions of higher probability of stimulation delivery to either the moving, or the resting, hand. It was hypothesized that attentional effects should be particularly apparent for the motor preparation period (see

predictions of the premotor theory, Rizzolatti et al., 1994, outlined in **Chapter 1**). While preparing to move however, participants responded more rapidly to tactile stimuli delivered to their resting hand only when it was very likely that stimulation would be delivered there, whereas a lack of facilitation was observed in responding to tactile events at the moving hand when the probability of stimulation was higher for the moving effector. Such results could be taken as evidence of a lack of attentional shifts to the effector of a goal-directed movement.

However, evidence supporting tactile attention shifts to the movement effector comes from studies that have investigated simple finger lifting movements. For example, participants respond more rapidly to tactile events presented in the motor preparation period at their fingertips, when a lifting movement of that finger has been previously planned, as compared to invalid trials, where the finger to be moved and the finger to receive stimulation are different (i.e., situated at different hands, hence a spatial effect; Juravle & Deubel, 2009). In a similar manner, electrophysiological studies indicate that ERPs recorded in response to tactile stimulation delivered when a participant directs his/her attention to a specific finger (i.e., to the left or, to the opposite right hand; Forster & Eimer, 2005), are very similar to the ERPs recorded in the motor preparation period of a finger lifting movement (Eimer et al., 2005). Moreover, differential parietal ERPs were found in the motor preparation time interval between two auditory tones which gave differential information on the saccade/finger flexion movement to be executed at the offset of the second tone: The ERPs associated with the finger movements were significantly enhanced when full information (effector and direction) was provided by the first tone, as compared to effector only

information (van der Lubbe et al., 2000). The fact that, at a behavioural level, tactile attention shifts to the movement effector in simple finger lifting movements, but not to the effector of a goal-directed reach-to-grasp movement could indicate that in assessing attention effects the specific task that happens to be used is important: Detecting or discriminating tactile events at a finger (from either hand) that was previously prepared to be lifted allows *spatial* attention shifts to the movement effector. However, tactile sensitivity was tested in **Experiments 2.1-2.5**, and **2.7** of this chapter by using a *non-spatial task*. That is, tactile sensitivity was assessed to a comparison in the stimulation delivered to both the moving at the resting effector. Alternatively, the attentional effects found for the simple lifting movements and the lack of attentional effects in the case of goal-directed movements could be explained by taking into consideration the locus of attention: Tactile attention could shift to the *effector* of a simple finger lifting movement (which, as argued before, represents a spatial task), whereas, visual attention shifts could be directed to the *goal-object* in the case of more complex goal-directed movements[8].

One last point of discussion concerns the different patterns of results obtained when measuring discrimination (**Experiment 2.5**) as opposed to the speed of responding to tactile events (**Experiment 2.6**). In fact, just such a distinction has already been made for the visual enhancement of touch (VET, enhanced tactile processing due to vision of the human body; Longo et al., 2008), which occurs with acuity measures of tactile performance, but not in speeded detection tasks (Press et al.,

[8] Furthermore, this alternative explanation directs the discussion to a potential hierarchy of the senses in their contribution to sensorimotor integration, with (spatial) vision leading over the less-spatial (as defined by the peripersonal space surrounding the body) touch. See also the discussion of **Experiments 4.1-4.3** on this.

2004). With respect to the movement execution period, participants responded significantly more rapidly to tactile stimulation in **Experiment 2.6** while moving; However, they were significantly worse at comparing the two stimuli in **Experiment 2.5** delivered in the same time period, as compared to a control condition in which they prepared the movement, but refrained from executing it. If tactile perception deteriorates while we move, this suppression effect may be paired with a speeding-up of participants' responses to tactile events. At the same time, motor preparation is characterized by a slowing of participants' responses to tactile stimulation paired with no change of perceptual sensitivity. Therefore, it could be argued that this dissociation between discriminating the quality of tactile stimulation and the speed at which one can respond to the very presence of tactile stimulation results from a compensatory phenomenon acting on tactile perception while moving.

Lastly, having argued in favour of sensory suppression during movement execution (**Experiments 2.1-2.5**), as well as in favour of a lack of attentional shifts to the movement effector during the preparatory phase of the movement (**Experiments 2.1-2.7**), in one last experiment of **Chapter 2**, it was investigated whether this attenuating effect influencing tactile perception during movement execution would generalize to tactile exploratory movements as well.

2.10. Experiment 2.8: Tactile exploration reveals the importance of what is felt during movement execution

2.10.0. Introduction

Experimental results such as those reported in **Experiments 2.1-2.7** could also be challenged in what regards *the movement relevance* for the tactile modality. In this respect, if goal-directed reaches were shown to impair what is felt during movement, then exploratory movements could provide an answer to the question of whether tactile information receives a lower weighting as soon as we start moving. Alternatively, however, tactile information could indeed be relevant for movement and thus, necessary to our overall interaction with the surrounding environment.

The motivation for the last experiment (i.e., for **Experiment 2.8**) of the present chapter therefore relates to a simple paradox: If, when moving, tactile perception is impaired (see the results of the experiments reported in **Experiments 2.1-2.5** and **2.7**)), then how could an exploratory movement account for tactile suppression? Just to consider an ecologically valid task, reading Braille for blind users implies specific, most often bi-manual, disjoint movements in order to extract tactile information (Hughes & Jansson, 1994); However, tactile suppression has also been reported for easily-displaceable Braille characters (Ziat et al. 2010; see also Keyson & Houtsma, 1995). Exploratory hand movements are used in order to identify 3D objects, as well as to identify specific characteristics or features of objects or our close surroundings. In daily life situations, where tactile information is needed to achieve our goals, they are amongst the first to be used.

For example, just imagine that you are about to buy a cashmere sweater: Provided that all of the visual attributes are the same, when deciding on the quality of the garment, you will move your hand and *feel* the material with your fingers. The

movement of the fingers across the surface of the material will eventually give you the necessary information as regards its perceived quality. Such exploratory haptic/tactile behaviours are associated in marketing research with a pleasurable *'need for touch'* that customers exhibit when evaluating products that they may be interested in purchasing (Peck & Childers, 2003). Indeed, this general liking for haptic input is present especially when interacting with clothing, novel, or high-quality products (see Spence & Gallace, 2011, for a review). Lastly, possibly mirroring the visual domain, exploratory movements have been compared to *'windows through which the haptic system can be viewed'* (Lederman & Klatzky, 1987, p. 344).

Experiment 2.8 was designed to test *the relevance of movement to what is felt*, by using an additional task that is specific to the tactile domain (i.e., a tactile exploratory movement), together with the goal-directed reaches used previously (i.e., in **Experiments 2.1-2.7**). One of the possible implications of the results of Experiments **2.1-2.7** is that touch may appear to be of little relevance to reaching movements. In turn, on a daily basis, tactile exploratory movements are used with the scope of extracting and analyzing important features of the objects we interact with. Therefore, by comparing the characteristics of tactile perception during the execution of exploration and reaching movements, one could extract the functional significance of what is felt while moving.

Experiment 2.8 was designed in order to test this hypothesis. The experiment consisted of a speeded goal-directed movement as a primary task, together with a non-speeded perceptual task, as a secondary task. The goal-directed movement involved simple reaching or exploratory hand movements (i.e., the same as the reaching movements, with the only difference being that contact with the table surface was maintained). For the perceptual task, tactile discrimination thresholds were measured

for vibratory stimuli delivered to participants' wrists while executing the movement and while at rest. Moreover, in another perceptual task, surface discrimination performance was measured (in a same vs. different task) for the materials covering the surface of the table, during the execution of the different movements (i.e., exploration and reach). This performance measure was intended to assess the specificity of exploratory movements. For both perceptual tasks, tactile perception was specifically tested during the movement execution period, where previous sensory suppression effects were reported (see **Experiments 2.1-2.5**, and **2.7**). The tactile vibratory discrimination and surface discrimination tasks could be performed either singly or together, both under active movement and passive conditions (i.e., no movement required, but with tactile stimulation provided by the experimenter, mimicking the surface contact specific to the reaching and exploratory movements).

For the tactile vibratory discrimination task (TD task), the first hypothesis predicted a deterioration in what is felt (i.e., higher discrimination thresholds) during the active execution of the movement (both reaching and exploration), as compared to a control rest condition. It was hypothesized that if the acuity of tactile perception deteriorates during movement execution, irrespective of the movement type, then no difference in TD task performance between the two active reaching and exploration movements would be found. However, if exploration brings about an enhancement in what is felt, then tactile sensitivity should be higher for exploratory movements, as opposed to it being diminished, and thus irrelevant, during reaching movements.

The surface discrimination task (SD task) was conceived of as a task that will give the best performance for exploratory movements. Therefore, a significantly improved level of discriminatory performance was predicted during the execution of exploration movements, as compared to simple reaches. Moreover, significantly

improved performance was expected for active movements of the hand (i.e., where participants actively explored the table surface with the purpose of gaining tactual information on its features), as opposed to the passive execution mode, that entailed no voluntary movement. Lastly, for both perceptual tasks, a significant deterioration in performance was expected under conditions of dual-task execution, as opposed to single task execution.

2.10.1. Methods

2.10.1.1. Participants

Eight participants (1 male, all right-handed) took part in this experiment. The mean age of the participants was 26 years (range 21-29 years). The experimental session lasted for approximately 150 minutes and participants received a £20 gift voucher in return for taking part.

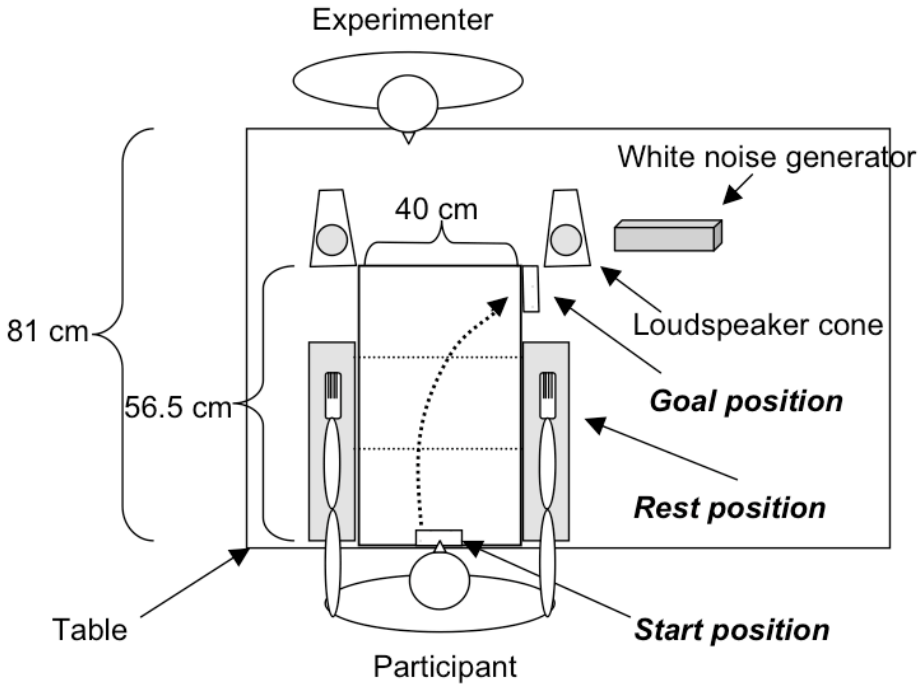


Figure 2.10. Experimental set-up used in **Experiment 2.8**. The participant is depicted with both hands/arms at the resting positions.

2.10.1.2. Apparatus

The participants were seated at a table (81 cm wide); the experimenter was seated/standing at the other end of the table. A rectangular piece of sponge-like material (24 cm long, 11 cm wide, and 2.5 cm high) was attached to the left side of the table in order for the participants to rest their left hand during the experiment (*left hand resting position*). On the participant's right side, a rectangular piece of wood (21.2 cm long, 17.2 cm wide, and 2.5 cm high) was attached to the table, together with an additional piece of spongy material (same physical measures) on top of it (*right hand resting position*). At the participant's chest edge of the table, between the two resting positions for the left and right hand, a rectangular object (6.5 cm long, 1.5 cm wide, and 3 cm high; *start position*) was positioned. The *goal position* was signaled with an identical object placed 19 cm in front of the right resting position. See Figure 2.10 for a depiction of the experimental set-up.

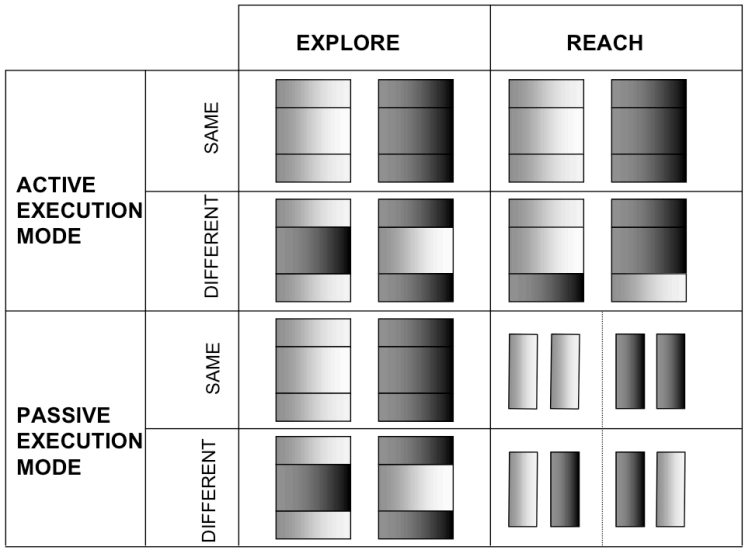


Figure 2.11. Schematic drawings of the types of boards used in **Experiment 2.8**, split according to the different experimental conditions. Dark shades of gray represent one type of material (i.e., cling film), and lighter shades of gray represent the other type (i.e., tinfoil).

On each trial, a carton board (hand made from painting board; 56.5 cm long, 40 cm wide, 0.6 cm high) covered in cling film, tinfoil, or a combination of the two materials, was placed in front of the participant, between the two resting positions. See Figure 2.11 for the different types of board used in the experiment.

Tactors were attached with tape to the ventral part of both of the participant's wrists and their wrists were then covered in several layers of thin sponge. The participants were blindfolded and wore closed ear headphones (Beyer Dynamic DT 531) for the duration of each block of the experiment. Two loudspeaker cones, one placed on either side of the table, delivered white noise throughout the experimental blocks. Depending on the task, the participants responded by means of two foot-pedals connected to the computer, as well as vocally, response that the experimenter entered into the computer.

2.10.1.3. Procedure

The experiment involved a speeded motor task (goal-directed reaching movement vs. exploratory movement) and two non-speeded perceptual tasks (tactile vibratory discrimination vs. surface discrimination). The motor tasks were designed either as active movements of only the right hand, or as passive movements.

2.10.1.3.1. Speeded motor task

Before the beginning of each trial, the participants rested their arms on the resting positions. The experimenter ensured the hands were at start and instructed them by saying 'Ready' and pressing a key on the keyboard to initiate the trial. At the experimenter's vocal signal, participants brought their hand to the start position (i.e., since they were blindfolded, they learned to feel the start position object positioned at

the edge of the table with the side of their index finger). At the start position, the participants were instructed to place their hand over the surface of the board such that they would feel the surface of the board with just their index, middle, ring, and little fingers. The thumb, as well as the palmar region of the hand, was not used during this experiment. After a random time interval following the experimenter's vocal instruction (500-750 ms), a short auditory signal was delivered over the headphones that participants were wearing (50 ms, 800 Hz) that acted as the go signal to initiate the movement.

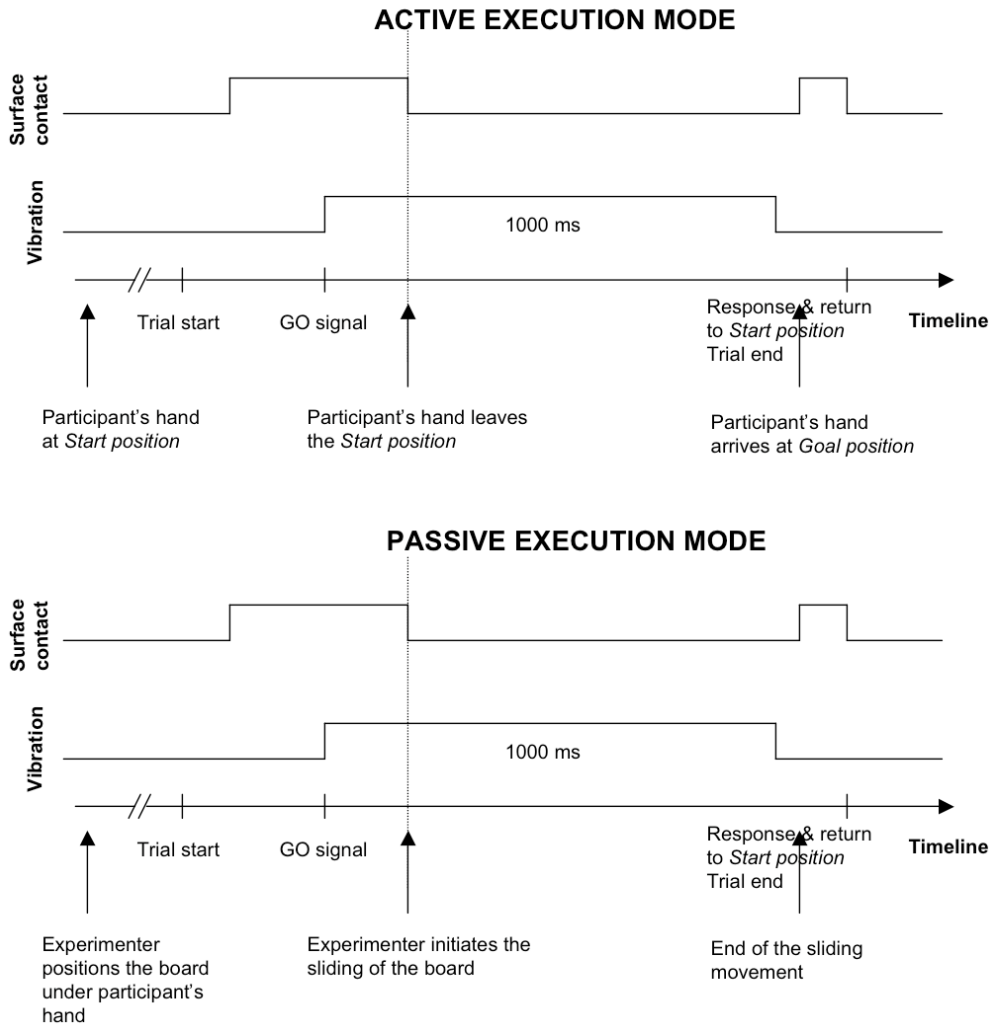


Figure 2.12. Trial timeline in the REACH movement conditions in **Experiment 2.8**. The vibration duration and the contact with the surface of the board are depicted for the two types of movement execution modes (active and passive). The EXPLORE movement conditions were identical to the depicted REACH conditions, with the only exception that the contact with the surface of the board was continuous throughout the movement execution phase.

In the ***speeded reaching movement condition***, the participants executed an outward movement with their right hand across the surface of the board. As such, if at the start of the movement their forearm was parallel to their torso, at the end of the movement, the participant's forearm formed an angle of approximately 90 degrees with respect to their torso. The reaching movement involved a 'jump' over the surface of the board, from the start position to the goal position. At the end of the movement, participants touched the goal position object with the side of their little finger. Once the goal position was reached, participants brought their hand back to the right hand resting position. See Figure 2.12 for a depiction of the trial timeline in the active and passive execution modes of the REACH movement conditions.

In the ***speeded exploratory movement*** condition, at the go signal, participants executed the same outward movement, this time, by keeping contact with the surface of the board until the goal position was reached. Participants also performed a control ***rest*** condition that required no movement of their hand. For this, they kept their right hand in the resting position and only performed the perceptual vibratory tactile discrimination task.

2.10.1.3.2. Non-speeded perceptual tasks

Two types of perceptual tasks were used in **Experiment 2.8**. In the ***tactile vibratory discrimination task (TD)***, shortly after the go signal, both of the tactors that the participants wore on their wrists were activated (250 Hz, 1000 ms). The participants made an unspeeded tactile intensity discrimination response: That is, they had to compare the right hand pulse to the left hand pulse and decide whether the intensity of right hand stimulation was stronger or weaker than that of the comparison pulse once

they had completed the movement task (and returned to the starting position). The participants were instructed to press one footpedal whenever a stronger pulse was presented to their right hand and the other footpedal whenever the right hand pulse was weaker. Response assignments for the left and right foot-pedals were counterbalanced across participants. In the ***tactile surface discrimination task (SD)***, participants had to indicate whether they perceived a change in the material covering the board (i.e., same material vs. different materials covering the table surface).

2.10.1.3.3. Single vs. dual perceptual task

The two types of non-speeded perceptual tasks could be performed, depending on the experimental condition, separately or together. Participants were informed at the beginning of each block of trials whether it was a single or a dual task block. For the ***single task*** blocks, the participants only performed a single perceptual task for the duration of a block of trials. For example, they performed an exploratory movement on each trial and at the end they either pressed one pedal or the other in order to respond to the quality of the vibratory stimulation, or alternatively, they gave a vocal response with respect to the quality of the surface of the board. For the ***dual task*** blocks, the participants always performed the vibratory tactile discrimination task as a first perceptual task. In random trials, after they made their pedal response for the first perceptual task, the experimenter requested their response to the second surface discrimination perceptual task. They again responded vocally and the experimenter inserted their response in the computer. Within an experimental block, participants didn't know in advance the trials in which their additional perceptual response would be required by the experimenter.

2.10.1.3.4. Active versus passive execution modes

Two types of execution mode were used in **Experiment 2.8**: active and passive. See Section 2.10.1.3.1 for a description of the active mode, which basically corresponds to the (active) speeded reaching or exploration movement executed by the participants. In contrast, the passive execution mode was introduced as a way to mimic movement, without the actual movement of the limb. In this respect, participants always kept their hands at the resting positions. In the ***passive exploration*** condition, at the beginning of each trial, the experimenter placed the board underneath the participants' fingertips. At the go signal, the experimenter touched their fingertips with the board and then slid it at a constant speed along the surface of their fingertips. In the ***passive reaching*** condition, the experimenter used two smaller boards (see Figure 2.11), one covered in cling film, and the other in tinfoil. The experimenter kept the boards with their lower corners superimposed in her left hand, such that they formed a V at an angle of about 45 degrees. At the beginning of the trial, depending on the condition, the experimenter positioned one of the ends of the board underneath the participant's fingertips. At the delivery of the go signal, she gently touched the fingertips with the prepared end, after which, she moved the V, such that the other end could be positioned underneath and touch the fingers as well. This is an example of the procedure for a trial that required the use of different materials. When the same material needed to be used for the passive reaching condition, the experimenter just paused shortly after the first touch and then performed the second touch with the same material.

Once the participants had made their response, the experiment progressed onto the next trial following a random inter-trial interval of 1500-2500 ms. The experimenter read the trial definition on the computer screen at the very beginning of each trial and changed the table board according to the up-coming condition.

2.10.1.4. Design

The experiment consisted of nine blocks of trials. Each block corresponded to an experimental condition. The manipulated variables were: Type of movement (reaching vs. exploration), Execution mode (active vs. passive), and Type of perceptual task (single vs. dual). Therefore, it was a 2 x 2 x 2 design; the ninth block consisted of the control rest condition for the tactile discrimination task. The order of the experimental blocks was counterbalanced across participants. See Table 2.5 for a summary of the experimental design.

Passive execution mode					Active execution mode			
Single task			Dual task		Single task		Dual task	
TD (rest)	SD (explore)	SD (reach)	SD+TD (explore)	SD+TD (reach)	SD (explore)	SD (reach)	SD+TD (explore)	SD+TD (reach)

Table 2.5. Experimental design in **Experiment 2.8**. SD stands for surface discrimination task and TD stands for the tactile discrimination task.

The design of the TD task was identical to that of the adaptive procedure used in **Experiments 2.1-2.5**, and **2.7**. The SD consisted of 28 trials per block. For half of the trials, boards consisting of the same material plates were used (i.e., 7 trials with cling film-only boards, and 7 trials with tinfoil-only boards). For the other half of trials, the boards were formed of different materials (i.e., 7 trials in which the covering material of the board changed from cling film to tinfoil, and 7 trials in which the material changed from tinfoil to cling film). The SD-only blocks consisted of the 28 randomly intermixed trials. The dual-task blocks had the 28 SD trials randomly intermixed amongst the TD trials.

2.10.1.5. Data analysis

Perceptual thresholds were calculated for the TD data, together with percentages of correct responses for the SD data. Depending on the experimental question, several analyses were performed that involved the use of repeated measures ANOVAs.

2.10.1.5.1. TD data analysis

For the TD analysis, three different ANOVAs were performed. In order to investigate whether the execution of movement interferes with what is felt, a first ANOVA was conducted with the factor Condition (rest vs. active exploration vs. active reaching) factor. The next step was to investigate whether not only movement affects tactile sensitivity, but also the concomitant tactile input delivered to a resting hand. For this, a second ANOVA was performed with the factor Task type (TD at rest vs. TD at rest plus passive exploration vs. TD at rest plus passive reaching). The third analysis was designed to investigate whether the movement type and the mode of movement execution gave rise to differential changes in tactile perception. For this, one ANOVA was conducted with the factors Movement type (exploration vs. reaching) and Execution mode (passive vs. active).

Lastly, for the dual-task conditions, bivariate correlations were conducted between the data from the two perceptual tasks, TD task and SD task, performed together under the dual task conditions. In order to investigate whether a relationship between the distribution of tactile thresholds in the TD task and the performance in the SD task arose from the dual-task situation, these primary correlations were followed by further partial correlations between the data from the two perceptual tasks performed together, while controlling for the data from the single task SD condition.

2.10.1.5.2. SD data analysis

For the SD analysis, one general 2 x 2 x 2 ANOVA was performed with the factors Movement type (exploration vs. reaching), Execution mode (passive vs. active), and Task type (single vs. dual). Furthermore, bivariate correlations were conducted for each type of movement, between the data collected under single and dual task conditions. In order to investigate whether a relationship between the distribution of correct responses in the SD task and that of the tactile thresholds in the TD task was explained by the simultaneous performance of the TD task, separate partial correlations were conducted between the same data while controlling for the variable TD at rest.

2.10.2. Results

2.10.2.1. TD results

Mean thresholds and individual data from all participants are presented in Figure 2.13. Figure 2.14 presents the TD threshold data plotted against the performance in the SD task for all the dual-task conditions in the experiment.

As expected for the TD task, the results indicated that tactile perception is deteriorated during movement [$F(2,14)=8.26$; $p=.004$]. Participants were significantly less sensitive in discriminating the quality of tactile stimulation while they were performing the active exploration movement ($p<.001$), as well as the active reaching movement ($p=.045$), as compared to the control rest condition, where no movement was performed. No significant difference was observed between the mean thresholds of the two active movement conditions, exploration and reaching ($p=.451$).

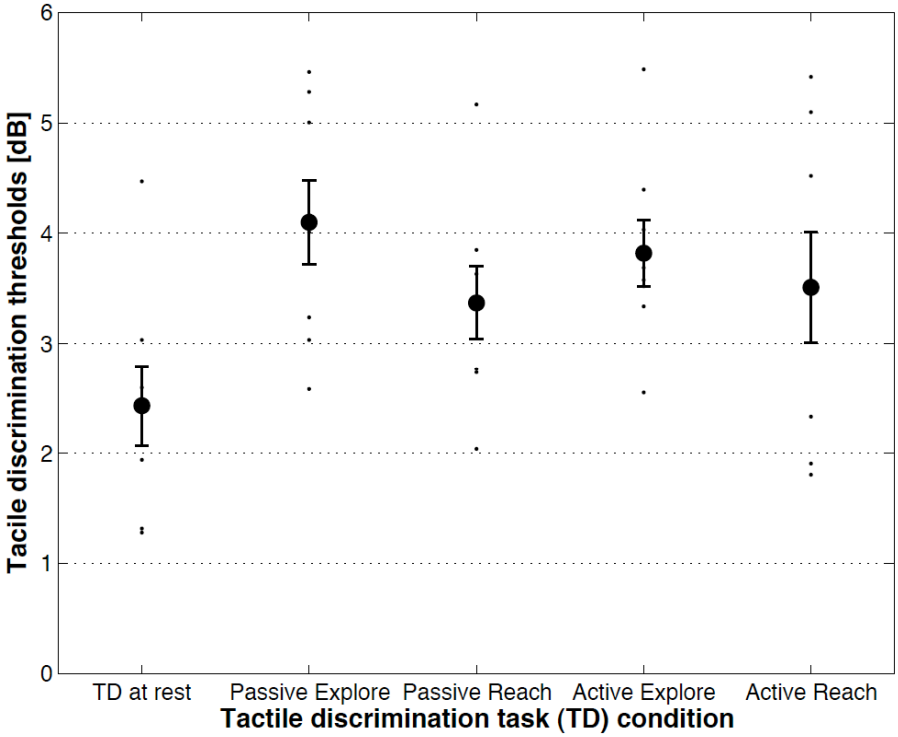


Figure 2.13. Scatter-plots of the individual threshold data together with the means for the TD task conditions from **Experiment 2.8**. Vertical error bars represent the standard errors of the means.

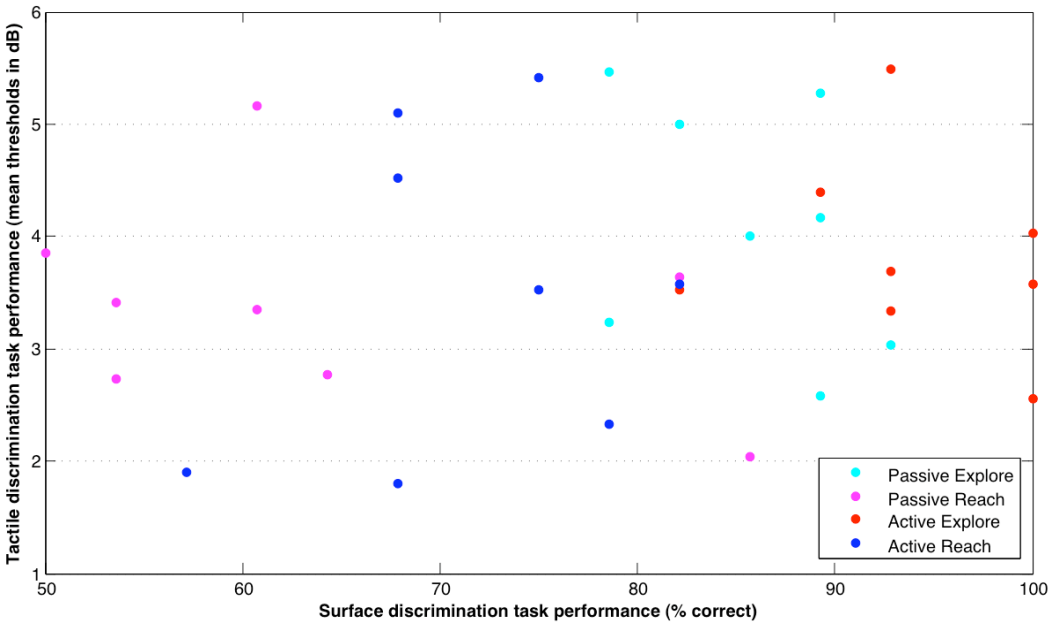


Figure 2.14. Tactile discrimination task performance (in dB) from **Experiment 2.8** plotted against the performance in the surface discrimination task (% correct). The dots represent the mean threshold data from individual participants.

With regard to the TD task performed at rest, the results indicated a significant effect of the type of task [$F(2,14)=18.95$; $p<.001$]. That is, participants were significantly more sensitive to the quality of tactile stimulation for the TD at rest, as

compared to those conditions in which the same task was performed while receiving 'passive exploratory input' (p=.003), or 'passive reaching input' (p=.001). Moreover, a significant difference was observed between the mean thresholds of the two passive dual task conditions: Tactile thresholds were significantly elevated (i.e., performance was significantly poorer) for the passive exploratory input, as compared to the passive reaching input (p=.030).

Lastly, the results showed no significant main effect of the movement execution mode [F(1,7)=<1; p=n.s.], movement type [F(1,7)=4.59; p=.069], nor any interaction between the two variables [F(1,7)=<1; p=n.s.], when comparing the data from the two movement types, across the two movement execution modes. No significant correlations were found between the distribution of the TD and that of SD performance under dual task conditions.

2.10.2.2. SD results

Percentages of correct responses for all the conditions at the intersection of the experimental variables are presented in Figure 2.15.

The results highlighted significant main effects of all experimental variables: Movement type [F(1,7)=44.71; p<.001], Execution mode [F(1,7)=10.19; p=.015], and Task type [F(1,7)=36.29; p=.001]. As such, participants' SD discrimination performance was significantly better under conditions of active movements, single tasking, and while exploring the surface of the board, as compared to reaching movements. See Figure 2.16 for a depiction of the significant main effects. No significant interactions between the experimental variables were found.

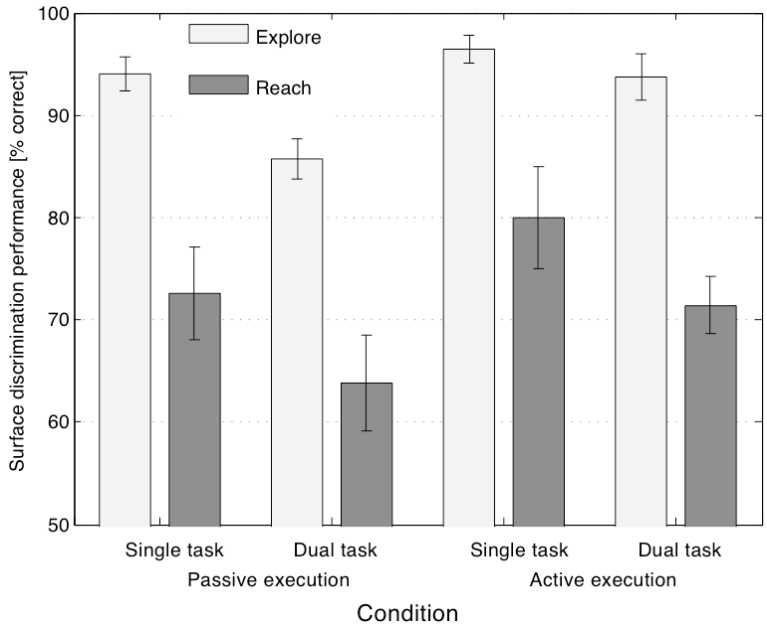


Figure 2.15. Percentages of correct responses for the different conditions in the surface discrimination task (SD) in **Experiment 2.8**.

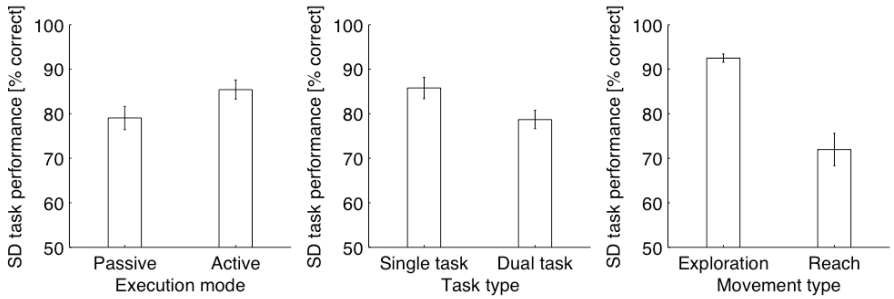


Figure 2.16. Significant main effects of Execution mode, Task type, and Movement type in the surface discrimination task (SD) in **Experiment 2.8**.

For the passive execution mode, a positive correlation was demonstrated between the Reach SD task performance under conditions of single and dual tasking (r=.853, p (one-tailed) =.007; R^2 =.727). When controlling for the performance in the TD performed at rest, the same strong correlation between the two variables was found (r=.851, p (one-tailed) =.008, R^2 =.724), suggesting that the variance found in the passive SD reaching condition was not explained by the additional TD task.

Similarly, for the active execution mode, a positive correlation was found between the Reach SD task performance under conditions of single and dual tasking (r=.679, p (one-tailed) =.032; R^2 =.461). When controlling for the performance in the TD performed at rest, the same positive correlation between the two variables was

found (r=.683, p (one-tailed) =.045, R^2 =.466), suggesting that the variance found in the active SD reaching condition was not explained by the performance of the additional task. No other significant correlations were found.

2.10.3. Discussion

Experiment 2.8 investigated the effects of goal-directed reaching movements, as well as exploratory movements, on tactile sensation. The results highlighted differential changes in tactile perception, depending on the type of movement performed (reaching vs. exploration), the movement execution mode (active vs. passive), as well as the type of perceptual task performed (single vs. dual). Here, some of the methodological issues raised are considered, followed by a discussion of the results of each perceptual task, and ending with conclusions of the findings and their implications.

2.10.3.1. Methodological considerations

Before the general discussion of the results of **Experiment 2.8**, some methodological issues need to be discussed first. These include the temperature cues provided by the experimental boards, the speed of movement used, the location of tactile stimulation delivery, and the dual-task effects given by the utilization of a dual perceptual task in some of the conditions.

2.10.3.1.1. Temperature cues

As mentioned in **Chapter 1**, the somatic information that we receive from the skin includes not only tactile information (that is tested in **Experiment 2.8** and throughout the rest of the thesis), but also information from other sub-modalities, such as, for example, the sense of temperature (see McGlone & Spence, 2010). Not surprisingly,

on a regular basis, when we interact with objects in our close surroundings, the different types of somatic information are combined into a unified percept of 'what something feels like'.

One perceptual task used in **Experiment 2.8** (i.e., SD, the surface discrimination task) utilized custom-built boards that were covered in one of two types of materials (i.e., cling film or tinfoil), or a combination or the two materials. To give an example, previous studies interested in the characteristics of tactile discrimination as it unfolds during exploratory movements utilized surfaces covered in sandpaper (e.g., roughness discrimination tasks, Heller, 1982). Sandpaper is appropriate for such a roughness discrimination task. However, when deciding on the materials that should be used for the present 'same vs. different task' used, the pleasantness of the feeling (Guest et al., 2011; Spence & Gallace, 2011) when interacting with the experimental boards was raised. Since repeatedly touching an experimental board covered in sandpaper over a period of two and a half hours could become rather uncomfortable, the decision to use more pleasant materials, and at the same time materials that we are all acquainted with (we interact with them more often than we interact with sandpaper), seemed to provide a reasonable solution.

Nevertheless, the more pleasant cling film and tinfoil used in **Experiment 2.8** come at a cost: their temperature cues. Tinfoil feels 'dry' and cold, as opposed to cling film, which is more 'sticky' and even warm, when comparing it to tinfoil. As such, for boards composed of different materials, the temperature cues could have helped participants in their performance of the discrimination task. Therefore, temperature cues need to be taken into account when considering the changes in tactile discrimination performance examined with the SD task.

2.10.3.1.2. Speed of movement

A second uncontrolled factor that should be mentioned here is the speed of movement. This factor needs to be discussed, since the degree of experienced tactile sensory suppression decreases as the speed of the movement decreases (Angel & Malenka, 1982; Schmidt, Schady, & Torebjörk, 1990). Following on from this, it has been argued that when performing exploratory movements, participants may adjust the speed of their hand movements such that the intended features of the surface are extracted (Chapman, 2009). As such, a slowing of the hand movement occurs during exploration, as opposed to the more rapid hand movement that occurs during reaching actions. On these grounds, it has been suggested that the known attenuation of tactile perception will occur for faster movement speeds, and not for the slower ones typically used in exploration. Indeed, in this respect, one recent study tested the critical speed of movement needed for sensory suppression to occur (Cybulska-Klosowicz et al., 2011). The authors had participants perform simple inward movements of their right hand, with the speed of the movement entrained to an oscilloscope. Brief electrical stimuli could be delivered to participants' middle fingers during the movement execution period, or else, in a control condition performed at rest. Participants made unspeeded judgments regarding the presence or absence of the weak tactile stimulation. In a blocked design, speeds ranging from very slow to ballistic movements were tested. For each participant, the critical speed at which tactile detection dropped to chance level was calculated. Not surprisingly, for all of the participants, the critical speed exceeded 200 mm/s, with a mean of 472 mm/s. Such a result was taken to show that tactile suppression occurs with movement speeds outside the typical range of 50-200 mm/s used in exploration (Essick & Whitsel, 1985). Moreover, the participants in Cybulska-Klosowicz and colleagues' study (2011) were asked at the end of each block, whether they would use the respective tested speed for

an exploratory movement. Most of the participants indicated that they would use speeds slower than 200 mm/s for exploration, but at the same time, a significant proportion of the participants indicated faster speeds as being appropriate for an exploratory movement. The authors had a good explanation for this: The participants did *not* have surface contact for the movement tested in their experiment, which made the evaluation of the speeds difficult. This begs the question of what exactly happens with tactile suppression when tested with specific exploratory movements, a question that was specifically addressed by **Experiment 2.8**.

2.10.3.1.3. Locus of tactile stimulation

Tactile perception was measured by means of two perceptual tasks: one TD task measuring tactile discrimination thresholds at participants' wrists, and another SD task, measuring surface discrimination at the participants' fingertips. One could criticize the present design on the grounds of not measuring tactile perception in both tasks at the same skin location. However, it would have been practically impossible to perform the two tasks together. Furthermore, tactile suppression has been shown to 'invade' the moving limb, such that when moving a finger, a decrease in what is felt is also present for the surrounding regions of the arm (Williams et al., 1998).

2.10.3.1.4. Dual-task effects in both TD and SD perceptual tasks

The two tasks used to measure tactile discrimination performance in **Experiment 2.8** could either be performed alone, or together, within the same experimental block. Given this experimental design, some deterioration in performance was expected when comparing conditions of single versus dual tasking. This was indeed the case: Participants demonstrated significantly higher tactile thresholds (i.e., poorer

discrimination performance) when the TD task was performed together with the SD task, under both active and passive execution modes for the tested movements. Conversely, participants' performance in the SD task was significantly lower when this accompanied the TD task, as compared to those conditions in which the participants only performed a single task.

2.10.3.2. Discussion of the TD task results

Given the experimental results outlined in **Experiments 2.1-2.7**, it was hypothesized that increased tactile thresholds (i.e., poorer performance) would be observed for the *active* goal-directed reaching movements, as well as for exploratory movements, as compared to thresholds measured in a control no-movement condition. This hypothesis was confirmed: Participants' performance deteriorated during movement execution (i.e., tactile suppression was observed). Moreover, the two types of active movements of the hand (exploratory or simple reaching movements) resulted in a similar deterioration of what was felt during movement, thus indicating that irrespective of the type of movement performed, tactile perception was affected.

Furthermore, tactile perception was significantly impaired during the *passive* execution modes for both tested movements (i.e., participants kept their hand at rest, while the experimenter touched it such that it mimicked the contact with the table surface from the active conditions), as compared to the control rest condition. Such a result could indicate that not only actively moving the hand triggers tactile suppression, but also the additional *distracting* tactile input provided to a resting hand (see also **Chapter 4** for a similar effect and discussion in the context of juggling movements). This distracting factor that gives rise to impaired performance in those conditions in which the two perceptual tasks were performed together could of course

be taken as a dual-task effect: The TD task performance was impaired when participants performed the concomitant SD task. In a similar vein, the necessity for participants *to divide* their attention between the two tasks could have contributed to the clear deterioration in TD task performance, when the additional tactile SD was performed. However, in the case of the passive movement execution mode, tactile discrimination thresholds were significantly higher for the exploratory movements, as compared to the reaching movements. Such a result hints that *distraction* was the more likely explanatory mechanism. Note, though, that the passive exploration task involved a sustained strike of participants' fingers with the experimental board, as opposed to the passive reaches that involved two temporally segregated touches, delivered by the experimenter. In this respect, the time allowed to get the needed tactile discrimination cues in this experiment (e.g., tactile memory, Gallace & Spence, 2009) could be taken as an additional factor accounting for the significant difference between tactile sensitivity measured under conditions of passive exploration and passive reaching.

Lastly, when comparing the data from the two movement types, across the two modes of movement execution, no significant difference in tactile sensitivity was observed for the two execution modes and the two movement types, nor was any interaction observed between the two variables. The latter result is particularly important, since it underlines the fact that a similar pattern of tactile suppression is found for the two types of movements, exploration and reaching. Such a finding could be taken to account for the fact that *a)* either participants did not adjust the speed of their movement, in order for the exploratory movement to be performed appropriately (see Cybulska-Klosowicz et al., 2011); or *b)* if participants adjusted their speed (i.e., they slowed down their movement), then speed alone does not delineate between a

suppressed state of tactile perception and a non-suppressed state. Following on from this, a discussion of the *movement relevance* in the tactile domain is needed.

2.10.3.3. Discussion of the SD task results

Since the goal of tactile exploration is to gain information concerning the tactual characteristics of objects that we come into contact with (i.e., the surface of the experimental board in this case), the first prediction with respect to the SD task entailed significantly higher discrimination performance for exploratory movements, as opposed to the simple reaching movements. This hypothesis was confirmed: Participants were significantly better at discriminating between the two materials covering the table surface when they performed exploratory movements, as compared to simple reaches. This is an important result, since it highlights *the relevance* of the movement chosen when measuring tactile performance during movement. This result is further strengthened by the positive correlations found for both active and passive reaching movements between the SD task performance under conditions of single and dual tasking: If performance declined for the single reach SD task, it also declined for the dual reach SD task (performed together with the TD task), and the variance in either of their distributions is not explained by the additional perceptual task. Therefore, with respect the relevance of the task, it appears that the goal-directed reaches may not be the ideal movements to test tactile perception during movement with.

Furthermore, as expected, participants' performance was significantly higher when actively performing the tested movements, as opposed to the passive execution condition. Note that for simple tactile features of objects (i.e., tactile roughness discrimination thresholds), it was observed that the movement execution mode, active

or passive, does not make a difference with respect to the performance on the task (Hsiao, O'Shaughnessy, & Johnson, 1993; Jones, 2009). These studies, however, have only used the natural exploratory movements in their design. In **Experiment 2.8** that contrasted exploration with reaching movements, when performing a purposeful movement (i.e., moving the hand on the surface of the board in order to get tactual information about it), performance is significantly higher as compared to simply receiving the same tactual information, in the absence of overt movement. Such a result thus highlights the importance of purposeful movement for tactile perception.

To summarize the discussion of the last experiment reported in **Chapter 2**, **Experiment 2.8** was designed to investigate at a behavioural level *whether* and *how* tactile suppression manifests itself during specific movements of the hand. To this end, a demarcation between *movement relevance* for what is felt during movement, as well as between *movement execution modes*, was used in order to obtain a comprehensive view with regard to what happens to tactual information during movement.

To consider what is felt in a moving hand first (i.e., the TD task measured at participants' wrists), tactile perception was attenuated during both active exploration and active reaching. At the same time, tactile suppression also occurs in the absence of movement, when additional tactile input (or distraction) is provided to a passive hand. Therefore, taken together, tactile suppression could result from the combination of active movement interference and passive tactile distraction. For the active execution modes, tactile sensitivity has a comparable decrement across reaches and exploratory movements. On the other hand, for the passive execution modes, tactile sensitivity was significantly lower during exploration as compared to reaching, thus suggesting that memory for touch could play a role in what is felt.

Second, when considering what is felt when moving one's hand across a surface (i.e., the SD task), exploration proves to be the appropriate movement to test tactile perception, since performance is significantly higher when exploratory movements are performed, as compared to simple reaches. Moreover, the active movement of the hand yields enhanced perceptual performance, thus suggesting that we feel more when we need to. It would appear, then, that the tactual information is prioritized when it is relevant for the movement being executed.

To summarize the findings of **Experiment 2.8**, tactile information is *attenuated* in a moving hand, irrespective of the type of movement used. The same holds for a resting hand that receives additional tactile distraction. However, tactile information is *enhanced* when the tactile percept is the result of an active purposeful goal-directed movement, such as that involved in tactile exploration. Therefore, tactile information is suppressed or enhanced depending of the task at hand, highlighting the importance of task relevance (i.e., the type of movement) in the context of tactile perception. See also General discussion in **Chapter 5**.

2.11. Summary and conclusions

The experiments reported in this chapter were designed to answer the following question: *'Does tactile sensitivity change over the time course of a goal-directed movement?'* The predictions for the experiments reported here were: **1)** tactile perception will be facilitated during the preparation phase of the goal-directed movement, and **2)** tactile sensitivity will decline during the execution phase of the tested movement. While the experimental data provides evidence in favour of a decrement in tactile sensitivity during movement execution (**Experiments 2.1-2.5**), the first prediction was not supported by the data (see **Experiments 2.5-2.7**). Even so, a

dissociation between discriminating the quality of what is felt (**Experiment 2.5**) and the speed of reaction to suprathreshold tactile events while moving (**Experiment 2.6**) was apparent during the movement execution phase. As such, if tactile sensitivity declines during movement execution, RTs to tactile stimuli are enhanced during the same time period. This dissociation is further considered in **Chapter 5**.

However, the fact that these behavioural investigations highlighted a lack of attentional influence on what is felt during the preparation of goal-directed movements raises the question on what type of *attention* it is that affects tactile perception during movement. The present data provides evidence that the mere preparation to move does not benefit from an enhanced tactile perception is the movement effector. Moreover, endogenously directing attention to either the moving or non-moving effector, results in an enhancement in what is felt there. However, this enhancement is most prominent over the execution phase of the movement. Therefore, the present data does not support the spatial account on tactile perception, as laid down in the premotor theory of attention. Rather, tactile perception, which is, by definition, inherent to the body, seems, at least from the present behavioural investigations on reach-to-grasp goal-directed movements, to be of little relevance during the execution phases of a goal-directed movement. Nevertheless, an interesting resolution to the relevance problem is given by the results of **Experiment 2.8**, highlighting that tactile information is indeed *attenuated* in a moving hand, irrespective of the type of movement used. The same attenuation effect is also present in the resting hand that receives additional tactile distraction. However, at the same time, the results of **Experiment 2.8** indicate that tactile information is *enhanced* when movement itself is the means of achieving it (i.e., tactile exploration), thus suggesting that moving in

order to feel makes more sense than moving and feeling at the same time. As such, note that when considering tactile attenuation during goal-directed movements, the *purpose* of the movement needs to be clearly stated: If **Experiments 2.1-2.5** in this chapter reported a decrement in what is felt over the execution phase of the movement, **Experiment 2.8** indicated that tactile information was enhanced over the same time period.

Chapter 3

Electrophysiological investigation of tactile perception during goal-directed movement

3.0. Introduction

The behavioural data on reach-to-grasp movements from **Chapter 2** were discussed within the framework of two theories, each predicting differential effects on perception during the course of movement execution. Accordingly, the act of preparing and executing a goal-directed action allows for different predictions to be put forward by the premotor theory of attention (Rizzolatti & Craighero, 2009; Rizzolatti et al., 1994) and the forward models of motor control (Miall & Wolpert, 1996; Wolpert et al., 1995): While the premotor theory predicts perceptual enhancement (i.e., resulting from the operation of an *attentional* mechanism), the forward model predicts perceptual suppression (i.e., as driven by an *attenuating* mechanism). Although the two theories appear to be at odds with each other, the two mechanisms they put forward need not necessarily be treated as exclusive. For example, the two theoretical stances could be brought together by first assuming that tactile information would not be important for goal-directed actions (i.e., thus it would fail to trigger an attentional shift to the movement effector). At the same time, they can be brought together by taking into consideration that the perceptual input is indeed attenuated by the internal model used to predict the consequences of an action (i.e., as predicted by the forward models). This fact raises the issue of *perceptual relevance for movement*. If the potentially non-relevant tactile information (i.e., which, according to the forward models, can be predicted from the self-generated action) is prone to

sensory attenuation during movement, then one would expect visual information (i.e., having an external generator) to be enhanced during self-generated movement. Such a result would support the forward models account.

Alternatively, if we were to assume that spatial attention 'travels' with the effector of the goal-directed movement, then perceptual input (i.e., either tactile or visual) should benefit from a facilitation of processing. Classical accounts on crossmodal attention have differentiated between modality-based and supramodal control mechanisms of selective attention: A supramodal, unitary attentional system would predict similar attentional shifts for all studied modalities (e.g., touch and vision in **Experiment 3.1** reported in this chapter), whereas a modality-specific control account would predict specific attentional shifts for each of the sensory modalities tested (Spence & Driver, 2004; see also Spence, 2010a).

Evidence for a supramodal attentional control system comes from patient studies (Farah, Wong, Monheit, & Morrow, 1989), as well as human electrophysiological studies (Eimer, 2004). For example, in one study (Eimer & Schröger, 1998; see also Eimer, 2001) participants had to detect infrequent auditory or tactile stimuli at a location indicated by a central visual pre-cue presented at the beginning of each trial. Depending on the condition, either audition or touch was denoted as the primary modality, and the participants were instructed to ignore the stimuli in the irrelevant modality, as well as the sensory stimuli delivered at the uncued locations. The results favoured a supramodal account of selective attention. In a further study designed to exclude the influence of visual attention on the previously found supramodal tactile and auditory shifts of attention (Eimer & Schröger, 1998), participants were instructed to detect infrequent visual or tactile targets presented in complete darkness, following a central auditory cue (Eimer, Van Velzen, Forster, &

Driver, 2003). The results highlighted once again that the ERPs sensitive to the direction of attentional shifts were highly similar *across* the tested modalities (i.e., vision and touch), thus supporting a supramodal account of selective attention (Eimer, 2001, 2004; Eimer & Van Velzen, 2002; Eimer et al., 2003). On the other hand, evidence for a 'separable-but-linked' modality specific attentional control systems comes from behavioural studies (Spence & Driver, 1996, 2004; Spence et al., 2000b; see also Chambers, Stokes, & Mattingley, 2004). By using the famous elevation-discrimination task (Spence & Driver, 1996) for auditory, visual and tactile stimuli, the authors demonstrate larger shifts of spatial attention within the primary relevant modality as compared to the crossmodal conditions, and suggest that there are dependencies between auditory and visual spatial attention and between tactile and visual attention, but the system is, however, not purely supramodal (Spence et al., 2000b; though see Eimer, Van Velzen, & Driver, 2002; Macaluso, Eimer, Frith, & Driver, 2003; see also Driver & Spence, 2004, for a more detailed discussion).

To return to the predictions for **Experiment 3.1**, the two explanatory theses (attention vs. suppression) could still be brought together if a *different temporal allocation* of the two mechanisms during action were to be assumed. As such, the different mechanisms (attention vs. attenuation) could become available and thus act on the perceptual system, at different points in time during the goal-directed action. This idea was tested at a behavioural level in **Chapter 2**. In this respect, if attentional facilitation were to be present during the preparatory phase, attenuation would reign over the motor execution period, potentially leaving place once again to facilitation in the post-movement period.

More importantly, the two theoretical accounts would predict opposing outcomes with regard to the perceptual processing in the movement effector (i.e.,

moving hand in **Experiment 3.1**). In this respect, if the *effector of the movement* were to be considered as a key delineator between the two contrasting mechanisms, then an attentional shift to the effector of the action would result in enhanced processing of perceptual information presented to a moving hand, whereas the estimates of the internal model would instead result in a diminished processing of the same information presented to a moving hand.

In **Experiment 3.1**, the exquisite temporal resolution provided by ERPs was utilized in order to investigate the neuronal correlates of tactile perception during the execution of goal-directed reach-to-grasp movements. Participants performed goal-directed reaches toward a foam object placed centrally on the table in front of them. A tactile-probe paradigm was used to deliver tactile stimulation to the index finger of participants' moving or resting hands (see Heinze et al., 1990; Mangun & Hillyard, 1988, for a similar probe paradigm in the visual domain).

In order to investigate whether a differential pattern of tactile ERPs would be present for the different phases of the movement, the tactile probes were delivered at different points in time during the movement: movement preparation, movement execution, or post-movement. Moreover, in order to assess the contribution of movement itself to what is felt during movement, in separate trials, ERPs were recorded without any sensory stimulation being applied to the participant's fingers. One last concern of the experiment presented in this chapter was to investigate whether the execution of goal-directed movements has a generalized influence on perception, which is not limited to the tactile modality. In this respect, in separate trials, visual probes instead of tactile probes were delivered to the index fingers of both moving and resting effectors during the various phases of the movement.

3.1. Experiment 3.1

3.1.1. Methods

3.1.1.1. Participants

Eighteen participants recruited among the student population of the University of Hamburg took part in this study. The data from two of the participants were excluded from all analyses (see data analysis section). The remaining 16 participants (9 male) had a mean age of 27 years (age range 22-45 years). They were all right-handed, had normal or corrected-to-normal vision, and normal hearing. All the participants reported normal tactile sensitivity on the hands, as well as no known neurological impairment. The experiment was conducted in accordance with the ethical guidelines laid down in the Declaration of Helsinki (2008). Participants gave their informed consent prior to taking part in the study. The preparation, together with the experimental session lasted approximately 4-4.5 hours, and participants were compensated with 8 EUR/hour or course credit for taking part in the study.

3.1.1.2. Apparatus

The participants were seated at a table (70 cm long, 70 cm wide, and 78 cm high) in a dimly-lit room. One rectangular foam block (15.5 cm long, 4 cm wide, and 4 cm high) was attached centrally on the table at a distance of 32 cm, directly in front of the participant (*goal object*). Another rectangular piece of foam (52 cm long, 10 cm wide, and 3 cm high) was attached to the table in order for the participants to rest the hand to be moved during the block (*start position*). Two additional pieces of foam (15 cm long, 12 cm wide, and 2 cm high) were placed on each side of the goal object, to rest the non-moving hand throughout the block (*resting positions*). Tactors were attached

with tape to the ventral part of the fingertips of the index fingers of each of the participant's hands. Participants also wore LEDs attached by means of adhesive pastels to the nails of each index finger. Furthermore, participants wore an Optotrack marker (Northern Digital Inc., Waterloo, Canada) on each of their index fingers, positioned on the nail, next to the LED, that allowed for the tracking of the movement of their hand. The tactors and the LEDs were driven by means of custom-built boxes connected to the main computer running the experiment. The auditory signals were delivered from two loudspeaker cones, placed on a table behind the participants. The movement of the participant's hand was monitored on-line using an Optotrack Certus motion tracking system with a sampling rate of 150 Hz (Northern Digital Inc.). One additional Optotrack marker, attached centrally on the table, 15 cm from the goal object, served as a central visual fixation point throughout the trial (see Figure 3.1 for a depiction of the experimental set-up).

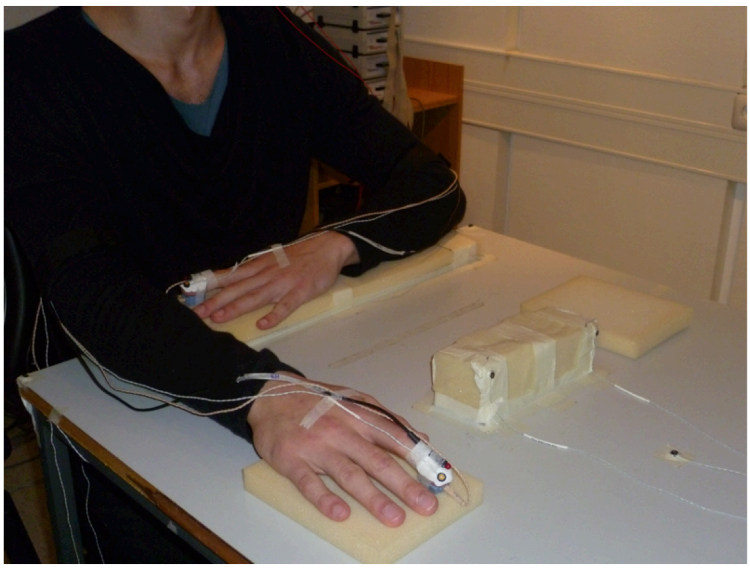


Figure 3.1. Experimental set-up in **Experiment 3.1**. The participant is depicted with his left hand at the start position and his right hand on the resting position.

3.1.1.3. Procedure

Each experimental trial consisted of an outward goal-directed reach-to-grasp movement to the goal-object. The participants had to listen out for three auditory signals presented from the two loudspeaker cones placed behind them. Each trial began with a beep (*prepare signal*, 600 Hz, 100 ms), instructing the participants to prepare the movement. After 270 ms, a second higher-pitched auditory signal (the *go signal*, 800 Hz, 100 ms) instructed them to initiate the reaching toward the goal-object. A third lower-pitched auditory signal (*return signal*, 400 Hz, 100 ms) was delivered 300 ms after their grasp of the goal object, instructing the participants to return their hand/arm to the start position. The experiment progressed to the next trial following an intertrial interval of 2000 ms. The coordinates of the moving hand were monitored on-line throughout the movement phases (start, reach, grasp, and post-grasp), such that, if the hand was not at the expected position, the trial was repeated.

For each trial, tactile pulse probes (250 Hz, 100 ms), visual LED illumination probes (100 ms), or omission probes (no stimulation, just 100 ms of recording) were delivered/recorded. These were randomly distributed throughout the block and participants were told to ignore them and just to perform the movement task.

For the ***moving hand***, the visual and tactile probes were presented to the participant's index finger at a different point in time, depending on the spatial location of the hand executing the movement. In particular, probes could be delivered either during the *movement preparation period* (100 ms before the go signal, when the hand was at the start position), during the *movement execution* period (when the hand was 13 cm (early position), 22 cm (mid position), or 30 cm (late position) away from the start position), or in the *post-movement* period (100 ms after the grasp of the goal object). The omission probes were recorded only for the moving hand with the same

timing of recording as for the delivery of the visual and tactile probes (preparation, early, mid and late execution, and post-movement).

For the ***resting hand***, the visual and tactile probes were presented to the participant's index finger at a different point in time, depending on the spatial location of the hand executing the movement. In particular, probes could be delivered either during the *movement preparation period* (100 ms before the go signal, when the moving hand was at the start position), during the *movement execution* period (22 cm (mid position) away from the start position), or in the *post-movement* period (100 ms after the grasp of the goal object).

The participants performed a short practice block of 10 trials in order to become acquainted to the goal-directed movements to be performed during the experiment. The practice data were not part of the final data analysis.

3.1.1.4. Design

The experiment comprised 20 blocks of 72 trials each, leading to a total number of 1440 trials. The moving hand was blocked, so that participants performed 10 blocks with the LH moving, and 10 blocks with the RH moving. All participants started with the LH moving. Within each block, a fixed number of probes were delivered for each experimental condition. That is, for the ***resting hand***, 6 tactile probes were delivered for the preparation, mid execution, and post-movement periods, giving rise to a total of 18 tactile probes per block. The resting hand also received visual probes; 3 visual probes were delivered for each of the preparation, mid execution, and post-movement periods, giving rise to a total of 9 visual probes per block of trials. For the ***moving hand***, 6 tactile probes were delivered for the preparation period, 4 tactile probes for each of the early, mid, and late execution periods, and 6 tactile probes for the post-

movement period, giving rise to a total of 24 tactile probes. As for the resting hand, the moving hand received 3 visual probes for each of the preparation, mid execution, and post-movement periods, amounting to a total of 9 visual probes per block. Furthermore, omission trials were also recorded for the preparation, early, mid, and late execution, as well as the post-movement periods. In total, 12 omission trials were recorded per block of trials for each of the movement periods. The experimental conditions were randomized within each block of trials. Participants took short breaks between blocks and a longer break in the middle of the experiment.

3.1.1.5. Electroencephalographic recording

The EEG was recorded continuously from 74 Ag/AgCl scalp electrodes mounted on an elastic cap with 74 equidistant electrode positions (passive electrodes; cap EC80#, Easycap Gmbh, Herrsching, Germany). The signal was referenced on-line to the left earlobe and re-referenced off-line to the right earlobe. The electrode impedances were kept under 5 kΩ. The electrodes were mounted in the cap according to the international 10-10 system (Oostenveld & Praamstra, 2001), an extension of the 10-20 system, with the following positions: Fpz, Fp1/2, AFz, AF7/8, AF3/4, Fz, F9/10, F7/8, F5/6, F3/4, F1/2, FCz, FT9/10, FT7/8, FC5/6, FC3/4, FC1/2, Cz, T7/8, C5/6, C3/4, C1/2, Cpz, TP9/10, TP7/8, CP5/6, CP3/4, CP1/2, Pz, P9/10, P7/8, P5/6, P3/4, P1/2, POz, PO9/10, PO7/8, PO3/4, Oz, O1/2, Iz, and O9/10.

Vertical eye movements were measured by means of an additional electrode placed under the left eye, with the same reference as the other electrodes. Horizontal eye movements were calculated offline by subtracting the signal recorded at F10 from that recorded at F9, electrodes positioned in the cap near the outer canthi of the eyes.

The electrode signals were amplified using three BrainAmp DC amplifiers with 32 channels each (Brain Products Gmbh, Gilching, Germany) and digitally stored using the BrainVision Recorder software (Brain Products Gmbh). The analog EEG signal was sampled at 5000 Hz, filtered on-line with a band pass of 0.1 to 250Hz and then down-sampled on-line to 500 Hz to be stored on disc. The signal was filtered off-line with a high cutoff at 40 Hz, 12 dB/oct, and a Notch filter of 50 Hz.

3.1.1.6. Data analysis

3.1.1.6.1. Behavioural data pre-processing

The behavioural data was inspected to control for trials in which RTs to initiate the goal-directed movement were slower than 1000 ms and trials in which the total duration of the movement was greater than 2000 ms. Trials with such slow RTs and such a long movement duration (9% of all trials) were excluded from the final ERP analysis.

3.1.1.6.2. EEG data pre-processing

As a first step in the ERP analysis, the EEG data pre-processing was conducted with VisionAnalyzer 2 (Brain Products Gmbh). The EEG signal was initially segmented into bins of 100 ms pre-, and 450 ms post-stimulus delivery. The vertical electro-oculogram segmented data was submitted to a blink artifact rejection (segments with an absolute voltage difference between maximum and minimum sample points higher than 60 μV were removed). Furthermore, a second artifact rejection was conducted on the remaining 74 scalp electrodes to inspect for movement and other amplifier artifacts (segments with an absolute voltage difference between maximum and minimum sample points higher than 100 μV, as well as segments with low activity for a period

of more than 100 ms were removed). The remaining data was then averaged by condition and baseline corrected (100 ms pre-stimulus baseline). Participants with more than 33% of trials per condition excluded were eliminated from the final analysis (this led to the removal of two participants).

The averages for each condition for each participant were exported to Matlab (Matlab 2008, MathWorks, Natick, MA, USA) and the remaining analysis was carried out using this software.

3.1.1.6.3. ERP data analysis

The average ERPs for each condition for each participant were separately calculated for the left and right stimulated sites. The ERPs were then collapsed over the left and right stimulated sites by inverting the electrode configuration of the left stimulated sites and then averaging over both stimulated sites (see Heed & Röder, 2010). Therefore, in **Experiment 3.1**, figures are displayed as if stimulation occurred to the right finger. Ipsilateral activity is thus shown over the right hemisphere and the contralateral activity over the left hemisphere. ERPs are plotted with the negative up.

Somatosensory ERPs have been shown to be maximal over contralateral sites to the stimulated hand (Desmedt & Robertson, 1977; Eimer et al., 2005; Röder et al., 1996). Following visual inspection of the data, and in accordance with the previous literature on somatosensory ERPs (see Luck, 2005), the mean amplitudes of the tactile N140 over the 80-200 ms post-stimulus onset time window were analyzed. For the visual N100, following a visual inspection of the data, a temporal window between 100-250 ms post-stimulus onset was chosen. The omission probes were assigned with the same temporal window as the tactile probes (80-200 ms). For these ERPs of interest, mean amplitudes (in [μV]) were exported.

As previous studies have demonstrated specific somatosensory ERPs modulations during movement preparation and execution in man (Forster & Eimer, 2007; Gherri et al., 2007; Huttunen & Hömberg, 1991), the statistical analysis was carried out over pairs of contralateral/ipsilateral electrodes: frontal-central (FC3/4), central (C3/4), central-parietal (CP3/4), and parietal (P3/4) for the tactile and omission probes. The visual probes analysis was carried for the occipital pair of electrodes PO3/4.

The ERP data were analyzed using repeated measures ANOVAs with the factors HAND (moving vs. resting), TIMING (preparation, execution, and post-movement), HEMISPHERE (contralateral vs. ipsilateral), and ELECTRODE PAIR (FC3/4, C3/4, CP3/4, P3/4). When an interaction proved to be significant, further ANOVAs were conducted that analyzed the ERP data separately for each factor level of one of the interacting factors. As such, four-way interactions between all experimental factors were split in a first step and the specific location where the effect arose from was then analyzed. For example, if an interaction between the hand that received the stimulation, the timing of stimulation delivery, the hemisphere, and the electrode pair was observed, this interaction was followed up with a separate analysis (with the factors of HAND, TIMING and HEMISPHERE), conducted at each electrode pair. Furthermore, significant three-way interactions found in the ERP data were broken down in a hypothesis-driven manner. To continue with the previous example, if a three-way interaction with HEMISPHERE was observed, separate ANOVAs (with the factors HAND and TIMING) were conducted for each hemisphere. Trivial main effects of the topographical factors of HEMISPHERE and ELECTRODE PAIR, as well as interactions between the two, are not reported throughout. Lastly, the two-ways interactions that were encountered in the data were

followed by post hoc pairwise comparisons, rather than separate ANOVAs. When comparing the various levels of the factor TIMING, paired-samples t-tests were conducted, instead of using the post hoc comparisons. These subsequent post hoc comparisons, as well as the paired-samples t-tests, were conducted using the Sidak adjustment for multiple comparisons; only the tests that survived the comparison are reported throughout. Mauchly's test of sphericity was used to ensure that the data did not violate the sphericity assumption. If the assumption was violated, then the Huynh-Feldt correction was applied to correct the degrees of freedom; corrected p values are reported.

A first analysis was conducted on the *tactile* ERP data with the factors HAND[9] (moving vs. resting), TIMING (motor preparation, execution, post-movement), HEMISPHERE (contralateral vs. ipsilateral), and ELECTRODE PAIR (FC3/4, C3/4, CP3/4, P3/4; Analysis 1.1). The same analysis was conducted on the difference waves (DWs, tactile-omission trials; Analysis 1.2).

In a subsequent step, the same statistical analysis was performed on the *visual* ERP data. The visual ERP/DWs analysis accounted for a confound in the experimental design utilized in **Experiment 3.1**. It is known that the visual ERPs depend on the visual field location of the eliciting visual stimulus (see Luck, 2005). The reach-to-grasp movement executed in the experiment reported in this chapter involved outward extensions of either the right or left hand. Due to the particular characteristics of the movement, in the preparation period, the visual stimulation was delivered on the (visual) contralateral side for both moving and resting effectors. However, in the post-movement period, the visual probe was received in the (visual) contralateral side for the moving hand, and the (visual) ipsilateral side for the resting hand. Therefore, the

[9] See **Appendix A1** for a further detailed analysis of tactile perception in the movement effector only.

visual ERP analysis involved separate ANOVAs for the resting and moving hand data, with the following factors: TIMING (motor preparation, execution, post-movement) and ELECTRODE (PO3/4) (Analysis 2.1). This analysis was followed by the DWs analysis (visual-omission trials), with the same factors (Analysis 2.2).

3.1.2. Results

3.1.2.1. Tactile probes at FC3/4, C3/4, CP3/4, and P3/4

The tactile ERPs/DWs analysis was conducted on the data from both moving and resting hands for the different timings of tactile probes delivery, at several pairs of electrodes. Therefore, the main ANOVA had four factors: HAND (moving vs. resting), TIMING (preparation, execution, and post-movement), HEMISPHERE (contralateral vs. ipsilateral), and ELECTRODE PAIR (FC3/4, C3/4, CP3/4, P3/4).

3.1.2.1.1. Mean tactile N140 amplitudes analysis (Analysis 1.1)

The somatosensory ERPs are presented in Figure 3.2, panels **a** to **d**, corresponding to each analyzed electrode pair (FC3/4, C3/4, CP3/4, P3/4).

The results of the overall ANOVA on the ERP data revealed a significant main effect of HAND [$F(1,15)=14.68$; $p=.002$], with the moving hand eliciting a significantly more negative N140, as compared to the resting hand. The timing of the delivery of the tactile probes significantly influenced the ERPs [main effect of TIMING: $F(2,30)=14.57$; $p<.001$]; post hoc comparisons indicated that the activity recorded in the *post-movement* period was significantly less negative, as compared to the *preparation* ($p=.002$) and *execution* periods ($p=.001$).

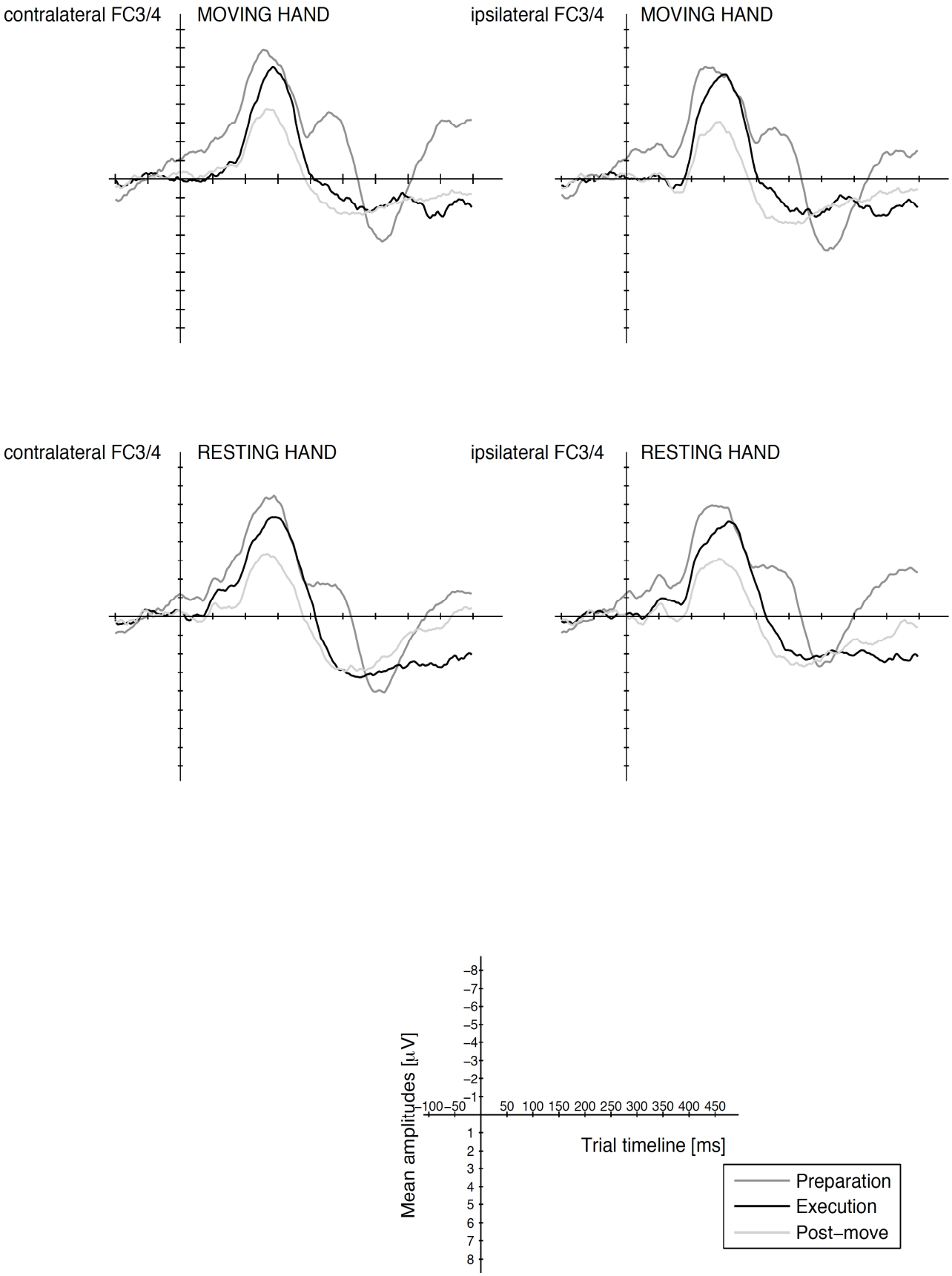


Figure 3.2a. Tactile ERPs recorded in **Experiment 3.1** at the FC3/4 electrode pair, for both the moving (upper rows) and resting hands (lower rows).

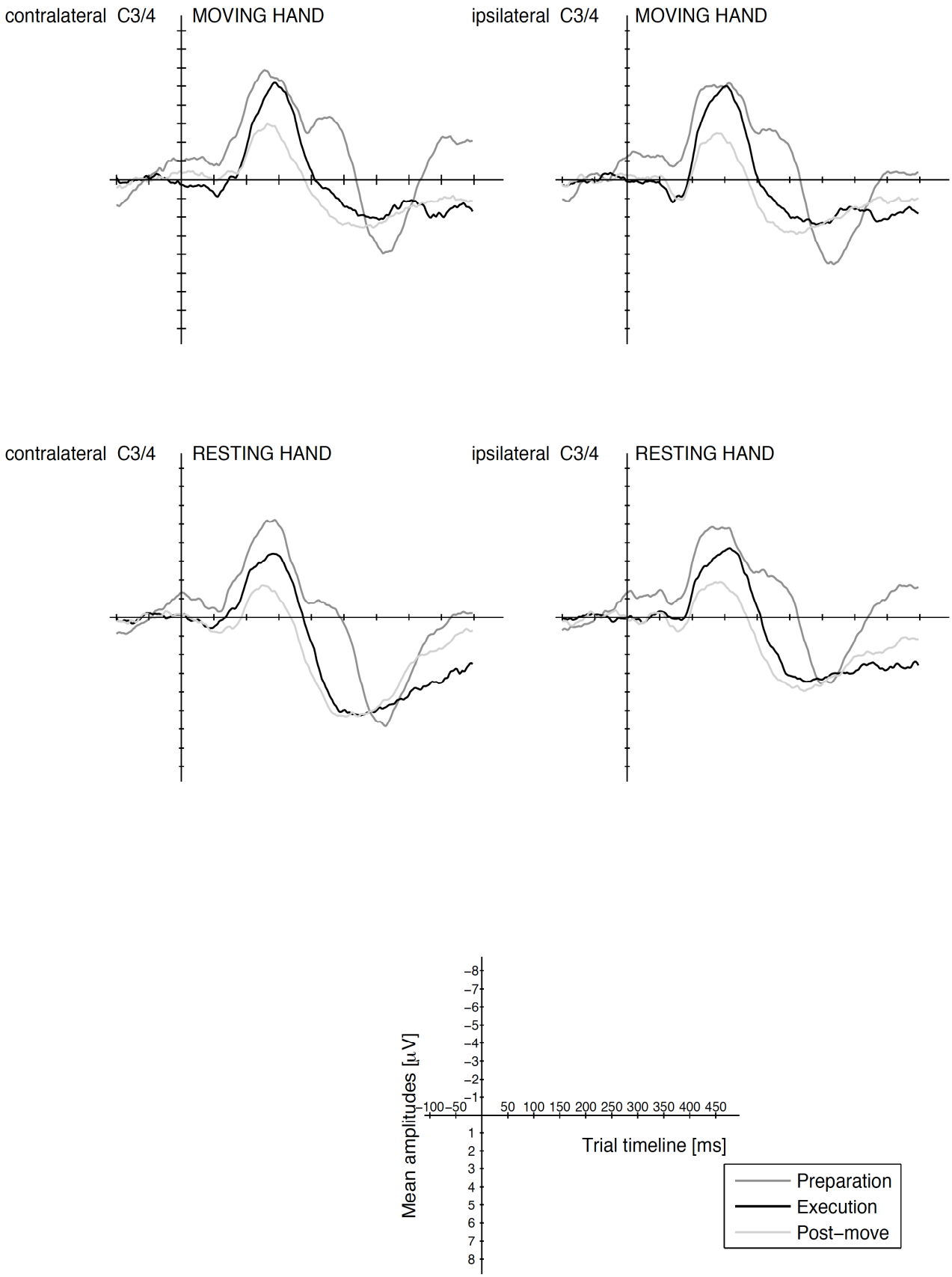


Figure 3.2b. Tactile ERPs recorded in **Experiment 3.1** at the C3/4 electrode pair, for both the moving (upper rows) and resting hands (lower rows).

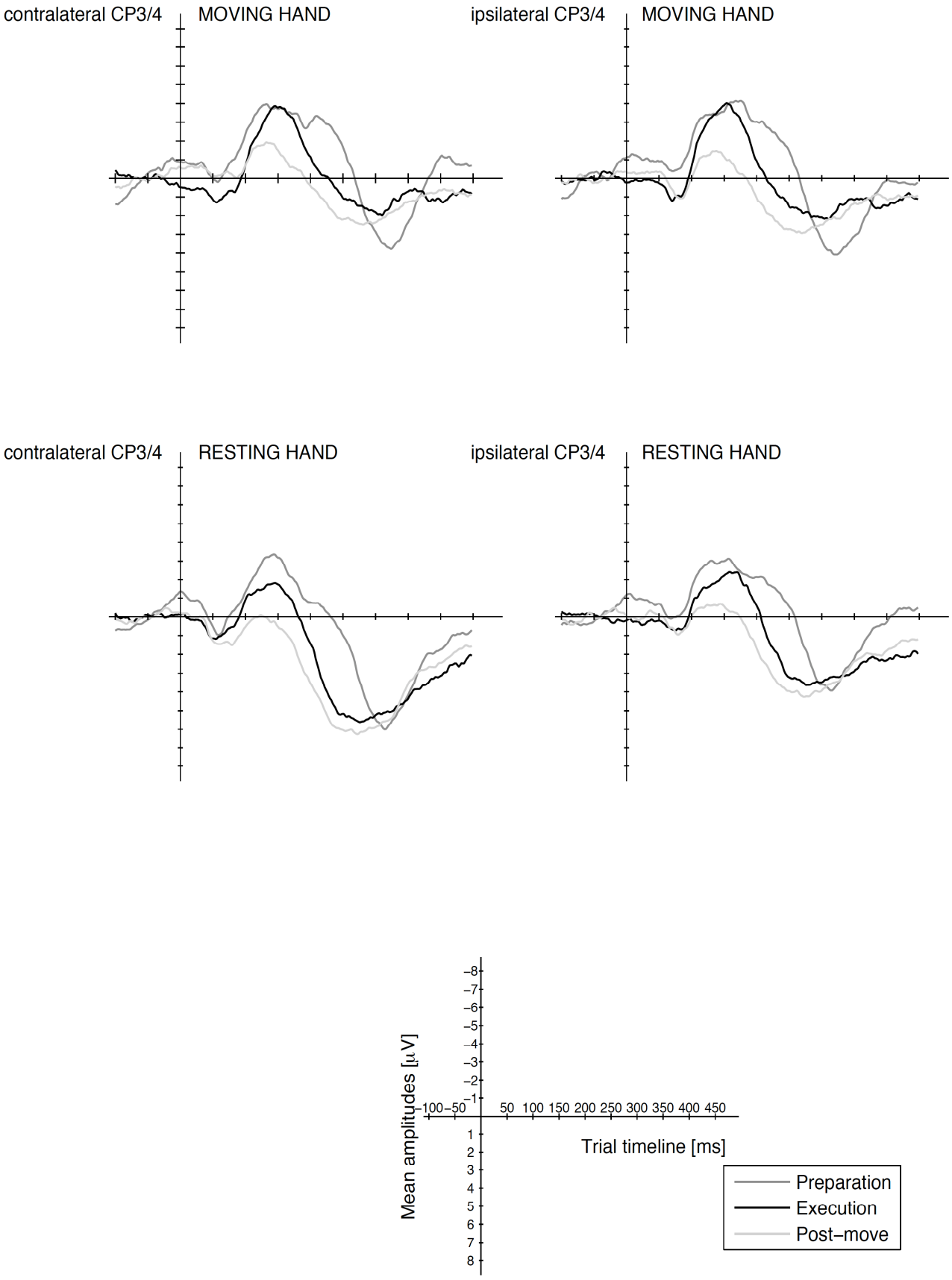


Figure 3.2c. Tactile ERPs recorded in **Experiment 3.1** at the CP3/4 electrode pair, for both the moving (upper rows) and resting hands (lower rows).

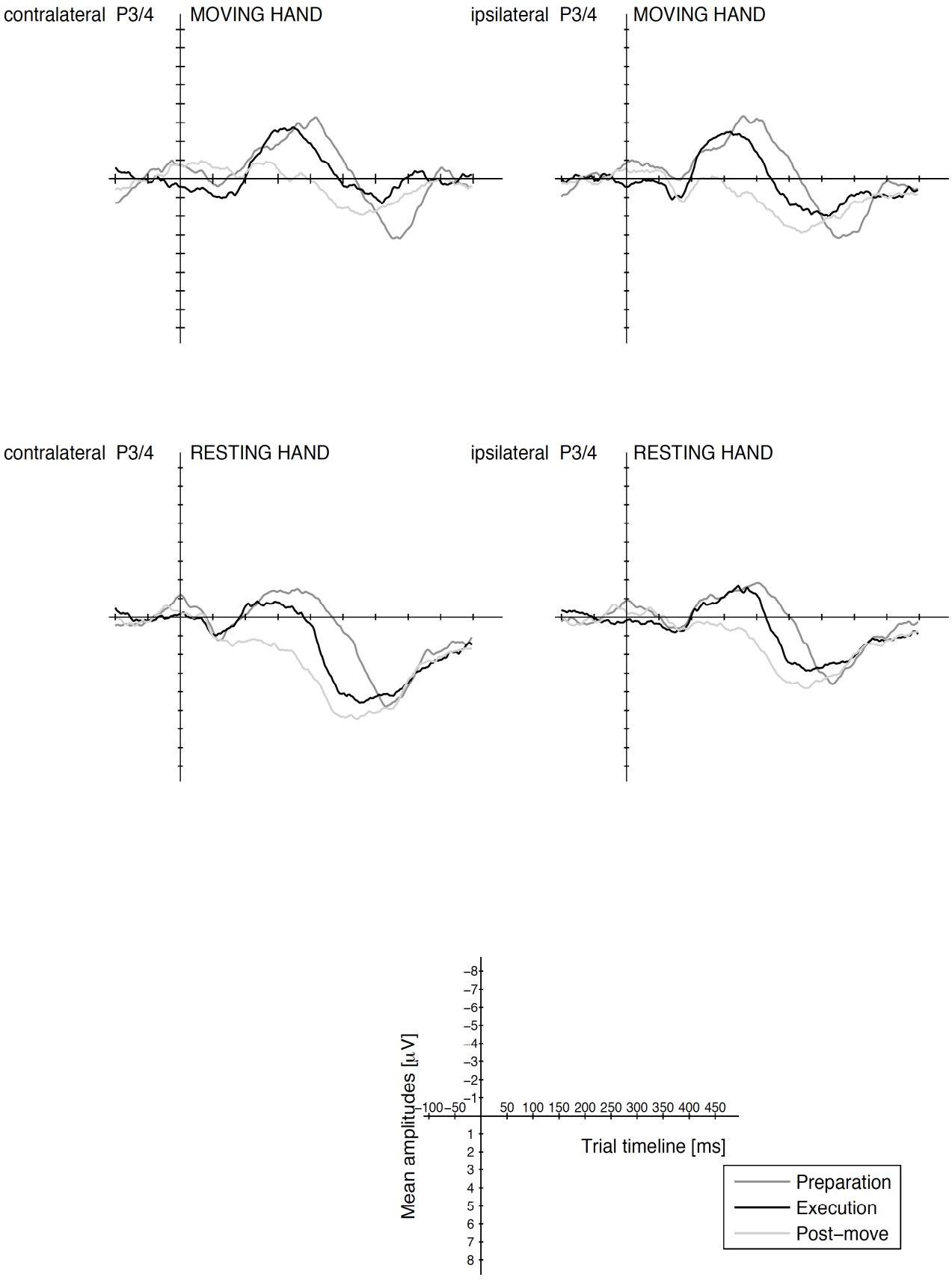


Figure 3.2d. Tactile ERPs recorded in **Experiment 3.1** at the P3/4 electrode pair, for both the moving (upper rows) and resting hands (lower rows).

A significant two-way interaction was found between HAND and ELECTRODE PAIR [$F(3,45)=22.29$; $p<.001$; $\varepsilon=.484$], which indicated that the moving hand N140 mean amplitudes were significantly more negative at **C3/4** ($p=.002$), **CP3/4** ($p<.001$), and **P3/4** ($p<.001$). A significant three-way interaction was found in the ERP data between HAND, TIMING, and HEMISPHERE [$F(2,30)=4.35$; $p=.022$]. The interaction between HAND and TIMING was nevertheless non-significant when separate ANOVAs were performed for the contralateral hemisphere data [$F(3,45)=1.03$; $p=.368$], as well as the ipsilateral hemisphere data [$F(2,30)=1.18$; $p=.315$; $\varepsilon=.794$]. A second three-way interaction was observed between HAND, TIMING, and ELECTRODE PAIR [$F(6,90)=3.14$; $p=.036$; $\varepsilon=.480$]. This interaction was followed with separate ANOVAs for each electrode pair with the factors HAND and TIMING. Results indicated that the interaction between the two experimental factors was not significant at all tested locations: **FC3/4** [$F(2,30)<1$; p=n.s.], **C3/4** [$F(2,30)<1$; p=n.s.; $\varepsilon=.791$], **CP3/4** [$F(2,30)<1$; p=n.s.; $\varepsilon=.769$], **P3/4** [$F(2,30)<1$; p=n.s.; $\varepsilon=.800$].

Finally, a four-way interaction between all experimental variables: HAND, TIMING, HEMISPHERE, and ELECTRODE PAIR [$F(6,90)=5.11$; $p=.011$; $\varepsilon=.354$] was observed. Separate analyses were conducted for each electrode pair with the factors HAND, TIMING, and HEMISPHERE.

The results highlighted a significant interaction between HAND, TIMING, and HEMISPHERE [$F(2,30)=4.50$, $p=.020$] for the **CP3/4** electrode pair. The resulting two-way ANOVAs from this interaction were thus conducted. The only significant interaction found was that between the factors of HAND and HEMISPHERE, over the post-movement period [$F(1,15)=7.02$, $p=.018$], with the moving hand eliciting

significantly more electronegativity over the contralateral hemisphere, as compared to the resting hand [$t(15)=-5.51$, $p<.001$, $r=.82$].

Furthermore, another interaction between HAND, TIMING, and HEMISPHERE [$F(2,30)=11.21$, $p=.001$; $\varepsilon=.723$] was observed at the **P3/4** electrode pair. The resulting two-way ANOVAs from this three-way interaction were therefore performed. The analysis highlighted a significant interaction between HAND and TIMING on the contralateral hemisphere [$F(2,30)=5.15$, $p=.012$]: Paired-samples t-tests indicated that the resting hand activity in the *post-movement* period was significantly less negative as compared to the resting hand activity in the *preparation* period [$t(15)=-4.46$, $p<.001$, $r=.10$], as well as the resting hand activity in the *execution* period [$t(15)=-5.85$, $p<.001$, $r=.72$]. Though a similar effect was observed for the moving hand, these results did not survive the correction for multiple comparisons.

3.1.2.1.2. Tactile-omission DWs analysis (Analysis 1.2)

The tactile-omission DWs are presented in Figure 3.3, panels **a** to **d,** corresponding to each analyzed electrode pair (FC3/4, C3/4, CP3/4, P3/4).

The tactile-omission DWs analysis revealed a main effect of HAND [$F(1,15)=10.98$; $p=.005$], with the moving hand eliciting a significantly more negative N140, as compared to the resting hand. The timing of delivery of the tactile probes significantly influenced the DWs data [main effect of TIMING, $F(2,30)=10.53$, $p<.001$]; post hoc comparisons indicated that the mean amplitudes of the N140 in the *execution* period were significantly more negative as compared to those of both the *preparation* ($p=.025$), and the *post-movement* periods ($p=.001$).

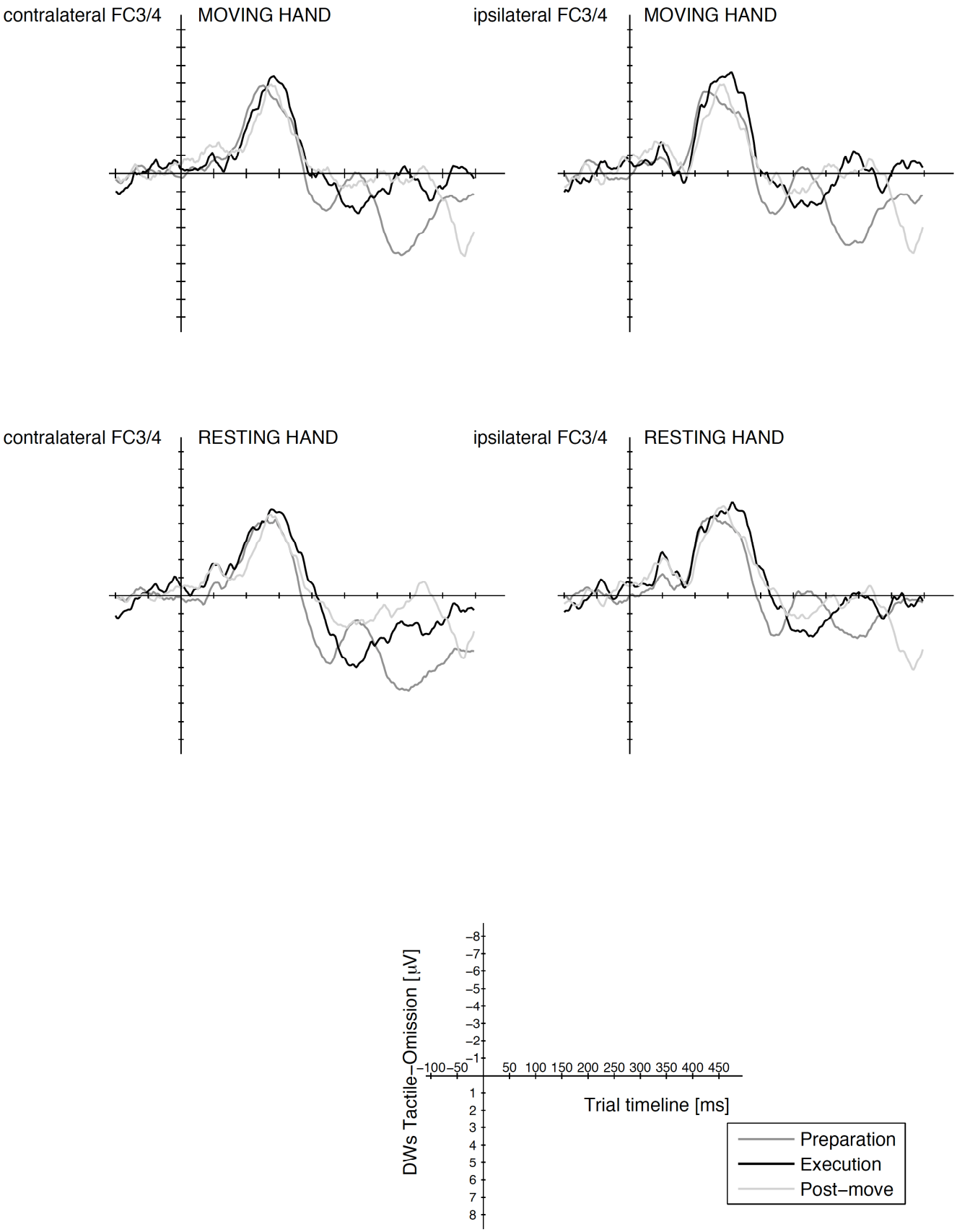


Figure 3.3a. Tactile-omission DWs derived in **Experiment 3.1** from the data recorded at the FC3/4 electrode pair, for both the moving (upper rows) and resting hands (lower rows).

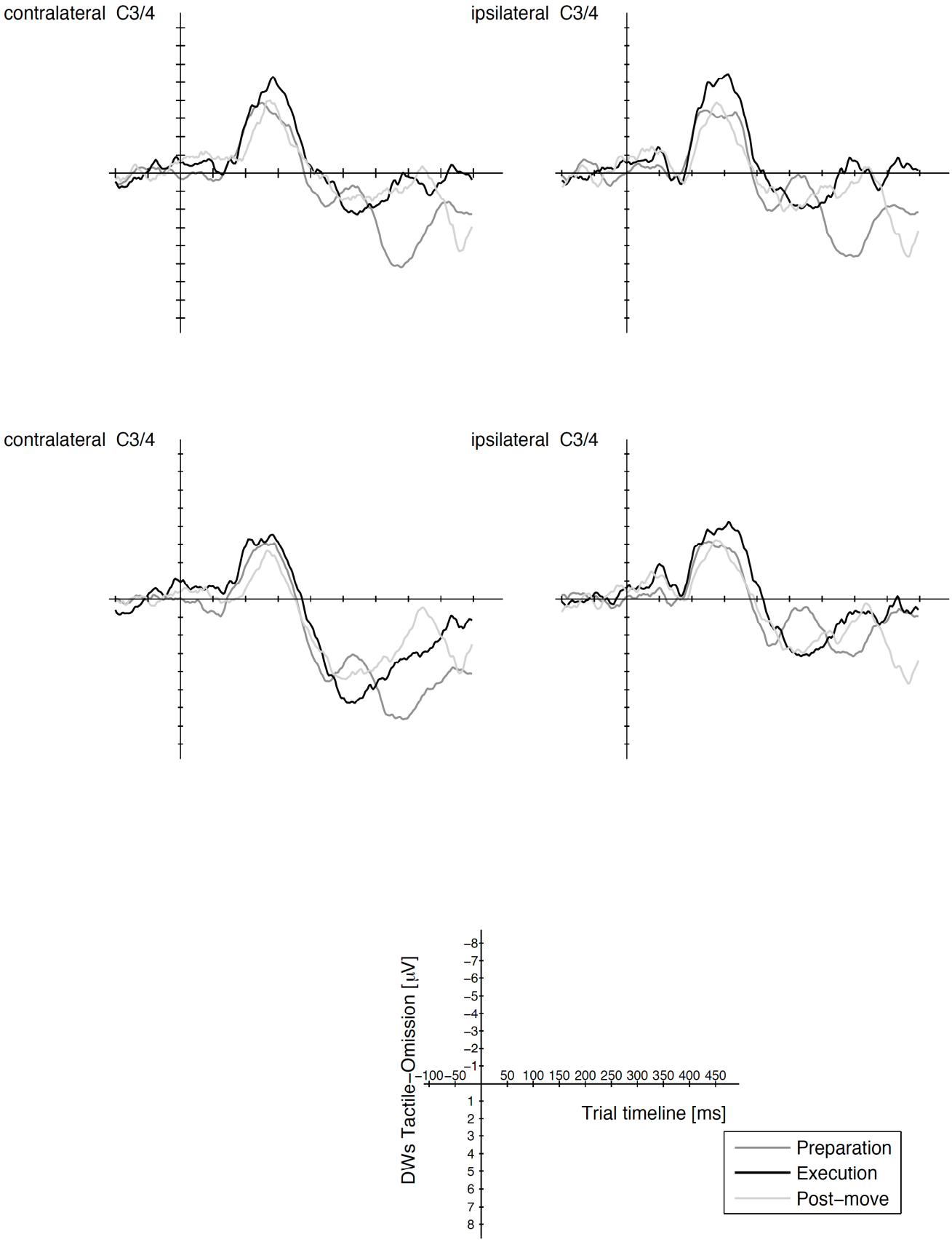


Figure 3.3b. Tactile-omission DWs derived in **Experiment 3.1** from the data recorded at the C3/4 electrode pair, for both the moving (upper rows) and resting hands (lower rows).

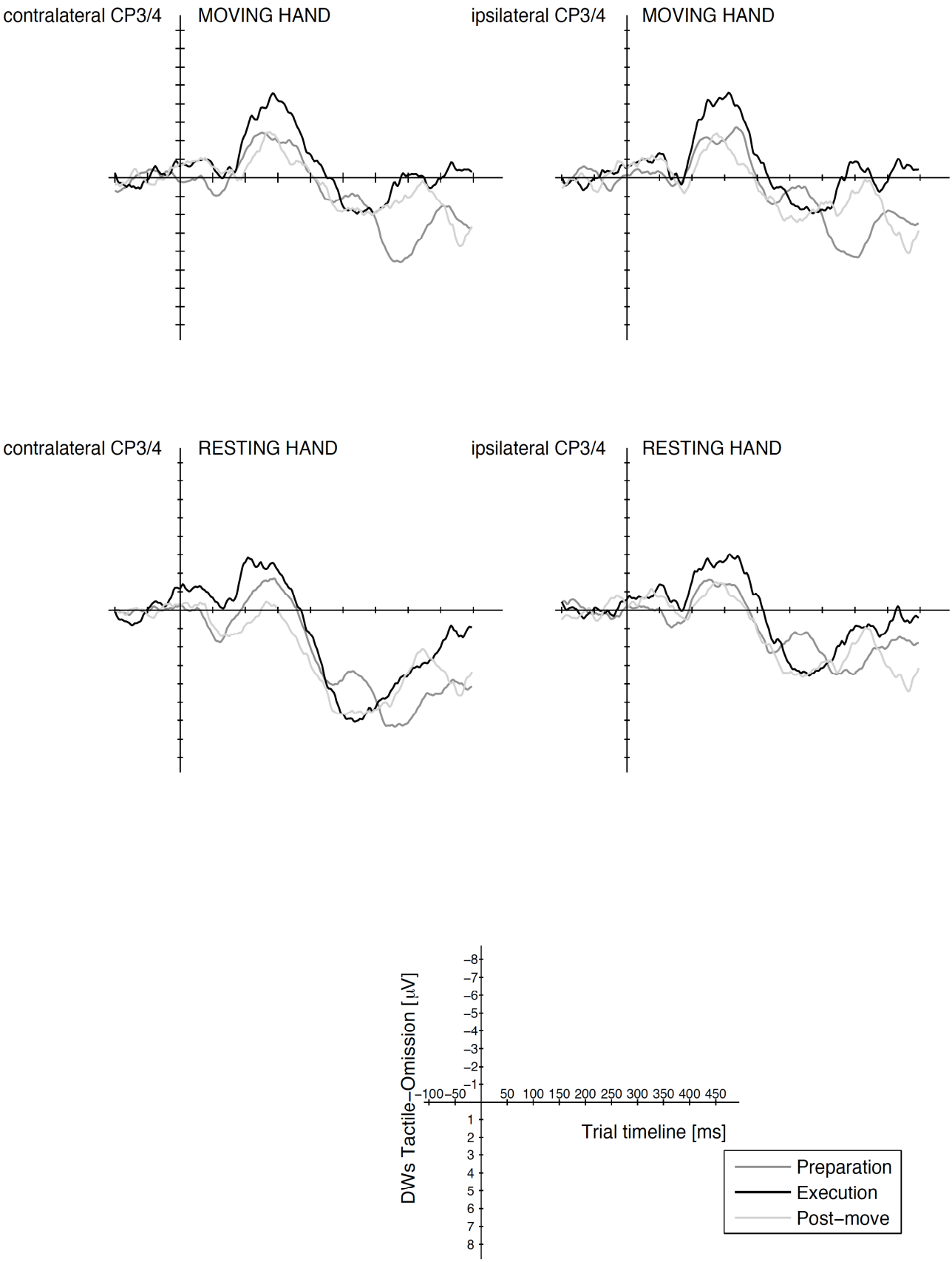


Figure 3.3c. Tactile-omission DWs derived in **Experiment 3.1** from the data recorded at the CP3/4 electrode pair, for both the moving (upper rows) and resting hands (lower rows).

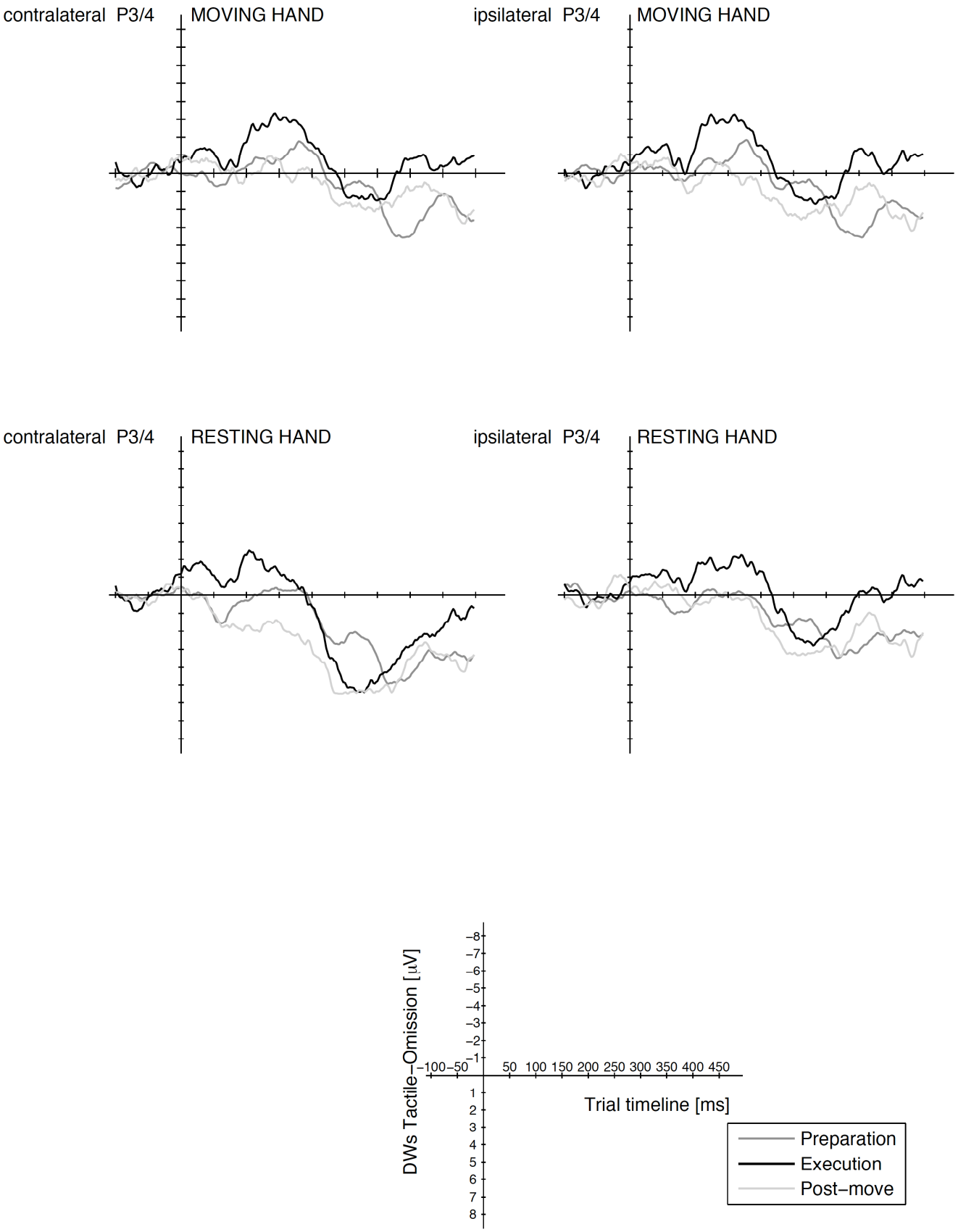


Figure 3.3d. Tactile-omission DWs derived in **Experiment 3.1** from the data recorded at the P3/4 electrode pair, for both the moving (upper rows) and resting hands (lower rows).

A first two-way interaction was observed between HAND and ELECTRODE PAIR [$F(3,45)=7.34$, $p<.001$; $\varepsilon=.428$]; post hoc comparisons indicated that the activity recorded for the moving hand was significantly more negative than that of the resting hand at the **C3/4** location ($p=.003$), **CP3/4** location ($p<.001$), as well as the **P3/4** location ($p=.004$).

A second two-way interaction was observed on the DWs data between TIMING and ELECTRODE PAIR [$F(2,30)=9.73$, $p=.002$; $\varepsilon=.782$]. Paired-samples t-tests were conducted between the different levels of the TIMING factor at each electrode site. The results indicated significantly more negative mean amplitudes of the N140 in the *execution* period as compared to both the *preparation* period [**FC3/4**: $t(15)=3.05$, $p=.008$, $r=.77$; **C3/4**: $t(15)=2.87$ $p=.012$, $r=.64$; **CP3/4**: $t(15)=2.73$, $p=.015$, $r=.58$; **P3/4**: $t(15)=2.95$, $p=.010$, $r=.65$], as well as the *post-movement* period [**FC3/4**: $t(15)=-3.28$, $p=.005$, $r=.77$; **C3/4**: $t(15)=-4.11$, $p=.001$, $r=.70$; **CP3/4**: $t(15)=-4.66$, $p<.001$, $r=.63$; **P3/4**: $t(15)=-4.96$, $p<.001$, $r=.55$].

A three-way interaction between HAND, TIMING, and HEMISPHERE was also documented [$F(2,30)=4.42$, $p=.021$] on the tactile-omission DWs data. The interaction between HAND and TIMING nevertheless proved not to be significant when separate ANOVAs were conducted for the contralateral hemisphere data [$F(2,30)<1$; p=n.s.; $\varepsilon=.725$], as well as the ipsilateral hemisphere data [$F(2,30)<1$; p=n.s.; $\varepsilon=.671$].

Finally, a four-way interaction was found between HAND, TIMING, HEMISPHERE, and ELECTRODE [$F(6,90)=5.56$, $p=.005$; $\varepsilon=.417$]. This interaction was followed up with repeated measures ANOVAs with the factors HAND, TIMING, and HEMISPHERE, for each of the electrode pairs (FC3/4, C3/4, CP3/4, and P3/4). A significant interaction between HAND, TIMING, and HEMISPHERE [$F(2,30)=12.10$,

p<.001] was observed at the **P3/4** electrode pair. For the contralateral hemisphere, a significant interaction between HAND and TIMING [F(2,30)=5.36, p=.010] was found. Paired-samples t-tests indicated that for the resting hand, the *post-movement* period was significantly less negative, as compared to both the *preparation* [t(15)=-4.97; p<.001, r=.66], and the *execution* periods [t(15)=-5.05; p<.001, r=.49].

3.1.2.1.3. Summary of the results of Analysis 1

The first analysis conducted on both moving and resting effectors for the different timings of tactile stimulation delivery over the various frontal to posterior electrodes (FC3/4, C3/4, CP3/4, and P3/4) highlighted an enhanced activity for the moving hand, as compared to the resting hand. This result was particularly evident at central to posterior electrodes (C3/4, CP3/4, and P3/4) for both somatosensory ERPs, as well as their counterpart DWs (i.e., derived by subtracting the movement-related information from the somatosensory ERPs).

Furthermore, with regard to the timing of the delivery of tactile stimulation, the ERP analysis indicated that the activity in the *post-movement* period was significantly less negative as compared to both the *preparation* and *execution* periods of the movement. While the DWs analysis confirmed the significantly diminished mean N140 amplitudes in the *post-movement* period, as compared to the movement *execution* phase, no significant difference was registered between the *post-movement* and *preparatory* phases. Instead, the DWs analysis revealed that the movement *execution* phase exhibited a significantly more negative N140 as compared to the *preparatory* phase of the goal-directed movement, in addition to the confirmed negative superiority over the *post-movement* phase.

Effects of the experimental variables at specific electrode locations were documented by this first analysis; these were particularly evident at the posterior analyzed brain electrodes. As such, the ERP data further confirmed the more negative N140 of the moving hand, this time for the contralateral **CP3** electrode only. However, this effect failed to reach statistical significance for the DWs data analysis. Lastly, both the tactile ERP and DWs analysis revealed that the resting hand N140 was significantly less negative in the *post-movement* period, as compared to both the *preparation* and *execution* phases of the movement, at the posterior **P3** electrode location.

3.1.2.2. Visual probes at PO3/4

This analysis was conducted on the visual ERPs/DWs separately for the moving and resting hands for the different timings of tactile probes delivery, at the PO3/4 electrode pair. Therefore, each ANOVA had two factors: TIMING (preparation, execution, and post-movement), and ELECTRODE (PO3 vs. PO4). See *ERP analysis section 3.1.1.6.3* for the rationale of the analysis.

3.1.2.2.1. Mean visual N100 amplitudes analysis (Analysis 2.1)

The visual ERPs at the PO3/4 location for both the moving and the resting hands are presented in Figure 3.4.

The analysis of the moving hand revealed a significant main effect of TIMING [$F(2,30)=3.69$, $p=.037$], with the *execution* period eliciting significantly more negative activity as compared to the *post-movement* period [$t(15)=-2.94$; $p=.010$; $r=.19$]. On the other hand, the same effect of TIMING failed to reach significance for the resting hand [$F(2,30)=3.16$; $p=.057$]. Nevertheless, a significant interaction between TIMING

and ELECTRODE was observed only for the resting effector [F(2,30)=8.10; p=.002]. As such, for the resting hand contralateral electrode **PO3**, a significant main effect of TIMING [F(2,30)=5.10; p=.012] was found, stemming from the less negative N100 exhibited during the *post-movement* period, as compared to the *execution* period [t(15)=-2.84, p=.012, r=.58].

3.1.2.2.2. Visual-omission DWs analysis (Analysis 2.2)

The visual-omission DWs calculated at the PO3/4 location for both the moving and the resting hand are presented in Figure 3.5.

The analysis of the moving hand visual-omission DWs revealed a significant main effect TIMING [F(2,30)=11.60, p<.001]. Paired-samples t-tests indicated that the visual DWs were significantly more negative in the *execution* period, as compared to the *preparation* [t(15)=-4.14, p=.001, r=-.13], and the *post-movement* periods [t(15)=-3.86, p=.002, r=-.12]. The same significant effect of TIMING was observed for the resting hand as well [F(2,30)=3.59; p=.040]. However, none of the subsequent tests survived the correction for multiple comparisons. Nevertheless, as in the case of the visual ERP data, the visual-omission DWs analysis revealed a significant interaction between the two factors of TIMING and ELECTRODE at the resting hand [F(2,30)=15.46; p<.001]. For the contralateral electrode **PO3** a significant main effect of TIMING was found at the resting hand [F(2,30)=5.62; p=.008]. Paired-samples t-tests indicated that the *post-movement* period N100 was significantly less negative as compared to both the *preparation* N100 [t(15)=-3.15, p=.007, r=.40], as well as the *execution* N100 [t(15)=-2.84, p=.012, r=-.33].

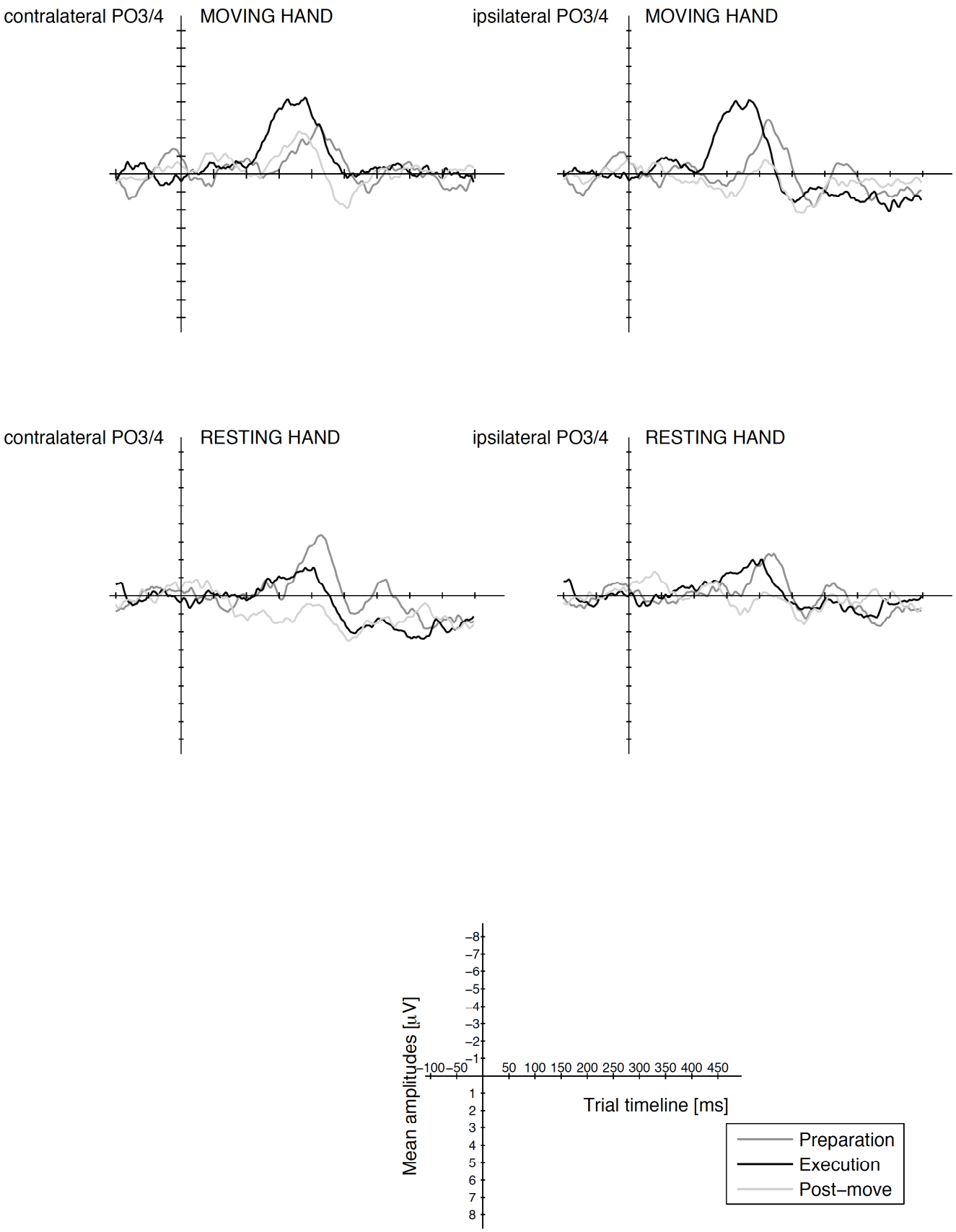


Figure 3.4. Visual ERPs recorded in **Experiment 3.1** at the PO3/4 electrode pair, for both the moving (upper row) and resting hands (lower row).

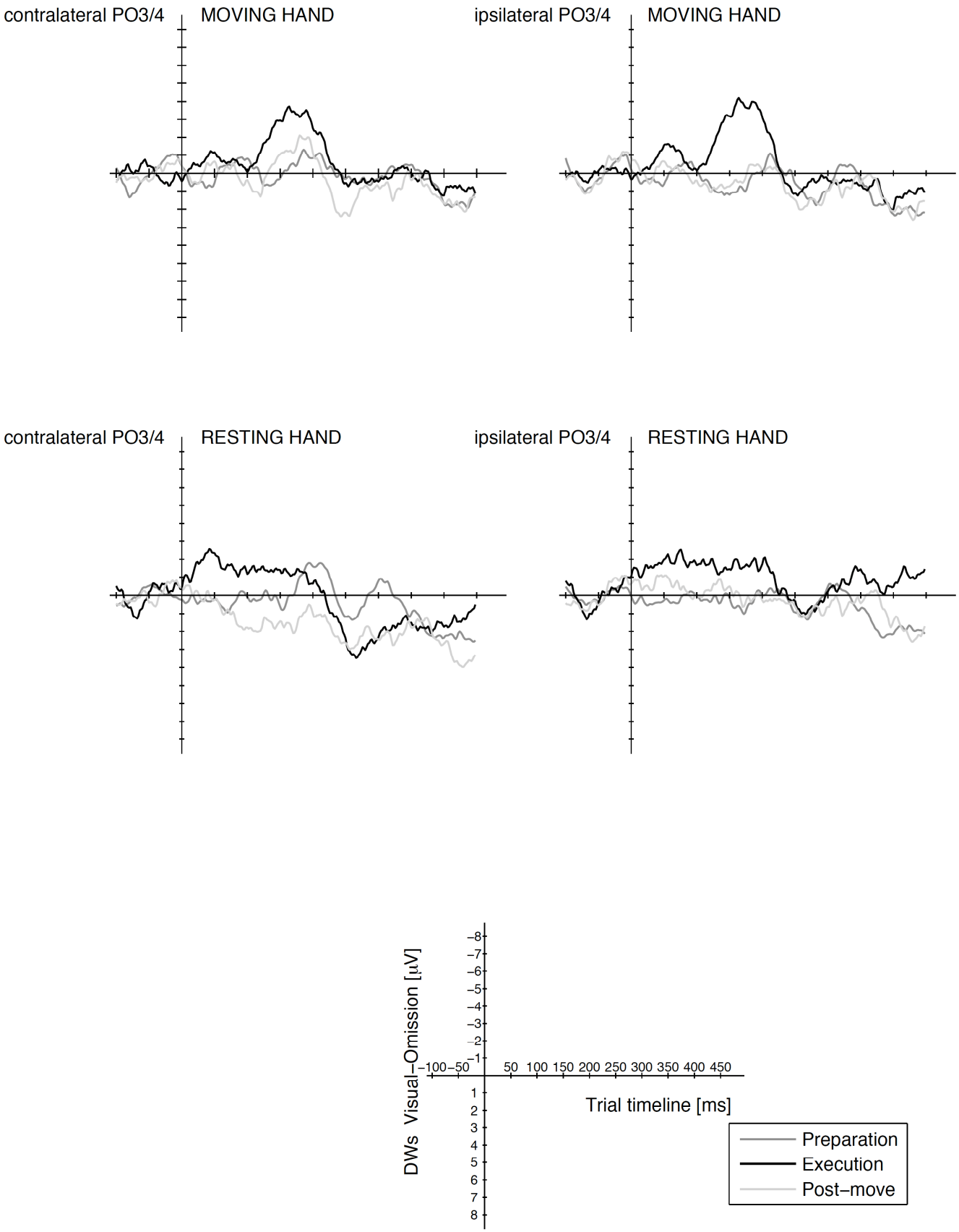


Figure 3.5. Visual-omission DWs derived in **Experiment 3.1** from the data recorded at the PO3/4 electrode pair, for both the moving (upper rows) and resting hands (lower rows).

3.1.2.2.3. Summary of the results of Analysis 2

The second analysis was conducted separately on the moving and resting effectors data for the different timings of tactile stimulation delivery over the occipital electrode pair PO3/4.

For the moving hand, the visual ERP results highlighted a bilateral significantly enhanced N100 for the motor *execution* period, as compared to the *post-movement* period. The same effect was evident on the visual-omission DWs data; Additionally, the DWs data also indicated that the *execution* period N100 was significantly more negative as compared to that of the *preparatory* phase of the movement.

A similar timing effect was present when analyzing the resting hand data, with the only difference being that for the resting hand the visual ERPs/DWs were lateralized and arose from the contralateral **PO3** electrode. As such, the ERP analysis revealed that the *execution* N100 was significantly more negative, as compared to the *post-movement* period. Furthermore, the DWs data indicated a significantly more negative N100 in the *execution* period, as compared to that of both the *preparatory* and *post-movement* phases of the reach-to-grasp movement.

3.1.3. Discussion

The goal of **Experiment 3.1** was to investigate by means of ERPs the neuronal correlates of tactile perception during the execution of goal-directed reach-to-grasp movements. For this purpose, ERPs were recorded in response to tactile and visual probes delivered at both participants' resting and moving hands, during the various temporal phases of the movement: movement preparation, movement execution, and

the post-movement period. Additionally, in a control condition, ERPs were recorded while participants performed the movement, but no sensory stimulation was received during the trial. Therefore, in order to characterize the modulations of tactile perception (i.e., the facilitatory attentional effect vs. the inhibitory suppression effect on tactile perception identified at a behavioural level in **Chapter 2**, see Introduction), the analyses performed on the somatosensory and visual ERP data had the goal of identifying whether attention/suppression effects are *effector-based*, *timing-based*, *modality-based*, or the result of a combination between (some of) the three explanatory factors. In the following, these factors will be considered in the light of the present results[10].

With regard to the first explanatory *effector-based* factor, the results of the **Experiment 3.1** highlighted a significantly more negative tactile N140 for the moving hand, as compared to the resting hand. This enhancement in negativity for the moving hand was particularly evident at the central and parietal electrodes. Indeed, one important function of the parietal lobe is spatial attention and its contribution to achieve awareness for stimuli from different modalities, together with sensorimotor transformations, has been well documented in patient studies (Eimer et al., 2002; Skakoon-Sparling et al., 2011; Torres et al., 2010; also see Critchley, 1949). Moreover, enhancements in electronegativity following sensory stimulation were previously attributed to a central attention-directing effect (Eimer et al., 2005; Forster & Eimer, 2007; Gherri et al., 2007). According to such an interpretation, it could be ascertained that at the neuronal level, the moving hand receives higher attentional prioritization as compared to the resting hand, over the time course of a goal-directed reach-to-grasp movement.

[10] The discussion follows the results of the DWs (somatosensory ERPs – movement-only ERPs), since this analysis provides a 'measure' of tactile perception during the various phases of a goal-directed movement, while at the same time excluding the movement-related interference from the data.

Furthermore, with regard to the second explanatory *modality-based* factor tested here, the results indicated that the same enhancement in electronegativity found for the tactile stimulation was present in the case of visual stimulation as well. This result thus provides evidence against the modality-based explanation of sensory relevance during movement (Bays & Wolpert, 2007). It appears as though both tactile and visual information receive similar prioritized consideration during the execution phase of a goal-directed movement. These results argue strongly in favour of taking spatial attention as the explanatory factor of what is felt during the execution phase of a reach-to-grasp goal-directed movement.

Lastly, when considering the results reported here from the perspective of the third *timing-based* explanatory factor, a differential pattern of activity was found, depending on the timing of tactile (but also visual) stimulation delivery: The execution phase of the movement was characterized by a significantly more negative tactile N140/visual N100 as compared to both the preparatory and post-movement phases. Traditionally, enhancements in electronegativity for tactile ERPs derived for stimulation delivered to a non-moving hand (Forster & Eimer, 2005; Van Velzen et al., 2002; Zopf, Giabbiconi, Gruber, & Müller, 2004), or in the movement preparation period at the movement effector (Eimer et al., 2005; Forster & Eimer, 2007; Gherri et al., 2007), have usually been attributed to a central attention-control mechanism acting on the investigated tactile perception. As an alternative to the attentional explanation, such an enhancement in activity could result from the peripheral input from the movement being processed at the cortical level during movement execution, as opposed to its preparation and initiation (see Urbano et al., 1998). However, note that the movement execution significantly enhanced negativity over the preparatory and post-movement phases was still present even when the movement-only activity was

subtracted from the tactile activity (i.e., the DWs analysis). Thus, if one were to consider such enhancements in electronegativity as an effect of an attention-directing process (Eimer et al., 2005; Forster & Eimer, 2007; Gherri et al., 2007), then it appears as though at a brain level, the execution phase of a goal-directed reach-to-grasp movement benefits from the highest attentional prioritization.

So far in the discussion of the **Experiment 3.1** data presented in this chapter, an attentional explanation with regard to what is felt during the execution of a goal-directed reach-to-grasp movement seems to start developing. The natural question that this result then raises is 'Why?' In answering this question, first of all, the type of attention responsible for the present results needs to be established. Given the type of task that the participants performed in **Experiment 3.1**, whereby each trial they had to perform the movement and ignore the presence or absence of all sensory events at their moving or resting effectors, the observed attentional effects could be included in the exogenous group of the attentional taxonomy (see Spence & McGlone, 2001; see also Spence, 2011). Indeed, the brain signaled the incoming sensory stimulation to a participant's hands by means of an enhancement in the electrophysiological ERP markers. However, another type of attention could be responsible for the present results: visual attention (see Sambo, Gillmeister, & Forster, 2009). Even though the experiment took place in a dimly-lit room and participants were asked to keep central fixation throughout the trial, benefits in the discrimination (Kennett et al., 2001), as well as detection of tactile stimulation (Tipper et al., 1998) were reported when participants were able to view their hand (i.e., note that for example, in the execution period, the moving hand crosses the frontal lower visual field in this experiment), even though the visual information was not relevant for the tactile task at hand. For example, enhanced negative somatosensory ERPs were reported when touch was the

relevant modality in a task where, though uninformative, vision of the hand was available (participants were required to perform either on a tactile or auditory discrimination task and could either see their arm, or another irrelevant object, Taylor-Clarke, Kennett, & Haggard, 2001). Furthermore, enhancement in what is felt has been reported even under conditions of complete darkness (Driver & Grossenbacher, 1996; Shore & Dhanoah, 2008; Shore, Gray, Spry, & Spence, 2005). However, note that when vision of the hand was not available (i.e., participants were blindfolded), the enhancements in early-mid latency negativities documenting spatial tactile attention (e.g., the N140 ERP highlighted in this chapter) were abolished (see Sambo et al., 2009).

The 'Why' question is especially more acute when considering the lack of sensory suppression found in **Experiment 3.1**. Earlier human electrophysiological studies have commonly reported an attenuation of very early somatosensory evoked potentials during movement (Cohen & Starr, 1987; Coquery, 1978; Dyhre-Poulsen, 1978; Rossini et al., 1999; Rushton, Rothwell, & Craggs, 1981), as well as during the imagination of a movement (Rossini et al., 1996). Similarly, other studies concerned with motor observation reported the attenuation of the 25 Hz band activity (i.e., the particular frequency band of the tactile stimulation used in the study) during the observation of movement (Voisin et al., 2011). However, in a similar fashion to Experiment 3.1 in this chapter, a bilaterally distributed mid-range latency (118-132 ms) enhanced somatosensory ERP during movement was reported - Nevertheless, the authors have rather interpreted it as a non-specific effect (Lee & White, 1974; see also Kida et al., 2006a). [11]

[11] Note that reports on auditory evoked potentials follow a different pattern, with long-range evoked potentials being reduced during movement (Tapia, Cohen, & Starr, 1987).

Strikingly, these studies highlight that early somatosensory ERPs are attenuated during movement, while mid-range ERPs are enhanced – with a recent study underlining a positive correlation between the size of attenuation of early ERPs and the size of enhancement in the late N140 (Nakata, Sakamoto, Yumoto, & Kakigi, 2011). Results such as these determined the authors to point towards possible different generators in the brain for the two outcomes of perceptual attenuation and perceptual enhacement, related to movement (Kida, Wasaka, Nakata, & Kakigi, 2006b; Kida et al., 2004; Nakata et al., 2003). Therefore, it could be hypothesized that different cortical brain regions/circuits may be involved in the processing of tactile information: premotor/prefrontal cortices could be involved in attenuating tactile information, whereas the parietal association cortex could be responsible for enhancing sensory information. The question still remains whether the same brain circuits are involved in attenuating/enhancing tactile perceptual information at same/different points in time during movement, or whether different brain regions act on what is felt simultaneously as opposed to at different points in time during goal-directed movement. See Chapter 5 for a further discussion.

The lack of sensory suppression in the experiment reported in this chapter raises the question of whether goal-directed reach-to-grasp movements are 'special' with respect to the processing of sensory information during movement. For example, recent studies that differentiated between simple reaching and grasping movements have highlighted enhanced processing of visual sensory information over the execution phase of the movement (van Elk, van Schie, Neggers, & Bekkering, 2010). Note that the enhancement in the somatosensory N140 is abolished when visual feedback from the hand is precluded (Sambo et al., 2009). Moreover, to consider the characteristics of the peripersonal space surrounding the body (Previc, 1998), the

incoming sensory information from the different sensory modalities is integrated so that it facilitates our interaction with the surrounding environment (Rizzolatti et al., 1997; see also Brozzoli et al., 2009).

The lack of sensory suppression found at a neuronal level in this chapter nevertheless involves a consideration of the particular task utilized: Participants were explicitly required to ignore the sensory events happening to occur while they executed the instructed task. Conversely, by utilizing tasks that required participants to discriminate the quality of the received sensory information, convincing behavioural evidence concerning the existence of tactile sensory suppression during movement execution was reported (Buckingham et al., 2010; Gallace et al., 2010; see also **Chapters 2** and **4** in this thesis). Such opposing results could suggest that during movement execution the brain does give priority to responding to incoming sensory stimulation (i.e., detecting their mere presence), as in the experiment presented in this chapter. However, the quality of sensory stimulation received during the execution of the goal-directed movement may not be important at this stage of the movement and thus is attenuated (see for example **Experiments 2.1-2.5** in **Chapter 2**, as well as in **Chapter 4**).

3.2. Summary and conclusions

The experiment presented in **Chapter 3** was designed to investigate at a brain level between explanatory factors of the different mechanisms (attention vs. suppression) raised in **Chapter 2** in order to explain what is felt over the time course of a goal-directed movement. To summarize, **Experiment 3.1** highlights the fact that the moving effector benefits from an enhanced sensory processing, as compared to the resting effector. Moreover, the experiment reported in this chapter singles out the

execution period, as the temporal stage that receives the highest sensory attentional contribution, as compared to the preparatory and post-movement phases. Lastly, attention affects the two modalities of touch and vision in a similar manner during the execution of the goal-directed reach-to-grasp movement. To return to the predictions raised in the Introduction of the present chapter, it appears as though at a neuronal level, attentional influences are greatest during the execution period of a goal-directed movement, they are effector-based and supramodal. The implications of the present results will be further discussed in **Chapter 5**.

Chapter 4

Investigation of tactile perception during the execution of naturalistic goal-directed movements

4.0. Introduction

The experiments presented in the last two experimental chapters (**Chapters 2-3)** were centered on goal-directed reach-to-grasp movements. In **Chapter 4**, the primary question was: *'Will tactile perception be similarly affected during the execution of other naturalistic movements as well?'* In order to answer this question, several types of bimanual movements were investigated: a sustained practiced bimanual movement (i.e., juggling), as well as the throwing, as opposed to the catching movements, of a basketball. As a starting point, the experiments reported here were conceived as exploratory experimental studies. However, since naturalistic movements were used, these studies allowed for the investigation of (tactile) perception and its importance to movement, when the executed movement is automatized (e.g., the juggling movement, **Experiments 4.1-4.3**). Moreover, any differences in what is felt during movement were also investigated in special groups that had training in the particular movements tested (e.g., intermediate/advanced basketball players in **Experiment 4.4**). Finally, **Chapter 4** was also intended to address the parallel between the self- versus externally-generated naturalistic movements of throwing and catching a basketball (**Experiments 4.4-4.8**).

4.1. Tactile perception while juggling

4.1.0. Some considerations on signal detection theory

When performing a search task in a real-world situation we can fail to find the target stimulus that we happen to be searching for. In such situations, we fail to detect the target of our search because we either select inappropriate aspects of the surroundings, we focus our attention on a small part of the environment or, we just unnecessarily divide our attention between stimuli or events that we do not wish to process.

When analysing two discrete states of the world (a *signal* is present and a signal is absent, or *noise*), states that cannot be easily distinguished, one usually refers to signal detection theory (SDT, Green & Swets, 1966; see also Macmillan & Creelman, 2005). The combination of these two discrete states and two categories of responses with regard to the presence of the stimulus (YES and NO) generates four classes of combined events: true positives, false positives, false negatives, and true negatives. The psychophysical model of SDT points toward two stages of information processing involved in target detection (Green & Swets, 1966): First, we gather *sensory evidence* concerning the presence or absence of the signal and second, we make a *decision* about whether this is a signal or not. As such, SDT allows researchers to derive measures not only of sensitivity, but also of response bias in the tested domain (i.e., tactile perception in this chapter), under various experimental conditions (i.e., movement preparation/execution, or rest).

Sensitivity (*d'*) provides a measure of the true separation between the signal (i.e., gap present in tactile stimulation, the method used in this chapter) and noise (i.e., gap absent). Sensitivity indicates how close the signal and noise are together and is supposed to provide a measure of only the sensory processes involved in the detection of a target. It therefore reflects the characteristics of the stimulus and is independent of response bias. In this respect, the larger the separation between signal and noise, the

more sensitive a participant will be.

On the other hand, the decision criterion, or response bias, provides a measure of the internal separation baseline for noise and signal and as will be discussed below, it can be influenced by a participant's motivations, expectancies, and any task pressures. Response bias is characteristic to the participant: In a YES/NO task, participants will likely favour one response or the other. SDT allows one to identify the criterion location (criterion *c*) in the decision space. Its distribution is centered on zero and extreme values are given by either very small or very large numbers of true positives (i.e., a YES response when a target was present) or false positives (i.e., a YES response when the target was absent). Given that zero constitutes the unbiased location, positive values of the criterion *c* indicate a tendency toward saying 'NO', whereas negative values indicate a tendency toward saying 'YES'. Moreover, another measure of response bias offered by SDT is the relative criterion location *c'*, a measure derived by scaling the criterion location to the measured sensitivity. If *c* is independent of sensitivity, *c'* is clearly influenced by sensitivity. When *d'* varies across conditions, the relative criterion *c'* provides a good measure of the strength of the criterion needed to obtain a certain amount of bias (see Macmillan & Creelman, 2005, for a discussion of the usefulness of the various criteria).

Several factors have been identified as having an influence on the sensitivity level and sensitivity decrement (Wickens & Hollands, 2000): *signal strength*, which brings in a reduction in sensitivity (sensitivity declines due either to a low probability of signal appearance, or when the signal is made more similar to the noise); the *uncertainty* with regard to the possible location or time of the target signal appearance, and *practice* as a way to improve sensitivity by making the task more automatic; these

practice automation effects occur unintentionally and make use of few cognitive resources.

The experiments reported in **Chapter 4** utilized the outlined measures of SDT (i.e., sensitivity, *d'*, and response criteria, *c* and *c'*) as dependent measures in order to investigate tactile perception during the execution of naturalistic goal-directed movements.

4.1.1. Experiment 4.1: Tactile sensitivity is diminished while juggling

4.1.1.1. Introduction

In **Experiment 4.1**, tactile perception was investigated in a complex, practiced bimanual task, namely juggling. The participants had to detect a short gap in an otherwise continuous tactile vibration under conditions of no movement (rest), and juggling. The juggling task was chosen as it seemed to provide a means of exploring the dynamics of tactile perception, the central concern of this thesis. Therefore, the first aim was to investigate whether a differential pattern of sensitivity would be observed for the successive 'catches' and 'throws' of the balls occurring during the hand movements used while juggling. Another exploratory hypothesis was related to the timing of the juggling: For this, the second goal of **Experiment 4.1** was to investigate whether the exact point in time during the trial when the target (i.e., the short time gap) was presented (whether at the beginning of the movement, the middle, or the end point) made a difference with respect to participants' sensitivity to it. Lastly, taking into consideration the sensory suppression experienced during movement, it was hypothesized that participants would be more sensitive to gaps in

tactile stimulation when their hands were at rest, as compared to the juggling condition in which a significant deterioration in participants' tactile perception was expected. At the same time, given the 'tactile uncertainty' favoured by the movement of both hands, a differential pattern in both criteria *c* and *c'* was expected during the active juggling phase, as opposed to the rest condition.

4.1.1.2. Methods

4.1.1.2.1. Participants

Ten jugglers (6 male, one left-handed) took part in this experiment (mean age of 24 years; age range 20-30 years). All of the participants reported normal touch, normal hearing, as well as normal or corrected to normal vision. The participants had been juggling for approximately 8 years on average (ranging from 3 to 20 years). All of the participants were comfortable with basic 3-ball juggling. The experimental session lasted for approximately 75 minutes and the participants received a £10 gift voucher in return for taking part in the study.

4.1.1.2.2. Apparatus

The experiment took place in a 1.6 m wide corridor. Illumination was provided by several ceiling lights. The participants had one tactor attached to their left wrist with an adjustable sports strap. The participants also wore disposable earplugs, as well as over-the-head earmuffs (Peltor H7A) for the duration of the experiment. The participants had a Wii Remote (Nintendo Co., Ltd., Kyoto, Japan) attached to their left forearm with another adjustable sports strap. The tactor cable was attached with Velcro to the participant's arm, so that it would not impede the movement of their hand. Both the tactor box and the Wii Remote were interfaced through Matlab on

Windows XP. The Wii communicated with the main computer via bluetooth (BlueSoleil v2) and the communication between the Wii remote and Matlab was interfaced through the open source library FWIINEUR [fWIIne v0.2; http://fwiineur.blogspot.com/, downloaded on 15/09/2009]. The auditory signals were delivered via the main computer loudspeaker. The participants gave a vocal response, which the experimenter entered into the computer. A set of three juggling balls (5 cm in diameter, 85 g each) was used.

4.1.1.2.3. Procedure

The experiment consisted of two sessions: A control (*rest*) session and an experimental (*juggle*) session. The participants first performed the control session and, after a short break, continued on to the main experimental session. The rest session lasted for approximately 8-10 minutes; the participants were seated in a comfortable chair and were offered a cup of tea. In each trial of the *rest session*, the participants heard an auditory beep (800 Hz, 100 ms) presented from the main computer loudspeaker placed on the floor, to their left. After 1000 ms, the tactor attached to their wrist vibrated for 2500 ms. Immediately after the termination of the vibration, a second auditory signal (800 Hz, 100 ms) indicated the end of the trial. The participants had to say whether or not they felt a gap in the vibration. In each trial of the *juggling session*, the participants had to stand with their forearms held at 90 degrees with respect to their body, with their palms oriented toward the ceiling holding the balls (two balls in one hand and the third in the other). An auditory signal (800 Hz, 100 ms) signalled that they should start juggling. The tactor started vibrating 1000 ms after the beep. The total duration of the vibration was 3500 ms. Once the tactor had stopped vibrating, another auditory beep (800 Hz, 100 ms) informed the participants that they

should stop juggling. At the end of the trial, the participants again had to give a response with respect to whether or not they felt a gap in the vibration. The experiment continued on to the next trial as soon as the experimenter (seated in a nearby experimental room outside of the participant's sight) had entered their response into the computer.

4.1.1.2.4. Design

The *rest session* consisted of one block of 120 trials. Given the fact that (in the absence of movement) the tactile detection task was very easy, the rest session was conceived of as a familiarization phase, so that the participants could get acquainted with, and hence easily remember, the signal for the following juggle session. In each trial, the Timing of the gap was manipulated: early (500 ms after the start of the trial), middle (1000 ms after the start of the trial), or late (1500 ms after the start of the trial). The second manipulated variable was the Gap duration: 0 (no gap), 10, 20, 30, 40, 60, 70, and 80 ms. The different gap timings, as well as the gap durations, were randomized across trials and participants.

The *juggling session* consisted of 6 blocks of 32 trials each, adding up to a total of 192 trials. Half of the trials were 'gap' trials (the vibration was interrupted very briefly) and half of the trials were 'no gap' trials (the vibration was continuous). The gap duration was a value drawn randomly from the interval (10 to 80 ms). Moreover, half of the gap trials were 'up' trials (the gap in the vibration was delivered while the participants' hand was moving upward) and the other half were 'down' trials (the gap in the vibration was delivered while their hand was moving downward). For each of the gap trials, the Timing of the gap (1000, 1500, 2000, or 2500 ms after the start of the vibration) was also manipulated.

4.1.1.2.5. Data analysis

For each of the participants, for each of the experimental (rest vs. juggle) sessions, the percentages of true positives (i.e., YES responses when a gap was present), as well as false positives (i.e., YES responses when a gap was not present) were calculated, split considering the manipulated experimental variables (Timing of the gap for both sessions, together with Type of movement for the juggling session). These percentages were then normalized and sensitivity measures (d_a/d'), as well as criteria c, and relative c', were derived according to SDT (Green & Swets, 1966; Macmillan & Creelman, 2005). See Table 4.1 for the exact equations used in deriving these measures. For the cases where accuracy was perfect (i.e., true positives in proportion of 1) or no false positives were registered in the data, the proportions of 1 and 0 were adjusted by 1/(2N), and 1/(1-2N), respectively, where N is the number of trials for a given condition on which the proportion was calculated.

	REST sessions (E 4.3 & E 4.2)	**JUGGLE sessions (E 4.1 & E 4.2) & E 4.3**
Sensitivity d'	$d_a = \left(\frac{2}{1+s^2}\right)^{\frac{1}{2}}[z(TP) - sz(FP)]$	$d' = z(TP) - z(FP)$
Criterion location c	$c = -\frac{1}{1+s}[z(TP) + z(FP)]$	$c = -\frac{1}{2}[z(TP) + z(FP)]$
Relative criterion c'	$c' = \frac{c}{d_a}$	$c' = \frac{c}{d'}$

Table 4.1. Equations used to derive the signal detection theory measures in **Experiments 4.1**, **4.2**, and **4.3**. *z(TP)* and *z(FP)* represent the normalized values of signal present and signal absent trials. The slope (s) is given by the ratio of the standard deviations of signal and noise trials (Green & Swets, 1966).

The data were explored and the assumptions of normality and homogeneity of variance were checked with the Kolmogorov-Smirnov and Levene's tests, respectively. If the normality assumption was violated, non-parametric tests were used

to analyze the data. Otherwise, repeated measures ANOVAs and t-tests were used to examine any differences between the experimental conditions. For these, Mauchly's test of sphericity was used to ensure that the data did not violate the sphericity assumption. If the assumption was violated, then the Greenhouse-Geisser correction was applied to correct the degrees of freedom; corrected p values are reported. Subsequent pairwise comparisons were conducted using the Bonferroni adjustment for multiple comparisons.

The sensitivity and criteria data from the rest session violated the normality assumption. Therefore, Friedman's ANOVA was used on the *d'* data with the within-participants factors of the Timing of the gap (500, 1000, and 1500 ms). The same analysis was then conducted on the two criteria data. The sensitivity data from the juggling session was normally distributed. Therefore, a repeated-measures ANOVA was conducted on the *d'* data with the within-participants factors of Timing of the gap (1000, 1500, 2000, and 2500 ms) and Type of hand movement (up vs. down). The criteria data calculated for the juggling session violated the assumption of normality. Therefore, related-samples Friedman's ANOVAs were conducted on the criterion *c* and relative criterion *c'* data.

Finally, Wilcoxon signed ranks tests were conducted on the amalgamated *d'* data from the two experimental Sessions (rest vs. juggling). The same analysis was repeated on the criteria data.

4.1.1.3. Results

Boxplots of the sensitivity and criteria data from **Experiment 4.1** are presented in Figure 4.1.

4.1.1.3.1. Rest session. Timing of the gap

The analysis revealed that the timing of the gap had no significant effect on the sensitivity data [$\chi^2(2)=4.2$; p=.135]. The same analysis revealed no significant main effect of the timing of the gap on the criterion *c* data [$\chi^2(2)=5$; p=.092] and failed to reach significance on the relative criterion *c'* data [$\chi^2(2)=3.8$; p=.187].

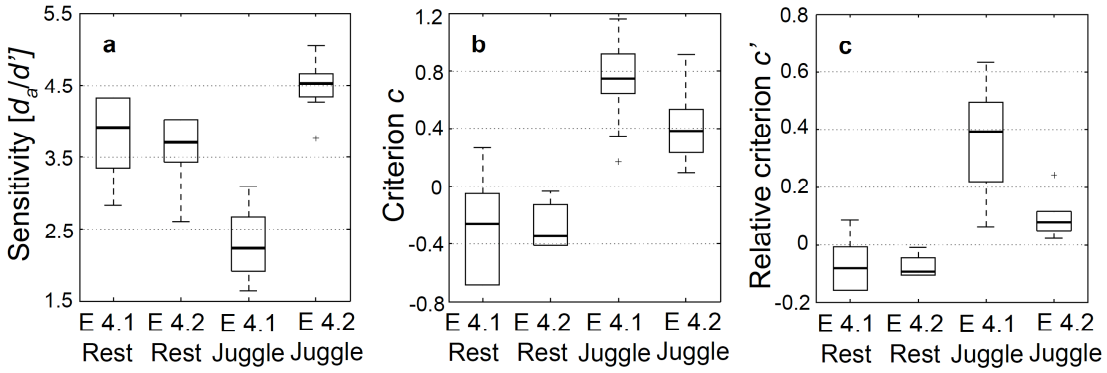


Figure 4.1. Boxplots of *d'* sensitivity data (a), criterion *c* data (b), and relative criterion *c'* (c) for **Experiments 4.1** and **4.2**. The box represents the middle 50% of the data; the whiskers extend to the upper (top 25%) and lower (bottom 25%) quartile respectively; the thick horizontal line denotes the median. Individual data with values higher than 1.5 times the inter-quartiles range are denoted with a '+' sign.

4.1.1.3.2. Juggle session. Timing of the gap

The analysis revealed that the timing of the gap had no significant effect on the sensitivity data [F(3,27)<1; p=n.s.]. The type of hand movement (up vs. down) was also non-significant in terms of the sensitivity data [F(1,9)<1; p=n.s.]. Moreover, the interaction between the two experimental variables (the timing of the gap and the type of movement) did not reach statistical significance [F(3,27)=1.33; p=.285]. Furthermore, Friedman's related-samples ANOVA revealed no significant difference in upward vs. downward movements of the hand for the tested timings of gap delivery on both criterion *c* data [F(7)=9.49; p=.219], as well as well as relative criterion *c'* data [F(7)=5.93; p=.548].

4.1.1.3.3. Juggle vs. Rest comparison

Participants exhibited significantly higher sensitivity when detecting a gap in the tactile stimulation when this was delivered to the hand at rest, as compared to the hand that was juggling (z=-1.94, p=.026, r=-.61). Participants did not, however, shift their criterion in deciding whether there was a gap in the tactile stimulus delivered either when the hands were at rest, or while moving, as highlighted by both criterion *c* data (z=-1.24, p=.117, r=-.39), as well as the relative criterion *c* data (z=-1.48, p=.075, r=-.46). Although the criteria effects obtained when comparing the two sessions did not reach statistical significance, note that they both exhibited an above average effect size.

4.1.1.4. Discussion

With regard to the exploratory aims concerning the dynamics of tactile perception during movement, the results of **Experiment 4.1** revealed no difference in detecting a short gap in an otherwise continuous tactile stimulus between the downward movements ('catches') and upward hand movements ('throws') executed while juggling. At the same time, no difference was found with respect to whether the gap occurred in the beginning, middle, or toward the end of the juggling trial. Taken together, these results suggest that when tactile suppression occurs, it is most likely uniformly distributed over the time-course of the sustained goal-directed movement, as well as the different types of hand movements used while juggling. However, when comparing the conditions of juggling and rest, the results confirmed the main hypothesis: Namely, that tactile perception was impaired when juggling, as compared to the rest condition (Gallace et al., 2010; see also **Chapters 2** and **3** of this thesis). This clear deterioration observed in tactile perception during movement can be attributed to the motor command and the sensory signals resulting from the performed

movement (Chapman & Beauchamp, 2006). Alternatively, a more general attentional mechanism could be responsible for the reported effects. Therefore, in order to test for attentional effects, in a second experiment, the same experimental paradigm was used in order to test for a possible deterioration in auditory perception while participants were moving. The participants in this study had to detect a short gap in a continuous auditory signal, under the same conditions of juggling and rest. If tactile attenuation occurred during movement so that other (external) stimulation is enhanced, as predicted by the forward models of motor control, then one would expect no deterioration in auditory performance during movement. However, if attention were responsible for the attenuating effects found on tactile perception during movement, then an equal amount of suppression should be found for the auditory task used in **Experiment 4.2**.

4.1.2 Experiment 4.2: Auditory sensitivity is not diminished while juggling

4.1.2.1. Methods

The methods used in this experiment were very similar to those used in **Experiment 4.1**. Therefore, only the differences are outlined here. Nine jugglers (6 male, all right-handed; mean age of 27 years; age range 24-34 years) took part, out of which two had already taken part in **Experiment 4.1**. The participants had been juggling for approximately 12 years on average (with a range of 3 months-20 years).

The participants wore closed ear headphones (Beyer Dynamic DT 531) for the duration of the experimental session. Since the first experiment did not indicate any effect of the type of movement (downward or upward) on sensitivity, The Wii Remote was not used in this experiment. Lastly, the 2500 ms vibration delivered in the rest

session and the 3500 ms vibration delivered to the participant's wrist in the juggling session of **Experiment 4.1**, were replaced with auditory signals (800 Hz, 65 dB) of the same duration. The participants now received a short tactile pulse (100 ms) as a signal to start and stop juggling. Their task at the end of the trial was to indicate whether they had heard a gap in the sound or not.

With regard to the analysis, since the rest session (as in the case of **Experiment 4.1**) violated the normality assumption, Friedman's ANOVA with the within-participants factor of Timing of the gap (500, 1000, and 1500 ms) was conducted on both sensitivity and criteria data. The data from the juggling session was normally distributed. Therefore, repeated-measures ANOVAs were conducted on the *d′* and criteria data with the within-participants factors of Timing of the gap (1000, 1500, 2000, and 2500 ms) and Type of hand movement (up vs. down). In a next step, Wilcoxon signed ranks tests were conducted on the amalgamated *d′* and criteria data from the two experimental Sessions (rest vs. juggling). A final analysis was conducted in order to compare the results of **Experiments 4.1** and **4.2**. For this analysis, independent-samples t-tests were used for normally distributed (sensitivity data in the juggle session of both experiments), or the non-parametric Mann-Whitney tests for not normally distributed data (criteria data in the rest and juggle sessions of both experiments).

4.1.2.2. Results

Boxplots of the sensitivity and criteria data from **Experiment 4.2** are presented in Figure 4.1.

4.1.2.2.1. Rest session. Timing of the gap

The analysis revealed that the timing of gap delivery had no significant effect on the *d'* sensitivity measure [$\chi^2(2)=2.66$; p=.44]. Moreover, this analysis did not reach significance on either criterion *c* data [$\chi^2(2)<1$; p=n.s.] or criterion *c'* data [$\chi^2(2)<1$; p=n.s.].

4.1.2.2.2. Juggle session. Timing of the gap

The analysis indicated that the timing of the gap had no significant effect on either the *d'* data [$F(3,24)<1$; p=n.s.], criterion *c* [$F(3,24)<1$; p=n.s.], or criterion *c'* [$F(3,24)<1$; p=n.s.].

4.1.2.2.3. Rest vs. Juggling comparison

The analysis revealed a significant effect of the experimental session on *d'* data [z=-2.31, p=.021, r=-.77], with participants exhibiting significantly higher sensitivity for detecting a gap in auditory stimulation delivered in the juggle condition, as compared to the rest condition. The same effect didn't reach significance for the criterion *c* data [z=-1.40, p=.161, r=-.46], and showed a marginally significant effect for criterion *c'* data [z=-1.89, p=.058, r=-.63].

4.1.2.2.4. Comparison of the results of Experiments 4.1 vs. 4.2

4.1.2.2.4.1. Rest session

There was no significant difference in participants' sensitivity between detecting a gap in tactile stimulation and detecting a gap in auditory stimulation at rest [U=36, p=.241, r=-.17]. Moreover, no significant difference was found between the criterion *c* adopted

in the rest sessions of **Experiments 4.1** and **4.2** [U=43, p=.443, r=-.03], nor was there any effect for the relative criterion *c'* [U=42, p=.412, r=-.05].

4.1.2.2.4.2. Juggling session

The analysis revealed a significant difference in the *d'* means from the juggling sessions of the two reported experiments [t(17)=-10.52, p<.001, r=.93], with participants being less sensitive to detect a gap in the vibration delivered to their wrist, as compared to a gap in the auditory signal. Moreover, a significant difference was found for the criterion *c* data [U=17, p=.010, r=-.52] from the juggling sessions of the two experiments, with participants being significantly less conservative in saying that there was a gap in the stimulation in **Experiment 4.2** as compared to **Experiment 4.1**. Finally, criterion *c'* data showed a similar significant pattern [U=7, p<.001, r=-.71]: If participants' criterion *c'* was more or less clustered around the zero-bias point for the auditory gap detection while juggling, their criterion was significantly shifted toward saying NO in the tactile gap detection task, performed in **Experiment 4.1**.

4.1.2.3. Discussion

The results of **Experiment 4.2** indicate that participants are significantly more sensitive to detect a gap in auditory stimulation while juggling, as compared to the rest condition. Such a result could be taken to support forward models of motor control hypothesis (Miall & Wolpert, 1996; Wolpert et al., 1995). According to such models, the movement of our limbs results in suppression for the information related to the movement itself (e.g., tactile information), but at the same time, it has been suggested that movement favours the enhancement of external stimuli (e.g., the auditory information tested in this experiment). However, the interpretation of the results of the

rest vs. juggle sessions of **Experiment 4.2** needs to be taken with some caution. Note that the sensitivity data of the rest sessions (in both **Experiments 4.1** and **4.2**) are derived from unequal number of true and false positives, a fact that most probably led to an underestimation of the real sensitivity performance for the two rest sessions, and consequently the significant difference between the two sessions in **Experiment 4.2**. Nevertheless, when comparing the normally distributed data from only the juggle sessions of **Experiments 4.1** and **4.2**, a significant deterioration in participants' performance was observed for **Experiment 4.1**. Results such as these could therefore be interpreted as a consequence of the motor command. More importantly, the results highlighted the fact that participants clearly shifted their criterion toward saying that no gap was present in tactile stimulation while juggling in **Experiment 4.1**, as compared to the auditory stimulation in **Experiment 4.2**.

In order to control for the limitations inherent in the rest conditions (of both **Experiments 4.1** and **4.2**), in **Experiment 4.3** participants performed the same gap detection task, this time by always keeping their hands at rest. Perceptual sensitivity, together with response bias, was tested with an equally balanced task comprising auditory and tactile conditions. It was hypothesized that participants would exhibit comparable sensitivity for the auditory and tactile gap detection tasks. However, at the same time, another factor that could account for the suppression found in the data could be intramodal tactile suppression. For example, the sensory feedback received when the ball touched the hand while juggling cannot be fully accounted for by the results of the rest condition of **Experiment 4.1**. Therefore, in order to control for this alternative explanation, in an additional condition in **Experiment 4.3**, participants performed the tactile gap detection task, while the experimenter rhythmically touched their palms with two juggling balls.

Additionally, one last aim of **Experiment 4.3** was to investigate whether the duration of the gap (a variable that was randomly allocated in both **Experiments 4.1** and **4.2**) influences the measured sensitivity, as well as criterion allocation.

4.1.3. Experiment 4.3: Tactile intramodal interference affects sensitivity, but not response bias

4.1.3.1. Methods

The methods used in this experiment were very similar to those used in **Experiments 4.1** and **4.2**, with a few exceptions. Ten participants (3 male, one-left handed; mean age of 27 years; age range 23-28 years) took part in this experiment. None of the participants was familiar with juggling at the time of participation. The experiment lasted approximately 40 minutes and participants received a £5 gift voucher in return for taking part in the study.

Experiment 4.3 consisted of three separate conditions, all involving the detection of a temporal gap in auditory stimulation (**Experiment 4.3a**), tactile stimulation (**Experiment 4.3b**), or tactile stimulation plus tactile interference (**Experiment 4.3c**). The order in which the conditions were presented was counterbalanced across participants. None of the three conditions involved movement of the participants' hands; the participants were seated at a table with both hands on the table surface, their palms facing upward.

In each trial of **Experiment 4.3c**, the experimenter, seated across the table in front of the participant, touched the participant's palms with two juggling balls. For this, the experimenter held a stick with one ball attached at either end. For the duration of the trial, the experimenter balanced the stick so that the balls touched the participant's palms in a rhythmical fashion; the balancing movement of the stick was

kept as constant as possible and the resulting touches were intended to mimic the touch of the balls from the juggle session, in the absence of any overt movement by the participant. The vibratory tactile stimulation, as well as the auditory stimulation, was the same as in the first two experiments. Each of the three conditions consisted of two blocks of 60 trials each. Half of the trials in each block were target absent trials (i.e., no gap in stimulation was delivered), while the other half of the trials were target present trials (i.e., a short time gap in the tactile or auditory stimulation was present). The only variable that was manipulated was the duration of the gap (20, 40, or 60 ms). Given the fact that the first two experiments of this chapter showed no significant difference in sensitivity, nor in response bias for the different timings of the gap delivery within the trial, in **Experiment 4.3** the timing of the gap was allocated randomly.

Lastly, the data analysis was conducted on the mean *d'*, as well as criteria *c* and *c'* data. If the data did not violate the normality assumption, in a first step, the data from each condition were analyzed with repeated measures ANOVAs with the factor of Gap duration (20, 40, or 60 ms). When the normality assumption was violated, the nonparametric Friedman's ANOVA was used instead. A second analysis was conducted on the amalgamated data from the three conditions, with the factor Condition (auditory, tactile, and tactile-ball interference). For this, a Friedman's ANOVA was used, which was followed-up with Wilcoxon signed ranks tests to investigate differences between the three conditions.

4.1.3.2. Results

Boxplots of the sensitivity and criteria data from **Experiment 4.3** are presented in Figure 4.2.

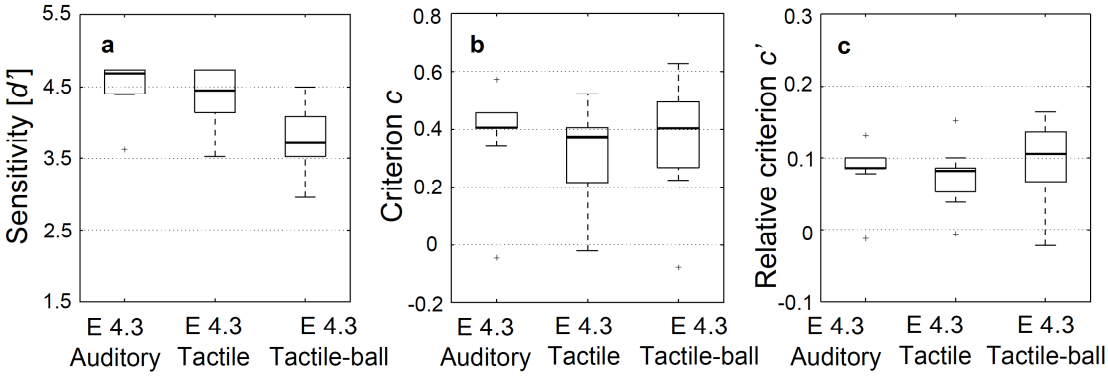


Figure 4.2. Boxplots of *d'* sensitivity data (a), criterion *c* data (b), and relative criterion *c'* (c) for **Experiment 4.3**. The box represents the middle 50% of the data; the whiskers extend to the upper (top 25%) and lower (bottom 25%) quartile respectively; the thick horizontal line denotes the median. Individual data with values higher than 1.5 times the inter-quartiles range are denoted with a '+' sign.

4.1.3.2.1. Experiment 4.3a. Gap duration

For the auditory condition, the Kolgomorov-Smirnov test indicated the violation of the normality assumption for all the measures of performance used. Participants showed no significant difference in their sensitivity in detecting the three different duration gaps [$\chi^2(2)=1.62$; p=.580]. Moreover, no significant difference was found for participants' criterion *c* [$\chi^2(2)=1.62$; p=.580], or criterion *c'* [$\chi^2(2)=2.37$; p=.457].

4.1.3.2.2. Experiment 4.3b. Gap duration

For the tactile condition, participants showed no significant difference in their sensitivity in detecting the three different duration gaps [F(2,18)=1; p=.387]. The same non-significant difference was found for participants' criterion *c* [$\chi^2(2)=2$; p=.556], and criterion *c'* [$\chi^2(2)<1$; p=n.s.].

4.1.3.2.3. Experiment 4.3c. Gap duration

For the tactile-ball interference condition, participants showed no significant difference in their sensitivity in detecting the three different durations of the gaps

[F(2,18)<1; p=n.s.]. The same non-significant difference was found for participants' criterion *c* [F(2,18)<1; p=n.s.], as well as criterion *c'* [F(2,18)<1; p=n.s.].

4.1.3.2.4. Comparison of the results of Experiment 4.3a vs. 4.3b vs. 4.3c

The analysis of the sensitivity data from the three conditions of **Experiment 4.3** revealed a significant main effect of condition [$\chi^2(2)=12.47$; p=.001]. Post-hoc tests revealed that participants' sensitivity in the tactile-ball interference condition was significantly lower as compared to the auditory condition [z=-2.86, p=.001, r=-.90], and the tactile condition [z=-2.36, p=.012, r=-.74]. No significant difference was documented between the sensitivity in detecting a gap in auditory versus tactile stimulation [z=-1.15, p=.199, r=-.36]. The criteria data revealed no difference between the three tested conditions on both criterion *c* [$\chi^2(2)<1$; p=n.s.], and criterion *c'* [$\chi^2(2)<1$; p=n.s.].

4.1.3.3. Discussion

The results of **Experiment 4.3** highlight comparable sensitivity when participants tried to detect a short temporal gap presented in tactile and auditory stimulation at rest. This result is important because it demonstrates that for the task used in the first three experiments of this chapter, performance at rest where equal numbers of target absent and target present trials were used (**Experiments 4.3a** and **4.3b**) was almost perfect. With regard to the familiarization rest sessions from **Experiments 4.1** and **4.2**, it has been shown that the different presentation probabilities can affect both sensitivity, as well as response bias (see Macmillan & Creelman, 2005). Moreover, the sensitivity values recorded in these two control conditions of **Experiment 4.3** are comparable to those from the juggle session of **Experiment 4.2**, suggesting that the hand movements

in the case of the auditory temporal gap detection task are not a factor that affects sensitivity. At the same time, the sensitivity data in the tactile ball interference condition was significantly lower as compared to the other two conditions. This result supports the claim regarding the tactile intramodal hypothesis, according to which not only the movement, but also the balls touching the hands, contributed to the deterioration in tactile sensitivity experienced while moving. However, more importantly, the criteria results of **Experiment 4.3** revealed no difference in participants' criteria allocation between the three conditions: Though slightly above zero, and thus indicating a tendency to respond 'NO', participants' criterion could be considered more or less, unbiased.

4.1.4. General discussion of Experiments 4.1-4.3

The first three experiments in this chapter investigated tactile suppression by using a complex bimanual juggling task. The first conclusion that can be drawn from the results reported here is that tactile suppression is a robust empirical phenomenon that appears during the execution of complex motor skills, such as basic 3-ball juggling. This outcome was to be expected. It has previously been shown that tactile perception deteriorates during the execution of simple finger movements (Voss et al., 2006), as well as during more complex goal-directed movements (Gallace et al., 2010; see also **Chapters 2** and **3** of this thesis). Recently, a study that investigated the detection of threshold vibratory stimuli during the execution of bimanual visual pointing movements showed a similar pattern of results, with the greatest suppression effects clustered around the onset of the movement (Buckingham et al., 2010). When considering the juggle session of both **Experiments 4.1** and **4.2**, performance clearly deteriorated for the tactile task, as compared to the almost perfect performance

observed in the auditory task. These results favour the forward models of motor control account, indicating that the experienced deterioration in what is felt while juggling most probably results from a combination of the motor command and the sensory signals resulting from the self-generated movements themselves (Chapman & Beauchamp, 2006).

The sensitivity measured at rest in the tactile ball interference condition nevertheless indicates that a tactile intramodal mechanism acts on tactile perception, and significantly disrupts performance, in the absence of movement. Indeed, in this respect, neuroimaging studies investigating tactile perception indicate that this tactile intramodal interference is most likely the consequence of inhibitory connections between the left and right somatosensory cortices (Hluschchuk & Hari, 2006; Kastrup et al., 2008; Klingner et al., 2010, 2011). Nevertheless, the magnitude of the deterioration in sensitivity for the juggle session of **Experiment 4.1** is clearly higher than that observed in **Experiment 4.3c**. This result suggests that although tactile intramodal interference contributes to the tactile suppression effects observed while juggling, it does not fully account for it. Moreover, if one considers the criteria data from all the conditions of the control **Experiment 4.3**, one can easily notice that while at rest, participants are no more inclined to say that the gap was absent when passively touched with the juggling balls (and thus having the tactile intramodal interference at play), as compared to the simple tactile gap detection.

On the other hand, participants' criterion was significantly shifted from the point of zero-bias in the juggle session of **Experiment 4.1**. This result is important because it indicates that movement itself is the delineating factor in defining tactile suppression, and consequently the criterion shift. Therefore, if participants were less sensitive in detecting a gap in the tactile stimulus while they were moving their limbs,

they were, at the same time, less inclined, or more conservative, in reporting it. This decisional component of sensory suppression provides evidence against a purely physiological cause (Williams & Chapman, 2002), and could be taken to argue in favour of a *decision-based* modulation of the phenomenon. At a neural level, it is known that sensory evidence concerning tactile stimulation accumulates in the somatosensory cortex (SI), while the primary motor cortex (MI) is involved in the preparation and execution of behavioural motor responses. Efferent signals for sensory suppression have been localized to the primary motor cortex (Voss et al., 2007), as well as the medial supplementary motor area (SMA, Haggard & Whitford, 2004), thus linking sensory suppression to the stage of motor planning and execution. Moreover, it has been shown that other adjacent brain areas that connect sensory input to motor output are also involved in the process of decision making. For example, Romo and Salinas (2001) have demonstrated that the activity recorded in primate motor areas correlates with their performance in decision-making tasks, suggesting that decisions may occur at a sensory-motor interface. Furthermore, decisional processes have been localized to the ventral and medial premotor cortex. As such, activity in these regions has been shown to be influenced not only by the quality of tactile stimulation, but also, and most importantly, the activity correlated with the monkey's behavioural response: For example, cells in the medial premotor cortex, a region also known as the SMA, showed enhanced firing patterns for tactile stimulation that was acknowledged by the monkey as a 'stimulus present trial', or a true positive response (de Lafuente & Romo, 2005; Romo et al., 2004). It appears that at a physiological level, the same brain areas usually involved in motor control are also involved in a decision-making process.

Lastly, the results outlined here, demonstrating suppression during juggling, allow the postulation of an interesting hypothesis. As highlighted in **Experiments 4.1-**

4.3 of this chapter, tactile perception deteriorates during complex goal-directed movements, such as basic 3-ball juggling. This phenomenon is independent of any contribution from overt visual attention, since direct visual input from the hand is not available while juggling. Some peripheral vision of the moving hands is, of course, still used while juggling, given that the eyes are needed to monitor the peaks of the juggling balls. Therefore, it seems that one has to consider the contribution of the other senses to the on-going sustained movement. In this respect, it could be that proprioception is the main 'pillar' of the rhythmical movement involved in three-ball juggling. Indeed, it has been shown that when moving in depth, people find it easier to localize the hand when it is positioned closer to the shoulder, as compared to when it is positioned at more distant locations (Van Beers et al., 1998). Moreover, older studies examining the acquisition of a new motor skill (e.g., fencing) have shown significantly improved performance under conditions of proprioception alone (i.e., under conditions of blindfolding), as compared to conditions of vision alone, or vision and proprioception combined (Jordan, 1972). From this viewpoint, juggling could be considered as a promising area to research how the senses come together/apart while moving. A possible demarcation between the traditional *spatial* multisensory integration at rest as opposed to a *movement-related* sensory interference could be further drawn: If information from the different sensory modalities is integrated according to the well-known spatial, temporal, and inverse effectiveness rules (Stein & Meredith, 1993; though see also Holmes & Spence, 2005b; Spence, 2012), it would appear that while moving we could at most speak of multisensory interference, or intersensory dominance.

To conclude, the first three experiments reported in **Chapter 4** provide evidence of tactile suppression occurring during the rhythmical execution of bimanual

movements, characteristic of 3-ball juggling. The reported attenuating effect on tactile perception is most likely a combination of the juggle movement itself (**Experiment 4.1**), and the sensory feedback of the juggling balls touching the hands while juggling (**Experiment 4.3**c). The deterioration in tactile sensitivity for the juggling session of **Experiment 4.1** was accompanied by a significant conservative shift in participants' criterion (i.e., they were more likely to give a 'NO' response). This result indicates a decisional component to tactile suppression, suggesting that suppression could already be triggered in the brain ahead of the motor command. Looking for tactile suppression in frontal areas would therefore provide a means of investigating the neuronal correlates of this phenomenon using a more brain-related method.

4.2. Tactile perception in throwing and catching

4.2.0. Introduction

In order to investigate the naturalistic movements of throwing and catching a ball, a series of experiments were designed that involved the measurement of both speeded responses to tactile stimulation during movement (**Experiments 4.4-4.7**), but also sensitivity and response bias evaluations (**Experiment 4.8**).

While the initial scope was exploratory, as with the juggling **Experiments 4.1-4.3** in this chapter, the main question of interest was *'Are there similar changes in what is felt in a movement effector for reactive movements (externally-generated movements, e.g., ball-catching in this chapter), as for the changes found when testing the self-initiated movements throughout the rest of this thesis?'*

At a behavioural level, self-initiated actions can clearly be dissociated from externally-generated actions. At a neural level, increased neural activation is seen in several brain regions during the execution of the two types of movement. For the

internally-generated actions, these include an extensive network of brain areas such as the left primary sensorimotor cortex, supplementary motor area, the anterior cingulate, the lateral premotor cortex, the left thalamus and putamen, parietal area 40, and finally, the right dorsolateral prefrontal cortex (Jahanshahi et al., 1995). The same areas are active during the execution of externally-triggered movements. The only difference being that a superior activation is observed in the dorsolateral prefrontal cortex in self-initiated, as opposed to externally-generated, movements (Jahanshahi et al., 1995; see also Deiber et al., 1999; Jenkins et al., 2000, for discussion of the role that frontal-medial regions play in motor preparation and motor execution). A stronger (electromyography) EMG signal has also been reported for self-initiated movements, leading Obhi and Haggard (2004) to suggest that these actions might simply be more forceful than their externally-generated counterparts.

Specifically with regard to the topic of tactile perception, a wealth of research has now been conducted on the tactile suppression that takes place during the execution of self-initiated movements (i.e., active movements), as compared to passive (hand) movements (e.g., see Williams & Chapman, 2002). Such studies have highlighted the typical pattern of gating results: Active movements seem to result in more suppression. However, to my knowledge, no other study has contrasted self-initiated versus externally-triggered movements, in order to highlight the respective characteristics of tactile perception in the two cases. Note that gating of other somatic inputs, such as, for example, thermotactile stimulation (i.e., as in judgments of 'coldness', VanDoorn et al., 2005), as well as painful stimulation (Helmchen et al., 2006) has been reported during the execution of self-initiated movements.

In the remaining experiments of this chapter, tactile perception was assessed during the execution of externally-generated movements (**Experiments 4.4-4.6**, and

4.8), as well as self-initiated movements (**Experiments 4.7-4.8**) with both measures of the speed of reaction to tactile events during movement (**Experiments 4.4-4.7**) and sensitivity and response bias measures (**Experiment 4.8**).

In **Experiment 4.4**, tactile perception was tested at different phases during the execution of a ball catching movement. The starting point was the differential pattern of RTs with respect to the various phases of the goal-directed reach to grasp movements outlined in **Experiment 2.6** of this thesis: Participants were slower to detect the tactile stimulus while preparing to move, as compared to while executing the move, as well as the post-movement period. Therefore, it was hypothesized that if the (reactive) externally-generated movements have a similar effect on tactile perception, then a similar downward RTs slope from preparation to post-movement (i.e., the catch of the ball, for **Experiment 4.4**) should be found. For this, in a first experiment of the series (i.e., **Experiment 4.4**), participants were instructed to catch a bouncing ball and to say 'BALL' in response to a tactile stimulus triggered at their wrist at certain hand positions during movement preparation and execution. This experiment also investigated whether long-term practice in ball-catching movements would be beneficial for what is felt during the execution of the movement. Therefore, in **Experiment 4.4**, several groups of participants were tested, ranging from those with very limited expertise with ball games, through to those with intermediate, and advanced training.

4.2.1. Experiment 4.4: Faster RTs to tactile stimulation while moving

4.2.1.1. Methods

4.2.1.1.1. Participants

Thirty participants (15 male, two left-handed) took part in this experiment (mean age of 25 years; age range 19-37 years). All of the participants reported normal touch, normal hearing, as well as normal or corrected to normal vision. The participants were distributed in 3 ball-expertise groups: *novices* (they had no ball experience or a very limited one from school sports); *intermediate* (played basketball or other ball sports – American football, baseball/softball, cricket, rugby, volleyball, netball – for 6 years on average), and *advanced* (participants had played basketball/baseball for 20 years on average, college 1st division or Première League athletes). The experimental session lasted for approximately 20 minutes and participants received a £5 gift voucher in return for taking part.

4.2.1.1.2. Apparatus

The participants had one tactor attached to their left wrist with an adjustable sports strap. The participants had also a microphone (Pro-Sound Uni-directional Dynamic YU-33 600Ω & 50kΩ) attached with thread around their neck and interfaced through a custom-built voice response key connected to the main computer. Moreover, the participants had the Wii Remote attached to their left forearm with another adjustable sports strap. A commercially available men's basketball (Adidas; approximately 75 cm in diameter) was used.

4.2.1.1.3. Procedure

In each trial, the participants were instructed to stand with their arms at their sides. The experimenter (the same for all participants) was located at a distance of

approximately 2.7 m in front of the participant, with the basketball in her hands, ready to throw. An auditory signal (800 Hz, 100 ms), that participants could hear as well, instructed the experimenter to throw the ball toward the participant. The experimenter ensured that the ball always bounced approximately 1.0-1.2 m in front of the participant. When the ball arrived in their vicinity, the participants reached for it and the movement of their hand triggered a 100 ms vibratory pulse to which they were instructed to give a speeded voice response by saying 'BALL'. The short vibration was delivered at one of four hand positions: in the *preparation* period of the movement, at two points in time during *movement execution* (i.e., first, when the hand formed an angle of 25º with respect to the body, and second, at an angle of 45º with respect to the body), and lastly, at the *catch* of the ball when the hand reached forward and formed a straight angle with the body. The experiment went on to the next trial once the experimenter pressed a key on the keyboard. At the end of the experiment, the participants filled in a short questionnaire about their athletic expertise (see **Appendix A2**).

4.2.1.1.4. Design

The experiment consisted of 160 trials. The manipulated variable was the Timing of tactile stimulation delivery: 40 trials were performed for each of the four timings (preparation, early movement execution, mid-movement execution, and catch). The order of the trials was randomized across trials and participants.

4.2.1.1.5. Data analysis

Outliers in the RTs from **Experiment 4.4** were excluded by using the z-score > 3 rule. This led to a rejection of 104 trials (0.02 %) of the data. The remaining data were

analyzed with a mixed factorial ANOVA with a within-participants factor of Timing of tactile stimulation delivery (preparation, movement execution, and catch), and the between-participants factor of Expertise (novices, intermediate, or experts).

4.2.1.2. Results

Mean RTs together with SEs for each level of the factor Timing of stimulation delivery, for each of the tested Expertise groups are presented in Table 4.2.

	Experiment 4.4						**Experiment 4.5**		**Experiment 4.6**		**Experiment 4.7**	
	Novices		Intermediate		Experts		Novices		Novices		Novices	
	M	SE	M	SE	M	SE	M	SE	M	SE	M	SE
Preparation	344	23	257	23	215	23	447	45	386	32	377	19
Early move	296	21	196	21	166	21	381	39	343	25	294	23
Mid move	286	21	192	21	173	21	390	47	348	30	277	23
Catch/Throw	353	27	271	27	224	27	493	58	331	25	259	21

Table 4.2. Mean RTs together with their standard error SE for **Experiments 4.4-4.7**, split according to Expertise and the Timing of sensory stimulation delivery. Note that in **Experiment 4.6** no movement was performed.

The results indicated a main effect of Timing of tactile stimulation delivery [$F(2,4)=26.49$; $p<.001$], with participants responding more rapidly to the tactile stimulus when this was delivered to the moving hand, as compared to preparation period ($p<.001$), and the ball-catching period ($p<.001$). RTs were comparable for the preparation and ball-catching phases ($p=.599$).

Moreover, a main effect of Expertise [$F(2,27)=9.02$; $p=.001$] was found, with novices being significantly slower than both intermediate ($p=.022$) and advanced players ($p=.001$). RTs were comparable for the intermediate and advanced players ($p=.668$). Lastly, no interaction was found between the two variables of Timing and Expertise [$F(4,54)<1$; p=n.s.] (see Figure 4.3).

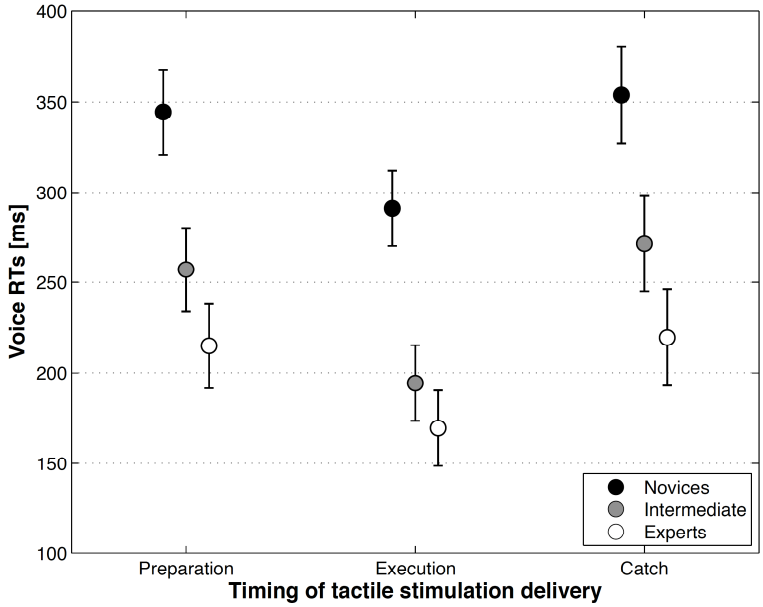


Figure 4.3. Mean tactile RTs for the three Expertise groups in **Experiment 4.4**. Vertical error bars represent the standard errors of the mean.

4.2.1.3. Discussion

One prediction for **Experiment 4.4** was that expertise in athletic tasks would influence the speed of reaction to tactile events during movement. This hypothesis was confirmed: Novices were slower than both intermediate and expert players, thus providing evidence for a significant advantage of expertise in athletic tasks (Aglioti, Cesari, Romani, & Urgesi, 2008; Yarrow, Brown, & Krakauer, 2009). This result is not surprising, considering that early in their training basketball players are taught to require the ball from their team mates by simply saying 'BALL'. However, although faster than novices, intermediate and expert players exhibited the same pattern of RTs for the different timings of stimulation delivery during movement.

Following on from this, the main prediction for **Experiment 4.4** was that a differential pattern of RTs would be observed for the various tested timings during the externally-generated movement at which stimulation was delivered. This hypothesis was confirmed: RTs were fastest during movement execution, as compared to both

preparation and catch; while no difference was observed between these last two periods.

Just to consider the preparation period, the present results mirror those found in the preparation period of the self-initiated goal-directed reaches (see **Chapter 2** of this thesis). A possible explanation could be the fact that the descending motor command exerts a disruption on the somatosensory cortices, and thus the observed slowing in RTs during the preparation period. Similarly to the goal-directed reaches investigated in **Chapter 2**, the movement execution period highlighted significantly faster RTs to tactile stimulation. Sensory suppression is known to appear in a moving limb (Bays et al., 2005; Voss et al., 2006; Williams & Chapman, 2002, see also **Chapter 2** of this thesis). Thus, the faster RTs found in the movement execution period of this experiment strengthen even more the possible demarcation between *speed* and *quality* in the tactile domain, suggested in **Chapter 2** of this thesis.

However, if the pattern of results reported in **Chapter 2** highlighted even faster RTs in the post-movement period, for the reactive movements of catching the ball investigated here, RTs were significantly slower, as compared to movement execution. One explanation for this effect could be the fact that the peripheral feedback from the ball touching the hand interfered with the concomitant tactile stimulation presented there (see **Experiment 4.3** on tactile intramodal interference, in this chapter). This intramodal interference could have resulted in a diminished tactile sensitivity, which in turn may have slowed down the responses to tactile events at the time of the catch of the ball. To test this hypothesis, in **Experiment 4.5** participants performed the same ball-catching task, however, this time they made a vocal response to an auditory event presented through headphones. It was hypothesized that if tactile intramodal interference is responsible for the slowing of RTs at the catch of the ball,

then RTs should be faster for auditory stimuli presented at the same timing during the externally-generated hand movement. However, if a more general attentional effect (e.g., a visual looming effect given by the approaching ball, see Franconeri & Simons, 2003; Hillstrom & Yantis, 1994; Makin et al., 2009) were to be responsible for the slowing of RTs at the catch, then tactile RTs should be comparable for tactile and auditory stimuli delivered at the catch of the ball. Since in **Experiment 4.4** all expertise groups showed a similar pattern of tactile RTs for the different timings of stimulation delivery, in **Experiment 4.5** only novices were tested.

4.2.2. Experiment 4.5: Faster auditory RTs while moving

4.2.2.1. Methods

The methods of **Experiment 4.5** were very similar to those of **Experiment 4.4**. Therefore, only the methodological differences are highlighted in this section. Nine participants (4 male, all right-handed; mean age of 25 years; age range 20-28 years) took part in this experiment. As mentioned, participants now responded to an auditory signal, delivered via headphones. The z-score > 3 rule led to an exclusion of 32 trials (0.02 %) of the total number of data points. The remaining data were analyzed with a repeated measures ANOVA with the factor of Timing of stimulation delivery (movement preparation, movement execution, and ball catching). An additional repeated-measures mixed ANOVA was conducted on the mean auditory RTs data from the novices with the within-participants factor of Timing of auditory stimulation delivery, and the between-participants factor of Experiment (**Experiment 4.4** vs. **Experiment 4.5**).

4.2.2.2. Results

4.2.2.2.1. Timing of tactile stimulation delivery in Experiment 4.5

Mean RTs together with SEs for each level of the factor Timing of stimulation delivery in **Experiment 4.5** are presented in Table 4.2.

The results indicated a main effect of Timing of stimulation delivery [$F(2,16)=11.79$; $p=.001$], with participants responding significantly more rapidly to the auditory stimulus when this was delivered during the execution period of the movement, as compared to both the preparation period ($p=.049$), and the timing of the catch of the ball ($p=.016$). No significant difference was found between mean RTs recorded in the preparation and catch periods ($p=.065$).

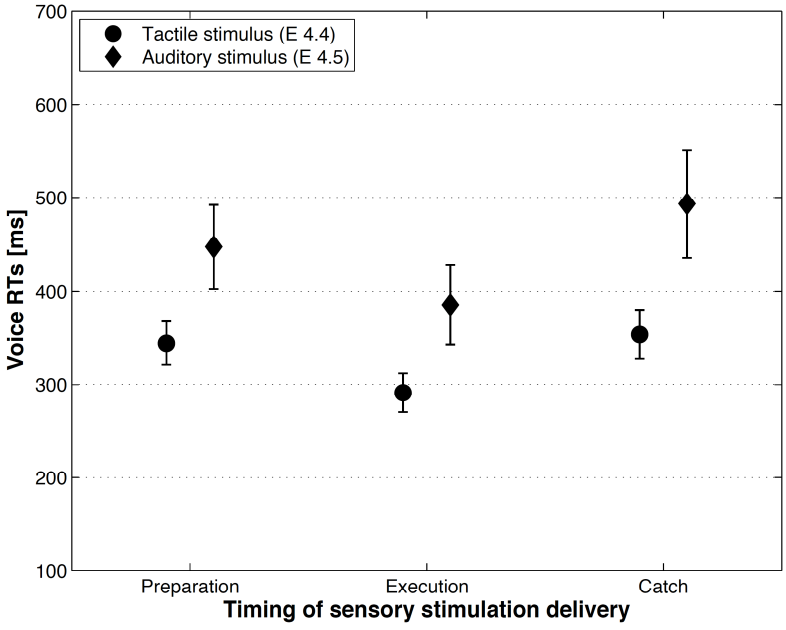


Figure 4.4. Mean tactile RTs from novice data in **Experiments 4.4** and **4.5**. Vertical error bars represent the standard errors of mean.

4.2.2.2.2. Comparison of the results of Experiments 4.4 vs. 4.5

When comparing the novice data from **Experiments 4.4** and **4.5**, a significant main effect of Timing of tactile stimulation delivery was found [$F(2,34)=15.73$; $p<.001$; $\varepsilon=.650$]. This result highlighted the previously found difference between the different

timings of stimulation delivery: Namely, the execution period was faster than both preparation (p=.003), and ball-catching periods (p=.002), whereas no significant difference was found between RTs in the preparation and ball-catching periods (p=.050). Nevertheless, no significant main effect of Experiment was found [F(1,17)=4.17; p=.057]. Moreover, no significant interaction between the two variables of Timing of stimulation delivery and Experiment was observed [F(2,34)=1.20; p=.313]. See Figure 4.4 for a depiction of the novice RTs data from the two experiments.

4.2.2.3. Discussion

Experiment 4.5 was designed to investigate a possible explanatory factor for the distribution of tactile RTs found in **Experiment 4.4**: faster RTs while moving, as opposed to both preparing and ball-catching. The results highlighted a comparable distribution of RTs in the novice group for the different temporal phases of the movement when sensory stimulation was delivered in **Experiments 4.4** and **4.5**.

Therefore, it could be argued that the slower RTs registered at the catch of the ball, for both the tactile and auditory stimuli, are an indicator of attentional capture, or attentional looming effect from the approaching ball (Franconeri & Simons, 2003; Hillstrom & Yantis, 1994; Makin et al., 2009). However, alternatively, another factor that could account for the slowing of RTs at the time of the catch of the ball could be a simple dual-task effect: At the time of the catch, participants perform a new action that follows from the goal-directed reaching for the ball, the particular *catch* of the ball. In order to test this question, **Experiment 4.6** was designed in which participants responded vocally to a tactile stimulus delivered at rest. This could be delivered at one of four different points in time after the initiation of the trial, time points that were

derived by averaging the timings of tactile stimulation delivery from **Experiment 4.4** (i.e., motor preparation, early movement execution, mid movement execution, and ball-catching). It was hypothesized that if a dual-task effect were responsible for the slower RTs observed at the time of the ball-catch, then in the absence of movement, this effect should be absent (i.e., no difference in RTs should be observed as a function of the timing of stimulation delivery). At the same time, if a difference in the tactile RTs for the different timings of stimulation used in **Experiment 4.6** were to be found, then other attentional factors (e.g., IOR, Klein, 2000; Spence et al., 2000a) could account for a temporal dissociation in the speed of reporting of tactile events.

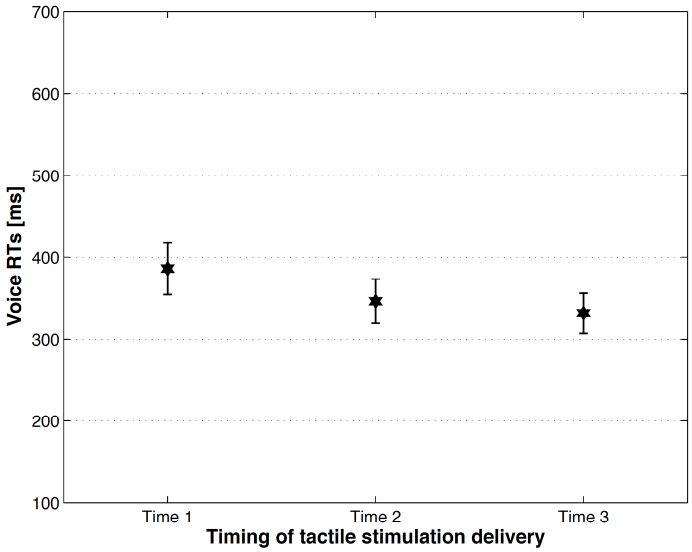


Figure 4.5. Mean novice tactile RTs in **Experiment 4.6**. Vertical error bar represent the standard errors of the mean.

4.2.3. Experiment 4.6: Comparable tactile RTs over the different temporal phases of stimulation, in the absence of movement

4.2.3.1. Methods

Since the methods of this experiment are very similar to those of **Experiment 4.4**, only the differences are highlighted. Ten participants (4 male, all right-handed; mean

age of 22 years; age range 19-28 years) took part. The experiment consisted of 100 trials, with 25 trials for each averaged timing of stimulation from **Experiment 4.4** (1010 ms, 1590 ms, 1760 ms, and 2210 ms after the beginning of the trial). The z-score > 3 rule led to an exclusion of 38 trials (0.04 %) of the total number of data points. The remaining data were analyzed using a repeated measures ANOVA with the factor Timing of stimulation delivery (Time 1, Time 2, and Time 3).

4.2.3.2. Results

Mean RTs together with SEs for each level of the factor Timing of stimulation delivery in **Experiment 4.6** are presented in Table 4.2. The results indicated that in the absence of movement, the timing of stimulation delivery did not influence tactile RTs [$F(2,18)=4.88$; $p=.050$; $\varepsilon=.545$]. See Figure 4.5 for a depiction of the RT data from the novices in **Experiment 4.6**.

4.2.3.3. Discussion

The goal of **Experiment 4.6** was to test whether a dual-task effect would be responsible for the slowing of RTs at the catch of the ball. In the absence of movement, the results highlighted comparable RTs for all the timings of tactile stimulus delivery. This result therefore supports the hypothesis that movement acts as a distraction on the performance of the perceptual speeded response task. It could therefore be argued that the slowing of RTs observed in in both the preparatory and catch phases of **Experiments 4.4** and **4.5** are a result of the movement.

To summarize the findings of **Experiments 4.4-4.6**, it appears as though the execution period of the movement favours speeded responses to sensory stimuli (e.g., tactile stimulation in **Experiment 4.4**, and auditory stimulation in **Experiment 4.5**).

Moreover, the preparation period highlights a significant slowing of RTs for both types of sensory stimuli tested in **Experiments 4.4** and **4.5**. This effect is most likely a result of the descending motor command. Lastly, the timing of the catch of the ball results in the slower processing of sensory stimuli delivered to the movement effector. Possible explanations for this effect are: *a)* movement itself acts as a distraction on the processing of incoming sensory stimuli (hypothesis tested in **Experiment 4.6**), and *b)* the approaching ball exerts a looming effect, or captures the participant's attention (hypothesis tested in **Experiment 4.5**).

In a next step, in order to further test hypothesis *b)*, an investigation was carried out in order to test whether this slowing of RTs would generalize across different types of movements. For this, in **Experiment 4.7**, self-initiated goal-directed movements were tested over the same time scale. That is, participants this time threw the ball to the experimenter and RTs were recorded for tactile stimuli delivered at different timings during the goal-directed movement: the preparation of the throw, movement execution, and release of the ball. It was hypothesized that if externally-generated and self-initiated movements affected tactile perception in a similar manner, then a similar pattern of RTs should be found for the self-initiated movements, as for their externally-generated counterpart. However, if different processes act on tactile perception during the preparation and execution of the two types of movements, then a difference in tactile RTs will be observed between self- and externally-generated movements. Note that as opposed to the externally-generated movements tested in **Experiments 4.4-4.5**, an attentional ball-looming effect could not account for the slowing of responses that could be potentially found at the time of the throw, since the ball leaves the peripersonal space, and thus could not be taken as incoming sensory stimulation.

4.2.4. Experiment 4.7: Faster speed of reaction to tactile stimulation delivered at the throwing of the ball

4.2.4.1. Methods

The methods of **Experiment 4.7** were similar to those of **Experiment 4.4**. Therefore, only the methodological differences will be highlighted here. Ten participants (2 male, one left-handed; mean age of 25 years; age range 22-31 years) took part in this experiment.

A first auditory signal (*prepare signal*, 100 ms, 400 Hz) instructed the participants to prepare to throw the ball at the experimenter. A second auditory signal (100 ms, 800 Hz), delivered 1100 ms later, acted as the *go signal* to initiate the throwing movement. Tactile stimulation was delivered to the participants' wrist at different points in time during the movement: in the preparation period (500 ms after the prepare signal), early execution period (immediately after the go signal), mid-movement execution (100 ms after the go signal), or at the release of the ball (200 ms after the go signal). Note that in **Experiments 4.4** and **4.5**, the experimenter always bounced the ball on the floor (in approximately the same location), so that it arrived at the participant's hand from roughly the same angle. For this reason, the bouncing of the ball was used in **Experiment 4.7**, when the participant threw the ball at the experimenter.

The z-score > 3 rule led to an exclusion of 39 trials (0.02%) of the total number of data points. The remaining data were analyzed using a repeated measures ANOVA with the factor Timing of stimulation delivery (movement preparation, movement execution, and ball throwing). An additional repeated-measures mixed

ANOVA was conducted on the tactile mean RTs with the within-participants factor Timing of stimulation delivery (movement preparation, movement execution, and ball catching/throwing), and the between-participants factor Experiment (**Experiment 4.4** vs. **Experiment 4.7**).

4.2.4.2. Results

4.2.4.2.1. Timing of stimulation delivery in Experiment 4.7

Mean RTs together with SEs for each level of the factor Timing of stimulation delivery in **Experiment 4.7** are presented in Table 4.2.

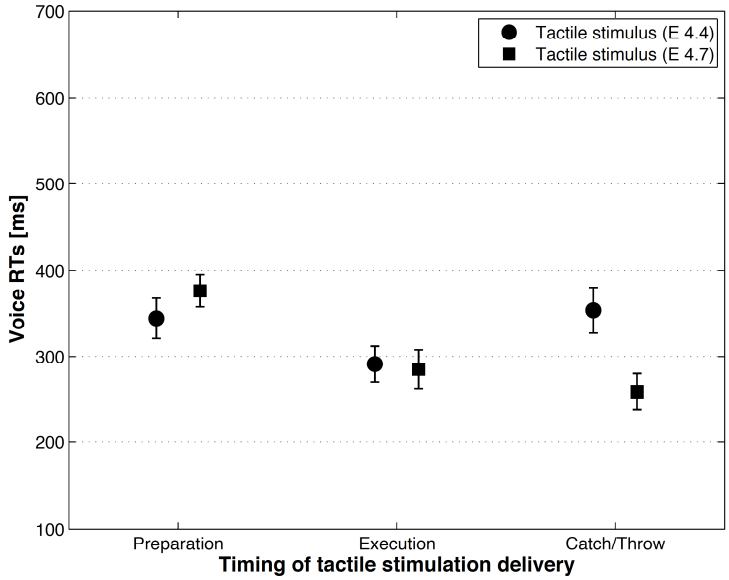


Figure 4.6. Mean novice tactile RTs in **Experiments 4.4** and **4.7**. Vertical error bars represent the standard errors of the mean.

The results indicated a main effect of Timing of stimulation delivery [$F(2,18)=21.28$; $p<.001$], with participants being significantly slower to respond to the tactile stimulus when this was delivered during the preparation period of the movement, as compared to both the execution period ($p=.009$), and at the timing of the throw of the ball ($p=.001$). No significant difference was found between mean RTs recorded during the execution and throw periods ($p=.156$).

4.2.4.2.2. Comparison of the results of Experiments 4.4 vs. 4.7

When comparing the novice data from **Experiments 4.4** and **4.7**, a significant main effect of Timing of tactile stimulation delivery was found [$F(2,36)=13.83$; $p<.001$]. Pairwise comparisons indicated that the preparation period was slower than both execution ($p<.001$), and ball-catching/throwing periods ($p=.001$); no significant difference was observed between the tactile mean RTs of the execution and catch/throw periods ($p=.762$). Furthermore, no significant main effect of Experiment was found [$F(1,18)<1$; p=n.s.]. Nevertheless, a significant interaction between the two variables of Timing of stimulation delivery and Experiment was observed [$F(2,36)=10.37$; $p<.001$]. Pairwise comparisons indicated that the mean tactile RTs registered in **Experiment 4.4** at the catch of the ball were significantly slower than the mean RTs recorded at the throw of the ball in **Experiment 4.7**. See Figure 4.6 for a depiction of the novice tactile RTs data from the two experiments.

4.2.4.3. Discussion

Experiment 4.7 highlighted enhanced RTs at the time of the throw of the ball. Furthermore, when comparing the data from **Experiments 4.4** and **4.7**, a clear difference in tactile RTs was observed with respect to the type of movement executed: The throw of the ball yielded significantly faster RTs to tactile stimulation, as compared to the catch of the ball. Therefore, it could be argued that different processes were at stake in the execution of self-initiated vs. externally-generated movements. Results such as these suggest that incoming *objects* (i.e., the basketball) entering our peripersonal space are prone to spark an attention-capture mechanism in the tactile domain. Alternatively, the *actor* (i.e., the participant) could be differentially biased in

responding to the presence of tactile events during the preparation/execution of simple ball-catches/throws.

Before taking a definitive stand (object-based vs. actor-based explanation) with regard to the implications of these results, the specific type of movement performed in **Experiments 4.4**, **4.5**, and **4.7** needs to be considered. In **Experiment 4.4**, the ball-catch movement was triggered after the ball bounced on the floor (approximately 1-1.2 meters in front of the participants). This particular characteristic of the design/movement ensured that the execution period of the movement was the same for all participants in **Experiment 4.4**. That is, participants would have to reach forward with their hands and catch the ball when this arrived in their vicinity. However, by using the same bouncing ball design in **Experiment 4.7**, it was impossible to have the same trajectory of the hand for the throwing movements. The movement utilized in **Experiment 4.7** when throwing the ball had a clearly diminished extent of the trajectory (i.e., the throw required at most a simple palmar push of the ball toward the bouncing location). If one considers this methodological confound, the present results highlighting faster RTs at the time of the ball-throw, but at the same time, no difference between the mean tactile RTs recorded during movement execution and ball-throwing periods, are not surprising at all: The throw of the ball could be considered as part of the motor execution period.

Therefore, in one last experiment to be reported in this chapter (**Experiment 4.8**), in order to eliminate this confound, the intermediate bouncing of the ball on the floor was eliminated. Participants performed simple chest passes (e.g., basketball chess passes) toward the experimenter (i.e., self-initiated throwing movements), or they caught the ball when this arrived in their vicinity following a similar chest pass from the experimenter (i.e., externally-generated ball catching movements). In a

control condition, participants performed the perceptual task while at rest. However, even for the simple chest passes, the extent of the throwing hand movements was significantly reduced as compared to the catching of the ball movement. For this reason, the time window for throwing, as well as catching, was differentially defined so that the movement execution period included the contact with the ball (i.e., at the catch), or the release of the ball (i.e., at the throw).

In **Experiment 4.8**, the power of SDT was used to examine the characteristics of tactile perception as they unfolded during the execution of self-initiated versus externally-triggered hand movements. Tactile sensitivity, together with response bias, was assessed at different points in time for the two movements: in the preparation period (i.e., when movement per se was not yet initiated), and the movement execution period. It was hypothesized that a decrement in tactile sensitivity would be observed during the movement execution period, together with a change in response bias (see **Experiments 4.1-4.3** in this chapter). Moreover, **Experiment 4.8** investigated, for the preparation period, whether a differential pattern of results from the SDT analysis would be observed when the movement resulted from the participant's own will, as compared to when it was externally-generated. By comparing the preparatory phases of throwing and catching movements, one could disentangle the potential perceptual and decisional processes acting on tactile perception.

4.2.5. Experiment 4.8: Perceptual and decisional attenuation of tactile perception during the preparation of self- versus externally-generated movements

4.2.5.1. Methods

4.2.5.1.1. Participants

Fourteen participants (5 male, one left-handed) took part in this experiment (mean age of 26 years; age range 23-32 years). None of the participants was a member of an athletic club. The experimental session lasted for approximately 40 minutes and the participants received a £5 gift voucher in return for taking part in the study.

4.2.5.1.2. Apparatus

The experiment took place in a wide, well-lit room. The participant and the experimenter were standing, facing each other, with a distance of approximately 2.7 m separating them. The participants had one tactor attached with an adjustable sports strap to the ventral part of their right wrist, which was then covered with several layers of thin sponge. The participant also wore closed ear headphones (Beyer Dynamic DT 531) for the duration of each block of the experiment. Two loudspeakers were positioned on a table on either side of experimenter's back. The participants gave a vocal response, which the experimenter entered into the computer.

4.2.5.1.3. Procedure

The experiment consisted of three conditions: A control (*rest*) condition, and two experimental conditions (a *catch* condition, and a *throw* condition) with the order of presentation of the conditions counterbalanced across participants. In the rest and catch conditions, the participants were instructed to start each trial with their arms at their sides. In the throw condition, participants started each trial with both hands holding the ball to their chest. Conversely, in the catch condition, the experimenter started the trial with both hands holding the ball. The vibratory signal at the

participant's wrist could be continuous (i.e., a no gap trial), or interrupted (i.e., a gap trial). When present, the temporal gap duration was set to 40 ms for all the three experimental conditions (see **Experiment 4.3** in this chapter).

Each trial started with an auditory signal (*start signal*; 50 ms, 400 Hz). This was followed after a random SOA (800-1200 ms) by a second higher-pitched auditory signal (*go signal*; 50 ms, 800 Hz). Immediately afterward, the tactor that the participants wore on their wrist was turned on (2000 ms, 250 Hz).

In the *catch condition*, the go signal was for the benefit of the experimenter. The experimenter threw the ball at the participant (i.e., a standard chest pass in basketball, aimed at participant's chest) and the participant was instructed to catch it when it arrived in his/her vicinity. Note that as opposed to **Experiments 4.4-4.7**, the ball pass was directed straight to participants' chest; that is, in this experiment, the ball did not bounce on the floor first. If a temporal interruption occurred in the catch condition, this could either be delivered in the preparation period of the catch movement (10 to 200 ms after the go signal), or in the catch movement execution period (700 to 1000 ms after the go signal). In the *throw condition*, the go signal was for the benefit of the participant. The participant threw the ball at the experimenter, who caught it when it approached. If the current trial was a gap present trial, then the gap in the vibration was delivered in the preparation period of the throwing movement (10 to 200 ms after the go signal), or during the execution of the throwing movement (200 to 700 ms after the go signal). In the control *rest* condition, just as for the experimental conditions, a 2000 ms vibration was delivered to the participants' wrist. If a gap occurred in the vibratory stimulation, this could be delivered either in the 'preparation' period (10 to 200 ms after the go signal), or in the 'execution' period (700 to 1000 ms after the go signal). Note that since hand movements were restrained

in this condition, the preparation and execution periods are so-called in order to match the experimental catch and throw conditions.

At the end of the trial, depending on the condition, the participant returned the ball to the experimenter (in the catch trials), or the experimenter returned the ball to the participant (in the throw trials). The trial ended with the participants' verbal response regarding the presence versus absence of the temporal gap in the vibration (YES/NO response). The experiment went on to the next trial once the experimenter pressed a key on the keyboard.

4.2.5.1.4. Design

Each of the conditions consisted of 2 blocks of 60 trials each, amounting to a total of 360 trials per experiment. Participants had short breaks in between the blocks. Half of the trials in each block were gap trials (the vibration was interrupted very briefly) while the remainder of the trials were no gap trials (the vibration was continuous). In half of the gap trials the vibration was interrupted in the preparation period, and in the second half the vibration was interrupted in the execution period. Therefore, the experimental variables were Condition (rest, catch, and throw), and Timing of the gap (gap delivered in the preparation period vs. gap delivered in the movement execution period).

4.2.5.1.5. Data analysis

SDT measures (*d'*, *c*, and *c'*) were calculated, split considering the manipulated experimental variable Timing of the gap (preparation vs. execution); see **Experiment 4.1** for the exact methodology. The data were explored and the assumption of normality was checked with the Kolmogorov-Smirnov test. The normality assumption

indicated violations for all levels of the experimental factors, aside from the execution period in both catch and throw conditions (for all tested measures *d'*, *c*, and *c'*), as well as the preparation period in the throw condition (for the *d'* and *c* measures).

Therefore, for each condition (rest, catch, and throw), for each SDT measure (*d'*, *c*, and *c'*), Wilcoxon signed ranks tests (or their parametric equivalent, paired-samples t-tests) were performed in order to compare the data from the preparation and execution periods. Furthermore, for each of the SDT measures, one non-parametric repeated measures of variance analyses (Friedman's ANOVAs) was conducted on the preparation period data with the factor Condition (rest vs. catch vs. throw). This ANOVA was followed up with Wilcoxon signed ranks tests in order to investigate differences between the three levels of the tested factor Condition. A Bonferroni correction for multiple comparisons was applied to these post-hoc tests; therefore all effects are reported at a 0.0167 level of significance.

4.2.5.2. Results

Boxplots of sensitivity and criteria data are presented in Figure 4.7.

4.2.5.2.1. Sensitivity (*d'*) results

As expected, the results indicated no significant difference between participants' tactile sensitivity in detecting a gap occurring at the beginning (i.e., preparation), or toward the middle (i.e., execution) of the vibratory stimulus [z=-.42, p=.673, r=-0.08] while at *rest*. Nevertheless, for the *ball-catch* condition, a significant difference was observed between the participants' perceptual sensitivity when trying to detect a gap in tactile stimulation, depending on whether this gap appeared in the preparation period or the execution period of the movement.

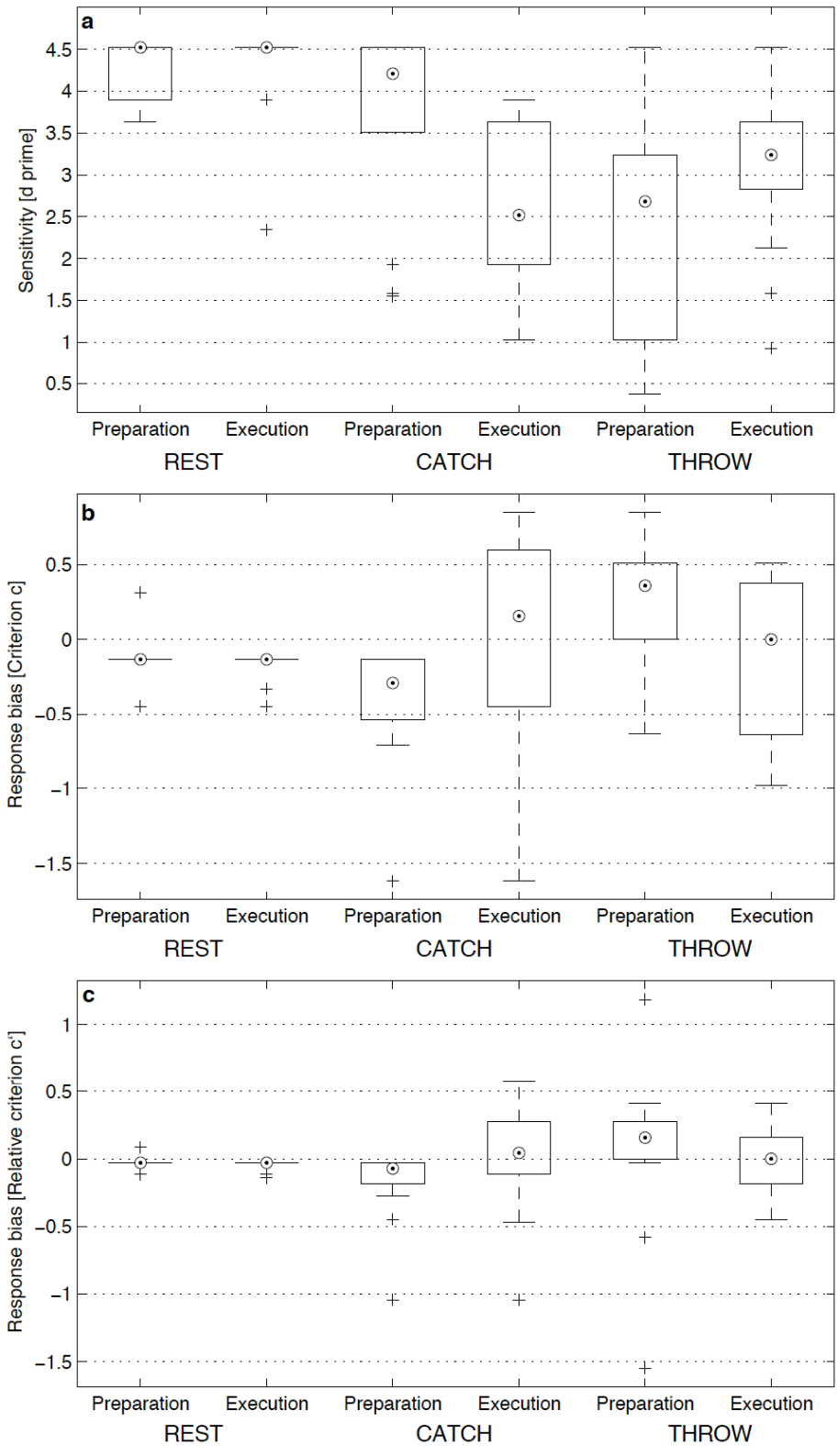


Figure 4.7. Boxplots of *d'* sensitivity data (**a**), criterion *c* data (**b**), and relative criterion *c'* (**c**), split according to the preparation and execution phases of the movement, for the three conditions (rest, catch, and throw) of **Experiment 4.8**. The box represents the middle 50% of the data; the whiskers extend to the upper (top 25%) and lower (bottom 25%) quartile respectively; the middle black dot surrounded by a circle denotes the median. Individual data with values higher than 1.5 times the inter-quartiles range are denoted with a '+' sign.

That is, participants were significantly more sensitive to the presence of the gap while preparing to catch, as compared to while catching the ball [z=-2.55, p=.011, r=-.48]. The throw condition indicated an opposite effect, with participants being significantly more sensitive to detect a gap if this occurred during the actual throwing of the ball, as compared to the preparatory period of the movement [t(13)=2.40, p=.032, r=.57].

For the *preparation* period, the results indicated a significant main effect of condition [$\chi^2(2)=21.35$; $p<.001$]. Post-hoc tests indicated that sensitivity in the preparation period of the throw condition was significantly lower, as compared to both the rest condition [z=-3.18, p=.001, r=-.60], and the catch condition [z=-3.18, p=.001, r=-.60]. Participants' sensitivity in detecting a gap in tactile stimulation did not differ between conditions of rest and preparing to catch a ball [z=-1.28, p=.200, r=-.24].

For the *execution* period, the results indicated that sensitivity in the execution period of the rest condition was significantly higher (thus, performance was better), as compared to that of both the ball-catching movement execution [z=-3.97, p=.001, r=-.75], and ball-throwing movement execution periods [z=-3.01, p=.003, r=-.56].

4.2.5.2.2. Criterion *c* results

The results indicated that for the *rest* condition, participants' criterion *c* did not differ for gaps occurring at the beginning (i.e., preparation), or toward the middle (i.e., execution) of the vibratory stimulus [z=-1.69, p=.092, r=-0.32]. However, participants were significantly more inclined to say that there was no gap in the tactile stimulation when this occurred while executing the ball-catching movement, as opposed to while preparing to catch the ball [z=-2.27, p=.023, r=-0.43]. Conversely, criterion *c* in the preparation period of the throw condition was significantly more positive, thus

showing that participants were more inclined to report that no gap was present in tactile stimulation when this occurred while preparing to throw the ball, as opposed to while executing the throwing movement [t(13)=2.50, p=.027, r=.47].

For the *preparation* period, the results indicated a significant main effect of condition on the criterion *c* data [$\chi^2(2)=19.14$; $p<.001$]. Post-hoc tests indicated that participants' criterion *c* in the preparation period of the catch condition was significantly more negative (i.e., participants were more inclined to give a YES response), as compared to both the rest condition [z=-2.82, p=.005, r=-.53], and the throw condition [z=-3.18, p=.001, r=-.60]. Participants' criterion to detect a gap in the tactile stimulation differed between the conditions of rest and preparing to throw the ball. However, that said, this comparison did not survive the correction for multiple comparisons [z=-2.27, p=.023, r=-.43].

No significant results were observed for the comparisons between the *rest* and *execution* periods of the two movements.

4.2.5.2.3. Relative criterion *c'* results

No significant difference was recorded between participants' criterion *c'* in detecting a gap occurring in the preparatory phase, as compared to the execution phase under conditions of rest [z=-1.90, p=.058, r=-.36], and throwing [z=-1.50, p=.133, r=-.28]. However, participants were more inclined to say a gap was present in tactile stimulation when this occurred while they were preparing to catch the ball, as opposed to when they were catching the ball [z=-2.34, p=.019, r=-.44].

For the *preparation* period, the results indicated a significant main effect of condition on the criterion *c'* data [$\chi^2(2)=12.76$; $p=.002$]. Post-hoc tests showed that participants were more inclined to say a gap was present in the tactile stimulus when

this occurred while they were preparing to catch the ball, as opposed to the rest preparation period [z=-2.82, p=.005, r=-.53]. Participants' criterion *c'* to detect a gap in tactile stimulation did not differ between the conditions of rest and preparing to throw a ball [z=-1.43, p=.152, r=-.27]. A comparison of participants' criterion *c'* between the conditions of preparing to catch and preparing to throw the ball revealed that participants were again more inclined to say a gap was present in stimulation when catching; however, once again, this comparison did not survive the correction for multiple comparisons [z=-2.13, p=.033, r=-.40].

No significant *c'* results were found for the comparisons between the rest and *execution* periods of the two movements.

4.2.5.3. Discussion

Experiment 4.8 investigated tactile perception during the execution of simple throwing and catching movements. The hypothesis was that a differential pattern of tactile sensitivity, together with changes in response bias, would be observed during the various tested phases of the movements. The results are in agreement with previous studies that highlighted decrements in what is felt during the execution of (self-initiated) goal-directed movements (Buckingham et al., 2010; Gallace et al. 2010; see also **Chapter 2** in this thesis), as well as with studies that found attenuation for other types of somatic stimuli during self-initiated movements (Helmchen et al., 2006; VanDoorn et al., 2005).

As predicted, the execution of both catching and throwing movements gave rise to significant decrements in participants' tactile sensitivity, as compared to the control rest condition. Tactile attenuation is a robust phenomenon, occurring during the execution of goal-directed hand movements (see **Chapter 2** in this thesis).

Moreover, with respect to goal-directed movements involving the particular throwing or catching of a ball, **Experiments 4.1-4.3** in this chapter have provided evidence that the observed decrement in tactile sensitivity results from a summation of movement-related gating and peripheral feedback from the ball touching the skin.

When the catch data were considered in isolation, a significant drop in participants' sensitivity was observed over the execution period (i.e., due to sensory suppression). However, the preparation period was unaffected; participants exhibited comparable levels of performance under conditions of rest and preparing to catch a ball. The participants were nevertheless more biased to report the presence of a gap in the preparation period of the catch, as compared to rest. Thus, during the preparation period of an externally-triggered movement, changes in response bias, rather than sensitivity are likely to be present.

This result underlines the fact that even if sensitivity remains unchanged, the 'noise' given by the prepared movement (van Beers et al., 2002) determines a change in participants' decision criterion: Participants were more liberal in reporting a change occurring in tactile stimulation. This result has even further implications if one considers accounts of tactile gating as just a result of mere action observation (Voisin et al., 2011). As such, even though the participants had not initiated their movement yet, they nevertheless observed the initiation of the throwing action from the experimenter's side. According to the (mirror neuron) simulation theory for mind-reading (see Gallese & Goldman, 1998, for a review; see also Heyes, 2010; Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010), when an observer perceives an actor initiating an action, his motor system should likely mirror-plan the same action. From this perspective, the decisional-only change observed in **Experiment 4.8** for the

catch trials might potentially reflect a mirror-like mechanism acting on the motor system during action observation and planning.

With regard to the data from the throwing condition, although a significant drop in sensitivity was present during the execution period (i.e., due to sensory suppression), the sensitivity decrement was even more pronounced during the preparation period of the throw. This result is in line with previous results that have indicated a greater level of preparation occurring during the execution of self-initiated movements, as opposed to externally-generated ones (Obhi & Haggard, 2004).

The most important result to emerge from the results of **Experiment 4.8** was highlighted by the comparison between the rest condition and the preparation periods of the two tested movements: catching and throwing. For both movements, the preparation period involved no movement of the participant's hands. That is, at the time of gap delivery, the goal-directed movement had not yet been initiated and the participant's hands were thus still at rest. However, if the preparation of the catching movement involved monitoring the experimenter initiating the throw of the ball at most, for the throw movement, the readiness to move was needed instead. That is, the difference between the two movements can be specified in terms of *the intention* to initiate a goal-directed movement. The results highlight a significant decrement in tactile sensitivity when participants prepared to throw, as compared to when they prepared to catch the ball. This effect was paired with a change in response bias (i.e., criterion *c* response bias: participants were more conservative when reporting a gap in tactile stimulation while preparing to throw, as opposed to catching preparation). Note that when sensitivity differs between experimental conditions, the appropriate measure of response bias is relative criterion *c'* (i.e., criterion *c* scaled by the corresponding sensitivity; Macmillan & Creelman, 2005). With this consideration in mind, response

bias data as highlighted by the relative criterion *c'* was clustered around zero, indicating 'no bias'. Furthermore, no significant difference between the allocation of criterion *c'* in the two preparatory phases was observed. Therefore, it appears as though a purely perceptual decline in tactile prowess occurs during the preparatory phase of a self-initiated goal-directed movement and the trigger for this is the intention to execute a movement.

Taken together, the results of **Experiment 4.8** therefore provide evidence that different types of attenuation act on tactile perception, as a result of the preparation to execute a goal-directed movement: If the preparation to perform an externally-generated action (i.e., catching the ball) triggers decisional attenuation (i.e., participants are more liberal to report a gap in stimulation, as compared to rest), but no change in sensitivity, the preparation to perform a self-initiated action (i.e., the throw of the ball) triggers perceptual attenuation (i.e., participants' sensitivity to tactile stimulation is diminished as a result of most probably, movement-related gating), but no change in response bias.

4.2.6. General discussion of Experiments 4.4-4.8

Experiments 4.4-4.8 investigated self- versus externally-generated movements by utilizing both speeded detection measures and non-speeded detection measures for perceptual stimulation delivered at different points in time during the executed movement.

The *preparatory* phase of both self- and externally-initiated movements highlighted a significant attenuation of tactile perception. If, for self-initiated movements, a decrement in sensitivity was observed, for the externally-generated movements, only a change in response bias was noticed (i.e., participants were more

inclined to give a YES response). Such results could be taken to represent the suppressive effect of the descending motor command, which diminishes what is felt in the movement effector. As such, in support of this interpretation emerging from **Experiment 4.8**, RTs to suprathreshold tactile stimulation do not differ between the preparation of a ball-catching (**Experiment 4.4**) or a ball-throwing movement (**Experiment 4.7**).

A clear deterioration in tactile sensitivity was observed over the course of the movement execution period of both ball-catching and ball-throwing movements. At the same time, the speed of participants' responses to tactile events was significantly enhanced over the same period. Such results argue for there being a trade-off between speed and quality in the tactile domain. This phenomenon ('faster to detect *it*, but less likely to say what *it* is during movement'), if further investigated and confirmed, would be a valuable contribution to the human factors industry, as well as sports interested in using the sense of touch benefits while moving.

Lastly, participants showed slower tactile RTs at the catch of the ball, as opposed to the ball-throwing movements. It can thus be argued with the present data that tactile perception is prone to exogenous attention capture, as given by a looming effect of the approaching ball (**Experiments 4.4-4.5**).

Taken together, then, these data suggest that tactile perception is differentially affected during the various phases of self- versus externally-generated movements. The data suggest that the attenuation found to affect tactile perception during movement preparation has a true perceptual cause for self-initiated movements, but only a decisional one for reactive externally-generated movements. Moreover, the sensory suppression known to appear during motor execution is compensated for by a

facilitation in the speed of participants' responses to sensory events over the same period.

4.3. Summary and conclusions

Chapter 4 has brought evidence that tactile perception is deteriorated during the execution of naturalistic movements, such as juggling and ball-catching, or ball-throwing movements. This decrement in tactile sensitivity has already started while preparing to move and continues over the execution period of the movement. The data suggest that this effect is a result of the motor command to execute the movement, as well as the peripheral contact with the ball. Moreover, perceptual sensitivity is genuinely affected only when the action results from one's one will (i.e., self-initiated actions). Otherwise, it is the expectation of a diminished tactile percept that affects our reports of what we feel. The data suggest that our perception is prone to attention capture by objects that 'invade' our peripersonal space. This effect generalizes over tactile and auditory perception. Lastly, **Chapter 4** highlights a natural compensation for the suppressive effect overtaking tactile perception: Even though we feel less while we move, we are faster to respond to incoming tactile stimulation. However, this compensatory effect is only present during movement execution, and not during movement preparation.

Chapter 5

General discussion

5.0. Introduction

All of the experiments reported in this thesis were designed to investigate the modulation of tactile perception at various time points during the course of goal-directed movements (see **Appendix A3** for a summary of the experiments presented in this thesis). Tactile perception was assessed by means of non-speeded discrimination and detection tasks, but also by speeded detection tasks (**Chapters 2** and **4**), and by means of ERPs (**Chapter 3**). The goal of this thesis was to try and characterize the changes that take place in tactile perception in the context of a goal-directed action (i.e., the reach-to-grasp and exploratory movements utilized in **Chapters 2** and **3**, as well as the catching and throwing of a ball in **Chapter 4**). These movements were investigated from the perspective of two mechanisms: a facilitatory one (attention) and an inhibitory one (suppression). The two mechanisms were thought to affect tactile perception differently, depending on the movement phase when sensory stimulation was provided. Several open questions were outlined in **Chapter 1** with regard to the dynamics of tactile perception during movement execution. Here, these questions are once again taken-up and the results are discussed with respect to the experimental evidence gathered in experimental **Chapters 2-4**.

5.0.1. Timing of tactile stimulation delivery during movement

The first prediction to be put forward in this thesis was that a differential pattern of tactile sensitivity would be observed over the different temporal phases of a goal-directed movement: It was hypothesized that tactile sensitivity would be higher during the preparatory and post-movement phases (i.e., both benefiting from the facilitatory effects of tactile, but also visual attention, as predicted by the premotor theory of spatial attention, Rizzolatti & Craighero, 2009; Rizzolatti et al., 1994), and it was expected to decline during the execution period of the movement (i.e., as predicted by forward models of motor control, Miall & Wolpert, 1996; Wolpert et al., 1995).

At a behavioural level, a differential pattern of tactile sensitivity was observed for the various phases of the goal-directed reach-to-grasp movement tested in **Chapter 2**. In line with previous accounts (Brozzoli et al., 2009; Buckingham et al., 2010; Gallace et al., 2010), tactile sensitivity was lowest (thus, the poorest perceptual performance was exhibited) over the execution phase of the movement in both **Experiments 2.1** and **2.2**. This decline in what was felt was explained by a combinatory influence of the motor command, together with the peripheral masking from the movement itself (Chapman, 2009; Chapman & Beauchamp, 2006). Moreover, contrary to the predictions of the premotor theory, **Experiment 2.3** demonstrated that attentional facilitation does not affect what is felt during the preparation and post-movement phases of the tested movement. Rather these periods can be characterized instead by a natural non-disturbed state of tactile perception. Furthermore, **Experiment 2.4** demonstrated that the decline in what is felt over the motor execution period at a behavioural level was not due to a (visual) attentional capture effect from the moving hand, but it evidenced a clear decline in tactual sensitivity (Bays et al., 2005; Voss et al., 2006). **Experiments 2.5-2.7** further investigated the potential attentional influences on tactile perception, with an emphasis

on the preparation phase, where these effects were expected to be particularly evident (Rizzolatti & Craighero, 2009; Rizzolatti et al., 1994). The results of these experiments highlighted that the mere preparation to move does not guarantee a shift of spatial attention to the moving effector (i.e., tactile sensitivity in the preparatory phase of the movement was comparable to that of the execution phase in **Experiment 2.5**). Interestingly though, the results on the speed of participants' responses to tactile events tested in **Experiment 2.6** highlighted a differential pattern of RTs: RTs decreased from the preparation phase to the execution, and then post-movement phase of the movement. Lastly, **Experiment 2.7** indicated that the increased thresholds found in the preparatory phase of the movement in **Experiments 2.5-2.6** were not due to an inhibitory attentional influence (i.e., IOR; Klein, 2000; Spence et al., 2000a), but instead stem from the motor command to execute the goal-directed movement (Bays et al., 2005; Voss et al., 2006; Walsh & Haggard, 2008). It can thus be concluded that the behavioural results pertaining to the timing of tactile stimulation delivery during the reach-to-grasp movement utilized in **Chapter 2** support an account in terms of tactile suppression during movement execution.

At a neuronal level, the experiment reported in **Chapter 3** of this thesis highlighted that the timing of tactile stimulation delivery significantly influenced somatosensory ERPs: Enhanced negative responses peaking approximately 140 ms post-stimulus onset were documented over the motor execution period of the movement, as compared to both the preparatory and the post-movement phases. Traditionally, following the delivery of tactile stimulation, such enhancements in electronegativity in a limb prepared to move have been taken to support a central attention-directing mechanism acting on tactile perception (Eimer et al., 2005; Forster & Eimer, 2007; Gherri et al., 2007).

Therefore, the experimental evidence regarding the timing of stimulation delivery in **Chapters 2** and **3** indicates a clear decrement in performance during movement execution at a behavioural level, whereas brain responses to tactile stimulation are significantly enhanced over the same movement period. At first glance, such results may appear contradictory. In order to grasp the meaning of such an outcome, the particular task utilized needs to be considered. The decrement in tactile sensitivity was observed in a discrimination task, where participants had to report on the quality of the tactile stimulation provided. As such, the task utilized for the reach-to-grasp movements in **Chapter 2** required participants' 'awareness' to the quality of tactile stimulation in a typical dual-task, including a movement task and a perceptual task. Conversely, the electrophysiological method of ERPs utilized in **Chapter 3** allowed participants to concentrate on the performance of the movement task (i.e., the reach-to-grasp movement) and ignore the sensory tactile events occurring at their fingertips, as already required by the experimenter (see Chapman et al., 1987, for a similar discussion). For this reason, the task used in **Chapter 3** could be regarded as not requiring participants' 'awareness' with respect to the quality of the incoming sensory events. However, their appearance, and thus novelty, triggered covert attentional-like processing at a neuronal level, a fact that was evidenced in the modulation of the somatosensory ERPs (Eimer et al., 2005; Forster & Eimer, 2007; Gherri et al., 2007).

To summarize the results of **Chapters 2** and **3** with respect to the timing of stimulation delivery over the time-course of a goal directed movement, it appears that the brain gives priority to incoming sensory events (i.e., the attentional ERP enhancement reported in **Chapter 3**). However, their particular quality does not seem

to play an influential role (i.e., the behavioural decrement in tactile sensitivity in **Chapter 2**) during the movement execution phase of a reach-to-grasp movement.

5.0.2. Does the effector of the movement receive attentional prioritization?

The second open question to be addressed by the experiments reported in this thesis was concerned with the location on the body surface where an enhancement or decrement in what is felt is more likely to appear: the moving versus resting effector of a goal-directed reach-to-grasp movement. It was hypothesized that a differential pattern of sensitivity would be observed in the moving/non-moving upper limbs. Accordingly, an attentional-based explanation would posit an enhancement in what is felt for the moving effector, whereas the forward models of motor control would predict a decrement in what is felt at the same effector.

In a first step, this discussion once again needs to consider the particular task utilized to assess sensitivity in **Experiments 2.1-2.5** and **2.7** from **Chapter 2** in this thesis. Sensitivity in these experiments was calculated by deriving comparison thresholds between the moving and resting effectors of the movement, and while keeping performance at a predefined level (79.4 % correct, see Levitt, 1970). While this method of assessing sensitivity to a difference in stimulation was successfully utilized in order to compare tactile performance across experimental conditions in **Experiments 2.1-2.5** and **2.7**, it came at the cost of not being able to have the direct post-hoc behavioural comparison of performance for the moving and resting effectors of the movement[12].

[12] Note that the experiments reported in **Chapter 4** assessed tactile sensitivity by means of a signal detection paradigm; therefore, these experiments assessed what was felt directly at the movement effector.

Nevertheless, the behavioural results of **Experiment 2.6** indicate that tactile events delivered to the resting effector benefit from faster processing (evidenced by faster RTs), as compared to those delivered to the moving effector. However, the electrophysiological results reported in **Experiment 3.1** indicate that at a neuronal level the ERPs in response to tactile stimulation delivered to the resting hand are significantly less negative as compared to those elicited at the moving hand. Once again, the behavioural and electrophysiological results from **Chapters 2** and **3** of this thesis appear to be at odds with each other. If the attentional explanation for enhancements in electronegativity (Eimer et al., 2005; Forster & Eimer, 2007; Gherri et al., 2007; Zopf et al., 2004) should be taken as the 'universal truth', then how can one account for the 'reversal' of results found at a behavioural level in **Experiment 2.6**? As argued before in **Chapter 2**, the slowing of participants' RTs in response to tactile stimuli delivered to the moving hand could be accounted for by accepting that the execution of the movement acted as a distraction on the performance of the concurrent perceptual task (i.e., speeded detection of incoming sensory stimulation), a typical dual-task effect (Pashler, 1992; Spence, 2008). Thus, if movement itself slowed down the speed of responding to the tactile events delivered at the moving hand, then it can be concluded that at a brain level the attentional effects are influencing the moving effector of a reach-to-grasp movement (as highlighted by the results of **Experiment 3.1**).

5.0.3. Modality-based versus supramodal accounts of perceptual modulation during movement

The third open question to be addressed by the experiments reported in the present thesis concerned the nature of the attentional versus attenuating mechanisms that evidently affect tactile perception during the various temporal phases of goal-directed

movements. In this respect, the experiments reported in **Chapters 3** and **4** investigated whether enhancement or attenuation in what is felt affect touch and stimuli presented in the other sensory modalities (i.e., vision in **Chapter 3** and audition in **Chapter 4**) in a similar manner. Since the experiments reported in this thesis focused on tactile perception, these investigations of visual and auditory perception were utilized here mainly as control measures for the tested mechanisms of attention and suppression, thought to influence tactile perception.

At a behavioural level, a distinction between speed and quality was observed: While **Experiment 4.2** indicated almost perfect performance in discriminating the quality of auditory information during movement (thus no decrement in performance was observed), the results of **Experiments 4.4** and **4.5** indicated that an attention-capture-like effect (or a looming effect from the approaching ball, see Franconeri & Simons, 2003; Hillstrom & Yantis, 1994; Makin et al., 2009) influenced both tactile and auditory perception in a similar manner. As long as the quality of sensory information is concerned, these data favour the forward model of motor control (see the argument in Bays & Wolpert, 2007). However, when the speed of reaction to tactile events is considered, the data support more a supramodal attentional-control mechanism exerting its influence during the execution phase of the movement (Spence & Driver, 1996, 2004).

Classic studies of crossmodal spatial attention and multisensory integration have differentiated between a supramodal attentional control mechanism affecting the tested modalities of vision, audition, and touch in a similar manner (Farah et al., 1989), and a modality-based attention-directing system. According to the latter, the attentional shifts could be controlled by modality-specific attentional mechanisms and these specific effects extend further to other sensory modalities (Spence & Driver,

1996, 2004). The electrophysiological data presented in **Chapter 3** indicate that, over the movement execution period, a supramodal attentional mechanism may have acted on both tactile and visual perception.

These behavioural and electrophysiological data collected from the various modalities of touch, audition, and vision bring the strongest support that the two mechanisms of attention and suppression are not mutually exclusive. Attention could be taken to account for signaling a change in the current state of the body and/or the environment, and this effect takes place preferentially during movement execution (where the strongest attentional effects were documented; see **Chapter 3**). On the other hand, suppression could be triggered (most probably once the presence of the sensory event has already been acknowledged by the brain) and then could act like a 'trimming' filter (i.e., it attenuates features of the sensory events that are not important for current purposes). This discussion will further be taken up in the conclusions section.

5.0.4. Insights regarding tactile perception from the execution of naturalistic goal-directed movements

The last open question to be addressed by the experiments reported in this thesis relates to the type of movement utilized and investigated whether a similar distribution of attentional versus suppressive influences on tactile perception were prone to generalize to the more naturalistic everyday movements (i.e., catching and throwing a ball in **Chapter 4**, but also the tactile exploration investigated in **Chapter 2**).

The naturalistic movements tested in this thesis indicated a similar pattern of suppressive influences acting on tactile perception during the motor execution period, as in the case of the 'laboratory-based' reach-to-grasp goal-directed movements. However, by making use of the signal detection theory measures, the experiments

reported in **Chapter 4** distinguished between the truly perceptual and decisional nature of such an attenuating effect found to affect tactile perception. In this respect, the deterioration in tactile sensitivity experienced while *juggling* in **Experiment 4.1** was accompanied by a significant conservative change in participants' response bias. Moreover, further experiments from **Chapter 4** that investigated the preparation phase of the movements involved in *throwing* and *catching* a basketball suggested differential tactile perception modulations for self- versus externally-generated movements: **Experiment 4.8** highlighted that the attenuation found to affect tactile perception has a genuinely perceptual cause for self-initiated movements, but only a decisional one for the reactive externally-generated movements. Although behavioural, results such as these are important because they hint at where in the brain the demonstrated suppressive effects could arise. Particularly, these results indicate that the tactile suppression found over the preparation period of an externally-generated movement, as well as over the execution period of a sustained juggling movement could already be triggered in the brain ahead of the motor command (e.g., in the premotor cortex, de Lafuente & Romo, 2005; Romo et al., 2004). At the same time, in a similar manner to **Chapter 2**, **Chapter 4** also indicates a natural compensation for this attenuating effect acting on tactile perception: Even though we feel less while we move, we can respond more rapidly to incoming tactile stimulation over the same phase of the movement.

Lastly, and most importantly, in terms of the perceptual relevance for the naturalistic goal-directed tested movements, the experimental data gathered in **Chapter 4** indicate that tactile perception may not necessarily be the key modality for goal-directed naturalistic movements, such as catching and throwing a ball. However, one last point of discussion needs to consider the naturalistic tactile exploration

movements investigated in **Chapter 2**. The results of **Experiment 2.8** highlighted the fact that tactile information is enhanced when the tactile percept results from movement execution (i.e., exploratory movements). Therefore, the results of **Experiment 2.8** concerned with the modulation of tactile perception during the execution of naturalistic movements highlighted that the *quality* of what is felt is prioritized over the movement execution period for exploratory movements. This was not the case for either the goal-directed reach-to-grasp movements tested in **Chapters 2** and **3**, or for the ball catching and throwing movements investigated in **Chapter 4**.

5.0.5. Neuronal correlates of what is felt during movement execution

The results of the experimental data reported in this thesis suggest that what is felt depends on the type of incoming tactile stimulation. In this respect, it could be hypothesized that for the cases when a fine discrimination of the quality of tactile stimulation is needed, the stimulus will first be processed in the primary somatosensory cortex (SI) and then will be further relayed to the second somatosensory cortex (SII). Here, the nature of the tactile stimulation will be assessed. Such a hypothesis is in line with the results of fMRI studies that reported a decrease in the BOLD signal in the parietal operculum (i.e., region that includes SII) for stimulation delivered to a moving limb (Parkinson et al., 2011). Furthermore, this study also indicated that this decrease in activity for SII was correlated with activity in premotor regions, such as the lateral premotor cortex, and the medial cingulate motor cortex (CMA) and supplementary motor area (SMA). The premotor regions have an important role to play in motor planning and the outlining of the motor sequence of the forthcoming goal-directed action. At the same time, it has been suggested that the pre-SMA might be the trigger region for the sensory suppression experienced prior to

movement start (Haggard & Whitford, 2004). It thus appears that SII receives inhibitory projections from the premotor cortex. Since a decision on the quality of stimulation is needed, it could be speculated that SII in turn projects back to the premotor cortex, as highlighted by monkey studies (de Lafuente & Romo, 2005; Romo et al., 2004). Furthermore, given the decisional component to tactile suppression described in **Chapter 4** of this thesis, one needs to consider other frontal brain areas that may be involved in the modulation of what is felt during movement. For example, by using a task that required participants to discriminate the frequencies of two successive tactile stimuli, human fMRI studies have reported significant activations in the left dorso-lateral prefrontal cortex (dlPFC), the anterior CMA, and bilaterally, in the insular cortices (Pleger et al., 2006). Most importantly, the activity in the left dlPFC was particularly sensitive to those trials in which participants gave a correct response in the tested tactile discrimination task.

Having established the potential involvement of SII in the gating of somatosensory sensation, the question is what happens in those cases where what is felt is actually enhanced (Burton, 2001; Nelson, 1996; see also the electrophysiological data from **Chapter 3**, as well as RTs data from **Chapters 2** and **4** in this thesis). A possible resolution[13] would be that for the simple notification of a tactile stimulus touching our hand (e.g., the ERP data in this thesis), or the behavioural detection of such a stimulus (e.g., the RTs data reported here) the neuronal processing would instead take place in SI. Such a task wouldn't necessitate the evaluation of SII, and thus it may be able to escape the decrement in what is felt (associated with motor

[13] Note that a more simplistic way to regard the dissociation between the behavioural and electrophysiological data on tactile perception modulations during the motor execution phase is to take into account the *timing of the decision:* When the 'decision' is made in real-time/during movement execution, tactile perception is enhanced. On the other hand, a post hoc judgment of the quality of what is felt will most probably involve a decrement in tactile perception, due to the comparison with the initial prediction on the consequences of movement.

prediction). Once the presence of the tactile stimulus is 'acknowledged' by SI, according to this alternative hypothesis, it could be further directly transmitted to the posterior parietal cortex regions responsible for attention.

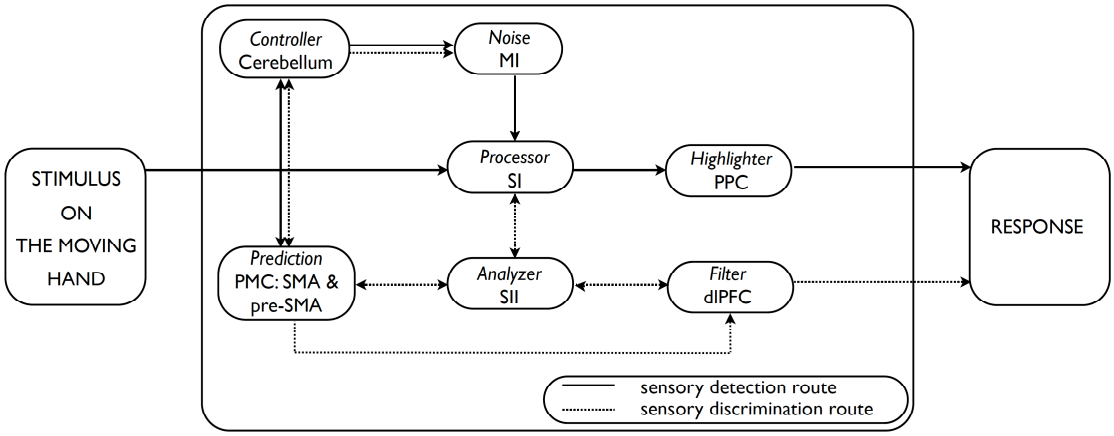


Figure 5.1. Hypothetical model on tactile perception modulations in the moving effector of a goal-directed movement. The stimulus arriving at the moving hand is first processed in SI (the Processor); SI also receives the Noise from the ongoing motor command and muscle afferents. The tactile stimulus is further fed to SII (the Analyzer); SII also receives projections from the premotor cortex, related to motor planning and sensory estimates of the movement (the Prediction). If the current perceptual task requires the observer just to detect the presence of a tactile stimulus, then the information processed in SI is further transmitted to the posterior parietal (PPC) centers (the Highlighter). Thus, the evaluation of the sensory information (as performed by the Analyzer, SII) could be by-passed. However, if a judgment on the quality of the incoming stimulation is needed, then the sensory information is passed on to the Analyzer (which is nevertheless biased due to the inherent motor Prediction). Therefore, before making a response, a final stop in the processing of the sensory information could take place again in the premotor/prefrontal cortex (the Filter). Thus, this hypothetical model posits that depending on the perceptual task, the final response can either be highlighted (attention), or filtered (suppression). Note that here the cerebellum is depicted as the Controller, given its steady involvement in motor control and training.

Another important region that is thought to represent the timing of our goal-directed actions is the cerebellum, with the neocerebellum being involved in the control and planning of voluntary movements, while the intermediate cerebellum is involved in regulating the quality of the movement (Gazzaniga et al., 2002). It has been argued that the cerebellum is a key predictive component in the conceptualization of the internal models of motor control (Desmurget & Grafton, 2000; Kawato, 1999). Single-cell recording studies highlighted activity in the cerebellar cortex when the monkey adjusts the grip for a slippery object (Dugas &

Smith, 1992). Human studies highlighted similar results: For example, a patient with cerebellar degeneration exhibited an impaired prediction of the consequences of his movements (Babin-Ratte, Sirigu, Gilles, & Wing, 1999). In this context, it is important to note that the cerebellum has extensive projections, through the thalamus, to the premotor and prefrontal cortices (Doya, 2000; Glickstein & Doron, 2008; Wise, 1985). Therefore, by its steady involvement in motor control, motor learning and training, as well as its connections to premotor/prefrontal areas in the brain, the cerebellum needs to be taken into account when considering the neural correlates of tactile perception during movement. See Figure 5.1 for a hypothetical depiction on what happens to a tactile event delivered to a moving hand.

5.1. Summary and implications of the results

This thesis brings strong behavioural evidence in favour of a differential temporal pattern of tactile perception modulations over the *time-course* of a goal-directed movement: Tactile sensitivity is significantly diminished over the movement execution phase, as compared to the motor preparation and post-movement phases, result arguing in favour of an attenuating mechanism that affects tactile perception (Brozzoli et al., 2009; Buckingham et al., 2010; Gallace et al., 2010). At the same time, at a neuronal level, the somatosensory ERPs were significantly enhanced over the same time period, a result that argues in favour of an attention-directing mechanism affecting tactile perception over the same movement phase (Eimer et al., 2005; Forster & Eimer, 2007; Gherri et al., 2007). This thesis also highlights that the *moving effector* benefits from attentional prioritization, suggesting that attention most likely 'travels' with the movement effector. Lastly, the experimental data gathered

here suggest that attention has a *supramodal* influence (Spence & Driver, 1996, 2004) on the modalities of touch, audition, and vision.

Most importantly, the experiments reported in the present thesis suggest that a demarcation between speed and quality must be made in the tactile domain, whenever movement execution is concerned: If the tactile stimulation impinging on our fingertips/palm/wrist/arm receptors is readily detected, its type/quality does not seem to play such an important role. Following on from this, a distinction between the presence of *some* external stimulation and the presence of a *particular* external stimulus is needed: The results of this thesis allow one to put forward the claim that the *presence* of a sensory event (tactile, visual, or auditory) will receive attentional prioritization during movement execution, just as postulated by the classical exogenous attention accounts on perception at rest (see Spence & Driver, 2004; Spence & McGlone, 2001). Nevertheless, when processing the *quality/type* of information being felt during the execution of reach-to-grasp movements, as well as other naturalistic movements involved in catching and throwing a ball, but also exploratory movements, a dichotomy based on *sensory-relevance* for movement is apparent: The characteristics of tactile stimulation that are not relevant to the motor task at hand will be suppressed, in order to highlight other incoming valuable sensory information. However, tactile information that is relevant to the motor task at hand, such as that used in active exploration, will be enhanced. From this perspective, the attentional/suppressive influences on what is felt during movement could be regarded as *context-dependent*. At the same time, such a stand allows the consideration of contributions from higher-order brain centers of decision-making and expectation on basic perceptual functioning. As such, from this perspective, the timely processing of sensory information during movement suggests that the incoming sensory information

may be used for the adjustment of the current motor plan, or the development of an alternative motor plan, if so required (e.g., the new motor plan needed when reaching for a steaming-cup of coffee).

Taken together, the data reported in this thesis have implications for the design of *warning* tactile signals in the human factors industry, ergonomics, industrial design, or sports science. These warning signals need to be delivered to the skin during the *execution* of various goal-directed movements (e.g., in designing training programmes in team sports such as cricket where a tight eye-hand coordination is required – tactile cues delivered during movement execution could inform the player of concurrent developments on the field to which he has no access at the specific movement time). Moreover, another newly emerging field is concerned with the use of all our senses, as well as their interaction for the benefit of marketing and advertising campaigns (Ariely & Berns, 2010; Lindstrom, 2005). Results such as the ones presented in this thesis have implications for consumer behaviour research (e.g., research on the sensory cues that drive a consumer to choose a specific product in the supermarket).

Furthermore, the advantages of the various *timings* of tactile stimulation delivery as highlighted by the experiments reported in this thesis could contribute to the understanding and the implementation of rehabilitation programmes for serious neurological conditions, such as strokes (Fridman et al., 2004), or movement disorders (e.g., Gilles de la Tourette syndrome, Ganos & Hummel, 2011). For example, a deterioration in tactile discrimination as compared to simple tactile detection has already been reported in Tourette patients (Belluscio et al., 2011), as well as stroke patients (Tyson et al., 2008). Therefore, the tight interaction between motor and perceptual function as well as its precise timing needs to be addressed when designing intervention/treatment plans for such neurological conditions.

Lastly and most importantly, the precise timing of movement-related perceptual function could be of use in translational research for the development of brain-computer interfaces (BCIs) designed to rebuild the lost movement/sensation abilities sometimes experienced following brain impairment (see Lebedev & Nicholelis, 2006; O'Doherty et al., 2011). For example, current machine-limbs decode the movement based on *spatial* visual information and consequently, perform the movement with respect to the goal of action. This process is highly time-consuming (it takes up to one second to plan and perform a reaching movement, Andersen & Cui, 2009; see also Wolpert et al., 2011). By taking into consideration the other sensory systems and the timing of their involvement in motor control as well as space construction, future neuroprosthetic devices could use their finer *temporal* resolution and perform the desired movement faster and more reliably.

5.2. General conclusions

To conclude, it appears as though the two mechanisms of attention and suppression tested throughout this thesis work *in parallel* over the execution phase of a goal-directed arm movement: one detects the novelty in the environment and promptly responds to it (attention), and the other filters those characteristics of the novel stimulus that are not relevant for the current task (suppression). Contrary to predictions made in **Chapter 1**, the preparatory phase of the movement does not receive facilitatory attentional influences. Rather, a truly perceptual decrement takes place in the preparatory phase of a self-initiated movement (i.e., reach-to-grasp movement, throwing movement), but only a decisional decrement (however, the tactile percept/report is still affected) in the case of externally-generated movements. Results such as these indicate that while moving, the cognitive system is readily

responding to incoming stimulation; Nevertheless, the type of such stimulation (its intensity, temporal structure, etc) is not important at this stage. Lastly, exploratory movements indicate that what is felt is highly relevant for movement, when the active movement itself is the means of achieving the tactile feeling.

5.3. Directions for further research

Future research needs to investigate further the brain networks related to the two mechanisms of attention and suppression that are involved in modulating tactile perception over the time course of goal-directed movements. As a first step, a reasonable follow up for **Chapters 2** and **3** of this thesis will be to design an EEG/MEG study conducted to test tactile performance by utilizing both detection (i.e., the presence of a stimulus), as well as discrimination paradigms. (i.e., the quality of the incoming stimulation). This study would hopefully provide a clear resolution on the distribution of both attentional and suppressive effects over the various phases of the goal-directed movement.

Furthermore, given the dissociation between attentional and suppressive effects on tactile perception as found in this thesis, an investigation into the trigger of these two mechanisms highlighted at a behavioural level is needed. This investigation can be achieved by using virtual TMS lesions (see Pascual-Leone, Walsh, & Rothwell, 2000; Sandrini, Umilta, & Rusconi, 2010, for reviews) over the premotor/posterior parietal association cortices for the various movement phases of interest (e.g., movement preparation and movement execution). Moreover, given the decisional component of tactile suppression observed in **Chapter 4** of this thesis, further research needs to investigate prefrontal contributions to the modulation of tactile perception during movement (Conte et al., 2012; Pleger et al., 2006; Rosenberg-Katz et al.,

2012). By stimulating 'the triggering brain location' of sensory suppression/attentional facilitation at various SOAs relative to the initiation of the movement, the reported behavioural effects could thus be abolished. This elimination of the attenuating/ facilitatory behavioural effects on tactile perception would potentially take place in a differential manner, depending on the particular task utilized (i.e., detecting the presence of a tactile stimulus vs. reporting its quality).

Lastly, another strand of research could further investigate the self- versus externally-generated movements from **Chapter 4** in the context of movement observation.

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Appendix A1

Supplementary material to Chapter 3

A1.0. Introduction

Appendix A1 provides supplementary material to the electrophysiological **Chapter 3**. First, some further general methodological considerations on EEG/ERPs are provided, which are followed by an additional analysis on the ERP data from the moving effector only in **Experiment 3.1** from **Chapter 3** of this thesis.

A1.1. Some remarks on the electrophysiological method

A1.1.1. What does the electroencephalography (EEG) exactly measure?

Electrophysiological activity can be classified into spontaneous (i.e., the continuous EEG recording of the overall activity of the brain) and evoked/event-related (i.e., the brain activity recorded in responses to a particular experimental stimulation).

The first step in understanding the underlying spontaneous EEG activity and where it arises from concerns the interaction between the basic components of the central nervous system (CNS): the neurons. The CNS is composed of two types of cells: the neurons and the supporting glial cells. The neurons' main function is to assure information transmission through the CNS. They do this by communicating with other neurons (i.e., they form synapses) and thus generating *action potentials*, or electrical signals, that are passed on from the point of initiation at the axon hillock through the axon until the end point of the axon, where synaptic contact is made. The

process by which the information carried through the action potential is passed on to the next cell is called *synaptic transmission*. From now on, I will focus on the postsynaptic cell with the scope of highlighting how the electrical signal is received at the other end.

The receptor binding determines the opening or the closing of specific ion channels; the resulting conductance (i.e., how permeable the cell membrane is to specific chemicals) causes the current to flow. As such, this postsynaptic current (PSC) is able to change the membrane potential (i.e., the difference in voltage between the inside and the outside of a cell) in order to give birth to a *postsynaptic potential* (PSP). The PSP can produce *depolarization* (i.e., the potential is more positive than the membrane potential) or *hyperpolarization* (i.e., the potential is more negative than the resting membrane potential). Therefore, the postsynaptic cell can be excited (i.e., an excitatory PSP (EPSP) occurs) or inhibited (i.e., an inhibitory PSP (IPSP) occurs).

On a regular basis, a CNS neuron usually receives thousands of synapses from other neurons. As such, the PSPs will sum in an algebraic fashion, such that an action potential will (or will not) occur. The resulting *summation* therefore depends on the relationship between excitation and inhibition.

To get to the point, this extra-cellular current flow described in the synaptic transmission is of key importance in EEG. When groups of many neurons become dipoles (i.e., they exhibit the postsynaptic activity described earlier), an *electrical field* evolves. It is widely accepted that the EEG (and thus, the averaged ERPs) measure the electrical potentials generated in the extra-cellular fluid when neurons synapse with each other.

Several conditions must be met for the electrical fields to propagate through the brain and the other layers of protective tissue around it, until the recording site on

the surface of the skin: A large number of neurons must be active at the same time, they must have a similar orientation and not be cancelled by other neuronal groups - e.g., active at the same time, but with an opposite orientation; Luck, 2005 - and lastly, they must be perpendicular relative to the surface of the skull (see Woodman, 2010). This last condition indicates that the EEG signal stems from the activity of the pyramidal neurons projecting onto the association cortices and gives the solution to the EEG *forward problem*: to compute the distribution of observed voltages for one or more dipoles, given that we know the location and orientation of their generator inside the brain. The *inverse problem* is far more tricky and it is the reason for the major drawback of EEG (i.e., its poor spatial resolution): to compute the location and orientation of one or more dipoles from a given voltage distribution. More exactly, the inverse problem states that if we do not know the number of voltage generators across the brain, but only the final voltage summation, we cannot identify their location.

A1.1.2. EEG recording and referencing

Electrophysiological recording and processing may be different from laboratory to laboratory (see Picton et al., 2000, for exact standards). This section describes the preparation of the participant in an EEG experiment.

The electrode caps follow the international 10/20 system (i.e., distances between consecutive electrodes expressed as percentages (20%) with the nasion and inion as markers, Jasper, 1958), though newer electrode arrangements are possible (e.g., the 10% enlargement used in **Experiment 3.1** of this thesis, Oostenveld & Praamstra, 2001). The caps come in different sizes, the participant's head is measured and the standard marker positions are identified. The cap is fixed with belts to the paticipant's body and the next step is the skin preparation. This involves the removal

of the fatty cover of the skin with alcohol and then the scrubbing with an abrasive substance. Lastly, electrolyte is filled in the prepared spot, between the skin and the electrode. Electolyte diffuses into the skin and facilitates the flow of current and thus makes the perfect wet connection between the skin and the electrode. Regarding the electrodes, the scalp electrodes most commonly used are the ones coated with silver chloride (AgAgCl), since they exhibit small impedance (i.e., resistance) to the passing electrical current.

Each of the scalp electrodes is connected into a socket of a differential amplifier; one electrode usually placed on the forehead is used to ground the system (in order to prevent amplifier drift, Nunez & Srinivasan, 2006). Another electrode is used as the on-line common reference for all electrodes (e.g., the common reference for **Experiment 3.1** presented in this thesis was attached to the left earlobe, while another electrode, which was used offline to re-reference the data, was attached to the right earlobe). This re-referencing process, which is usually used with electrode montages that cover the whole head, involves an 'averaged ears' reference, such that when recording, one earlobe is used as the common reference, while the other earlobe is recorded together with the other electrodes, as an active electrode. Consequently, off-line, all the electrodes are re-referenced to only half the other earlobe site (see Nunez & Srinivasan, 2006, Chapter 7, for a discussion on the 'ideal' reference).

A1.1.3. Data processing and filters

The amplified EEG signal is passed onto an analog-to-digital converter and afterward to a digital filter. The filter selects the frequencies of interest and thus tunes down all the unwanted frequencies. As such, the filter can be low-pass (i.e., a high-frequency filter) that cuts off the high frequencies, or high-pass (i.e., a low-frequency filter) that

cuts the low frequencies and lets the high frequencies pass. Filtering allows for the removal of any artifacts related to the recording system (i.e., broken or improperly attached electrodes) as well as physiological ones (i.e., the corneoretinal potential; the electrocardiogram artifact; the pulsation artifact; high amplitude muscular artifacts, or skin conductivity artifacts due to sweating or drying of the skin).

A1.1.4. Relevant ERP components and their interpretation

As mentioned earlier in this chapter, the continuous EEG signal can be classified into spontaneous and evoked/event-related potentials. The ERP technique is currently widely used and involves averaging across multiple instances of brain responses to a particular stimulation across trials for a single participant, and across participants for a specific study. Averaging weakens the irregularities in the signal that are not related to the sensory stimulus of interest. See Figure A1.1 for an example of ERP-specific averaging.

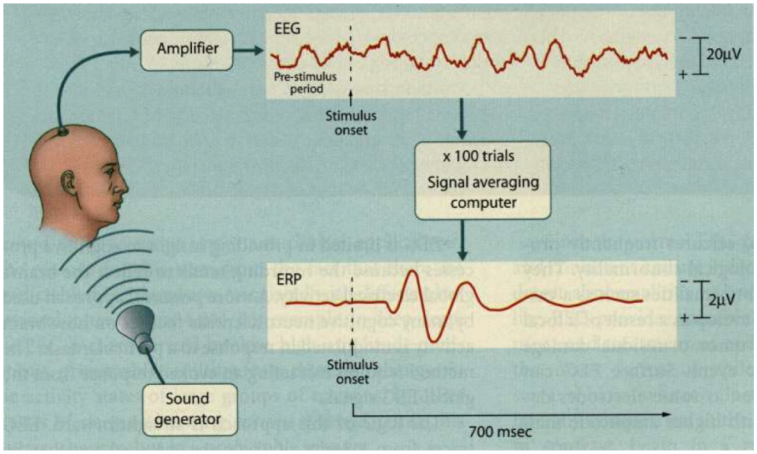


Figure A1.1. Example of EEG data averaging with the resulting smooth ERP waveform. Figure taken from Gazzaniga et al. (2002).

By averaging, one obtains from the initial irregular EEG signal a clear wave with positive and negative deflections that can be noticed over a period of few

hundred milliseconds pre/post-stimulus onset. These 'ups' and 'downs' are the ERP components that are of interest to the cognitive neuroscientists.

Components have been classified by their polarity (i.e., either negative or positive), by their latency (i.e., the time in milliseconds when they appear post-stimulus onset), by their position in the sequence, or by scalp distribution. Moreover, ERPs have been divided into either exogenous (i.e., reflecting characteristics of the stimulation modality, features, or intensities of the stimulation) or endogenous (i.e., reflecting expectancy processes on the participant's side, the novelty, or the relevance of the specific stimulation). Their naming follows similar conventions, such as: P100 for a positive component appearing 100 ms post-stimulus onset or N100 for a negative component with the same latency. Alternatively, components are named by their polarity together with their order in the sequence, e.g., P1, followed by N1, followed by P2, etc (see Luck, 2005, for a discussion). Naming, as well as plotting (e.g., plotting the negative waves up as tradionally happens, versus plotting the ERPs with the positive waves up) differs from lab to lab. In this thesis, ERPs are denoted by their polarity and latency; ERPs are plotted with the negative up.

A1.1.4.1. Somatosensory evoked potentials

Following tactile stimulation, the electrophysiological brain responses first exhibit a very early in latency component (N10), most probably reflecting action potentials, rather than postsynaptic activity; this component is shortly thereafter followed by other early subcortical components with latencies as short 20 ms, and, later on, by short to mid latency components (20-100 ms; e.g., the N100 with which peaks at approximately 150 ms together with the P200, peaking at about 200 ms post-stimulus onset, are referred to as the vertex potential, Luck, 2005). Somatosensory ERPs have

been shown to be maximal over the hemisphere contralateral to the stimulated hand (Eimer et al., 2005; Forster & Eimer, 2007; Röder et al., 1996; Van Velzen et al., 2002).

A1.1.4.2. Movement-related potentials

Movement ERPs have been studied extensively during *the preparation* to execute a required response (e.g., a button press in a psychological experiment), or just simple finger or hand movement. This is not surprising considering that the continuous EEG signal is very sensitive to movement artifacts. Preparing to perform a voluntary motor action therefore triggers two motor components: the early and late contingent negative variation (CNV) and the lateralized readiness potential (LRP); the late CNV is considered to be identical to the LRP (Leuthold et al., 2004). This component is usually the result of unimanual activation of the primary motor cortex (see Eimer & Coles, 2003; Kutas & Donchin, 1980).

A1.1.5. Why use ERPs?

Given that the right experimental question is asked and a well-studied ERP is singled out for experimentation, measuring ERPs proves to be a very satisfying method.

The biggest advantage of ERPs is their temporal resolution. Neuronal signals propagate at such a high speed that ERPs allow researchers to unveil processing in real time, with a temporal resolution of 1 ms or even better. Nevertheless, this comes at the cost of a very poor spatial resolution: Since we don't know where exactly the activity is coming from and how the different excitatory or inhibitory processes influence our derived components, we cannot be confident when drawing conclusion about their meaning (i.e., functional significance, Luck, 2005).

Luck (2005) lists a series of other advantages in using ERPs as a method: They provide a continuous measure of the processing between the presentation of a stimulus and the overt response and therefore allow researchers to investigate which stages of processing are influenced by the experimental manipulations, they even provide a measure for the processing of sensory stimulation in the absence of a behavioural response (e.g., ignored stimuli), and lastly, they are less costly when compared to other imaging methods.

Aside from the research environment, the benefits of EEG have long been used in clinical settings in the diagnosis of sleep disorders, epilepsy, and in acknowledging brain death. Lately, exciting BCIs have been developed with the purpose of augmenting or restoring sensory or cognitive functions (see Lebedev & Nicholelis, 2006; O'Doherty et al., 2011).

A1.2. Analysis A1: Timing of tactile stimulation delivery during movement

This additional analysis was carried out on the data recorded at the **moving hand only**.

The analysis was performed on the tactile ERP data with the factors TIMING (motor preparation, early execution, mid execution, late execution, and post-movement), HEMISPHERE (contralateral vs. ipsilateral), and ELECTRODE PAIR (FC3/4, C3/4, CP3/4, P3/4) (see Analysis A1.1).

In a second step of Analysis A1, difference waves (DWs) were calculated (by subtracting the omission trials (i.e., movement only trials) from the tactile trials). These DWs were then submitted to the same statistical analysis with the factors TIMING, HEMISPHERE, and ELECTRODE PAIR (see Analysis A1.2).

The somatosensory ERPs, together with the omission activity, as well as the DWs (tactile-omission) from this supplementary analysis are presented in Figure A1.2, panels **a** to **d**, corresponding to each analyzed electrode pair (FC3/4, C3/4, CP3/4, P3/4). The tactile ERP waveforms indicate a negative deflection peaking between approximately 140 ms post-stimulus onset (i.e., the tactile N140), for each of the timings of tactile stimulation delivery. In the preparation period, the go signal to initiate the movement was delivered immediately after the omission probe. This auditory signal resulted in a specific auditory early negative ERP component, usually found over frontal and central sites (see Hansen & Hillyard, 1980; Lange et al., 2003). This auditory evoked potential is especially visible in the preparation period of the omission trials. For this reason, difference waves were calculated and given higher weight in the interpretation of the present results.

A1.2.1. Tactile probes: Mean N140 amplitudes (Analysis A1.1)

Analysis A1.1 revealed a main effect of the TIMING of tactile probes delivery [$F(4,60)=8.10$; $p<.001$]; post-hoc comparisons indicated that the activity in the *post-movement* period was significantly less negative as compared to that recorded in the *preparation* ($p=.008$), *mid execution* ($p=.009$), and *late execution* ($p=.010$) periods.

A significant interaction between TIMING and ELECTRODE PAIR [$F(12, 180)=3.12$; $p=.034$; $\varepsilon=.257$] was observed. Paired-samples t-tests were conducted between the different levels of the factor TIMING at each electrode site. Results indicated significantly more negative mean amplitudes of the N140 in the *preparation* period as compared to the *late execution* period [**FC3/4**: $t(15)=-3.44$, $p=.004$, $r=.82$; **C3/4**: $t(15)=-3.60$, $p=.003$, $r=.71$; **CP3/4**: $t(15)=-3.15$, $p=.007$, $r=.41$; **P3/4**: $t(15)=-2.99$, $p=.009$, $r=.42$], as well as the *post-movement* period [**FC3/4**: $t(15)=-4.60$,

p<.001, r=.85; **C3/4**: t(15)=-4.42, p<.001, r=.74; **CP3/4**: t(15)=-4.13, p=.001, r=.56; **P3/4**: t(15)=-3.74, p=.002, r=.54]. In a similar manner, the *early execution* period exhibited significantly more negative N140 mean amplitudes as compared to both the *late execution* period [**FC3/4**: t(15)=-3.06, p=.008, r=.80; **C3/4**: t(15)=-4.02, p=.001, r=.76; **CP3/4**: t(15)=-4.25, p=.001, r=.58; **P3/4**: t(15)=-4.93, p<.001, r=.58], as well as the *post-movement* period [**FC3/4**: t(15)=-4.03, p=.001, r=.83; **C3/4**: t(15)=-4.72, p<.001, r=.77; **CP3/4**: t(15)=-5.18, p<.001, r=.65; **P3/4**: t(15)=-5.65, p<.001, r=.63].

Moreover, at anterior electrodes locations, a significant difference was registered between the *mid execution* mean N140 amplitudes and the *post-movement* N140 mean amplitudes; the mid execution period indicated significantly more negativity at the **FC3/4** electrode pair [t(15)=-3.37, p=.004, r=.87], as well as the **C3/4** electrode pair [t(15)=-3.11, p=.007, r=.83]. Furthermore, the *early execution* period was significantly more negative, as compared to the *mid execution* period at the posterior electrodes **CP3/4** [t(15)=-2.98, p=.009, r=.74] and **P3/4** [t(15)=-3.35, p=.004, r=.66].

Finally, a three-way interaction between TIMING, HEMISPHERE, and ELECTRODE PAIR [F(12,180)=5.82; p<.001; ε=.483] was observed on the tactile ERP data. This interaction was followed with separate ANOVAs with the factors TIMING and HEMISPHERE at each of the electrode pairs.

A significant interaction between the TIMING of tactile stimulation delivery and HEMISPHERE [F(4,60)=3.34, p=.015] was found at the **CP3/4** electrode pair. For the contralateral hemisphere, paired-samples t-tests indicated that the *post-movement* mean N140 amplitudes were significantly less negative as compared to the *preparation* [t(15)=-3.03, p=.008, r=0.62], as well as the *late execution* periods [t(15)=-3.35, p=.004, r=.65]. For the ipsilateral hemisphere, the *post-movement* N140

mean amplitudes were significantly less negative as compared to the *preparation* [t(15)=-4.29, p=.001, r=.74], the *early execution* [t(15)=-3.35, p=.004, r=.65], and the *late execution* mean N140 amplitudes [t(15)=-4.59, p<.001, r=.76].

The same significant interaction between the TIMING of tactile stimulation delivery and HEMISPHERE [F(4,60)=9.51, p<.001] was also found at the **P3/4** electrode pair. For the contralateral hemisphere, paired-samples t-tests indicated that the *post-movement* N140 mean amplitudes were significantly less negative as compared to the *mid execution* [t(15)=-3.05, p=.008, r=.62], and *late execution* N140 mean amplitudes [t(15)=-3.89, p=.001, r=.71]. The *early execution* mean N140 amplitudes were significantly less negative than the *late execution* ERPs [t(15)=3.45, p=.004, r=.67]. For the ipsilateral hemisphere, significantly less negative mean N140 amplitudes were found for the *post-movement* period as compared to the *preparation* period [t(15)=-4.03, p=.001, r=.72], *mid execution* period [t(15)=-4.96, p<.001, r=.79], and the mean N140 amplitudes for the *late execution* period [t(15)=-4.34, p=.001, r=.75].

A1.2.2. Tactile-omission DWs analysis (Analysis A1.2)

The statistical analysis on the tactile-omission DWs data revealed a significant two-way interaction between TIMING and ELECTRODE PAIR [F(12, 180)=11.58; p<.001; ε=.278]. Paired-samples t-tests were conducted between the different levels of the factor TIMING at each electrode site. Although several significant differences between the mean N140 amplitudes of the different movement periods were found, none of them survived the correction for multiple comparisons.

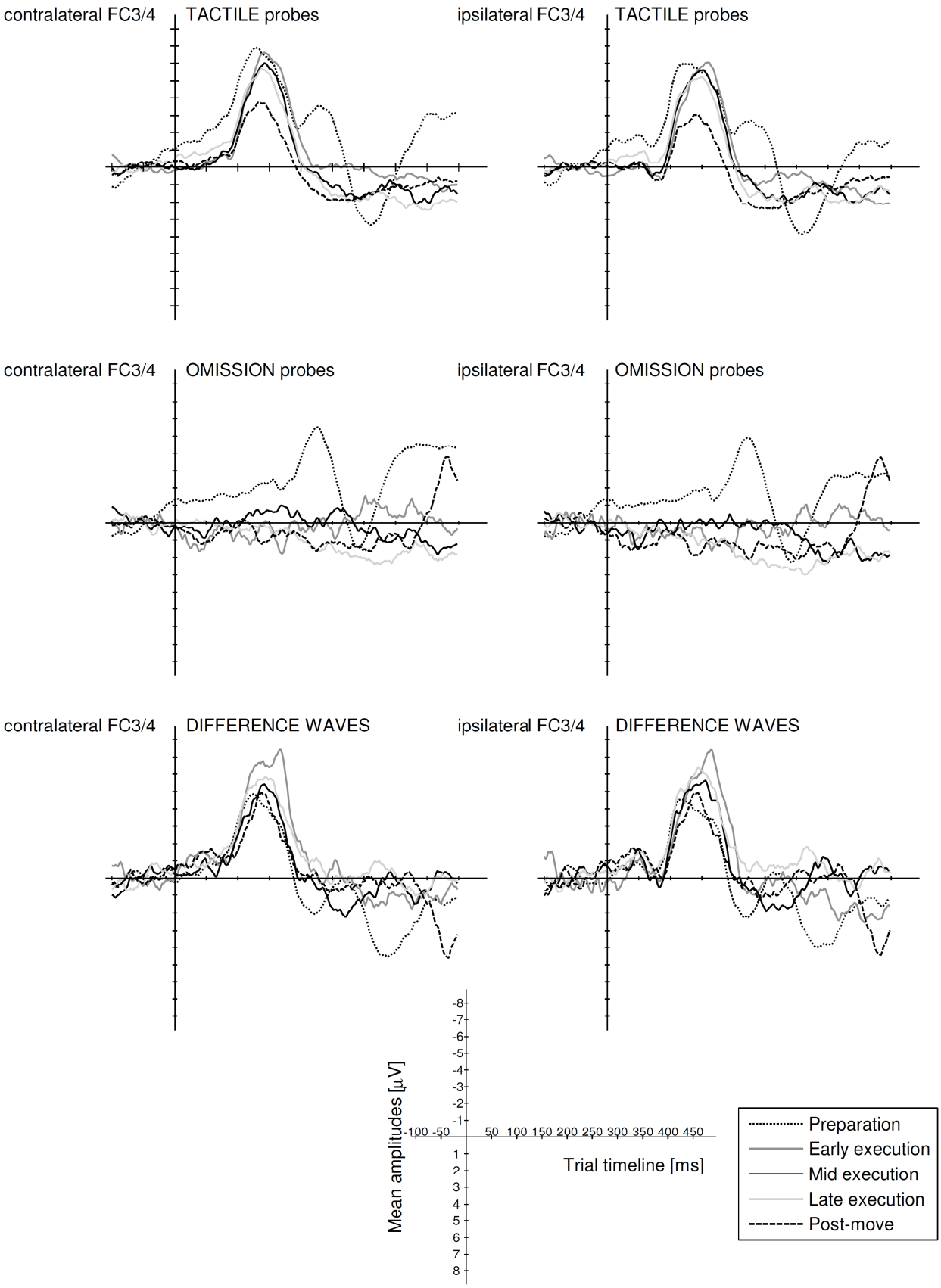


Figure A1.2a. Moving hand tactile ERPs, omission waves, and tactile-omission DWs at the FC3/4 electrode location in **Experiment 3.1**.

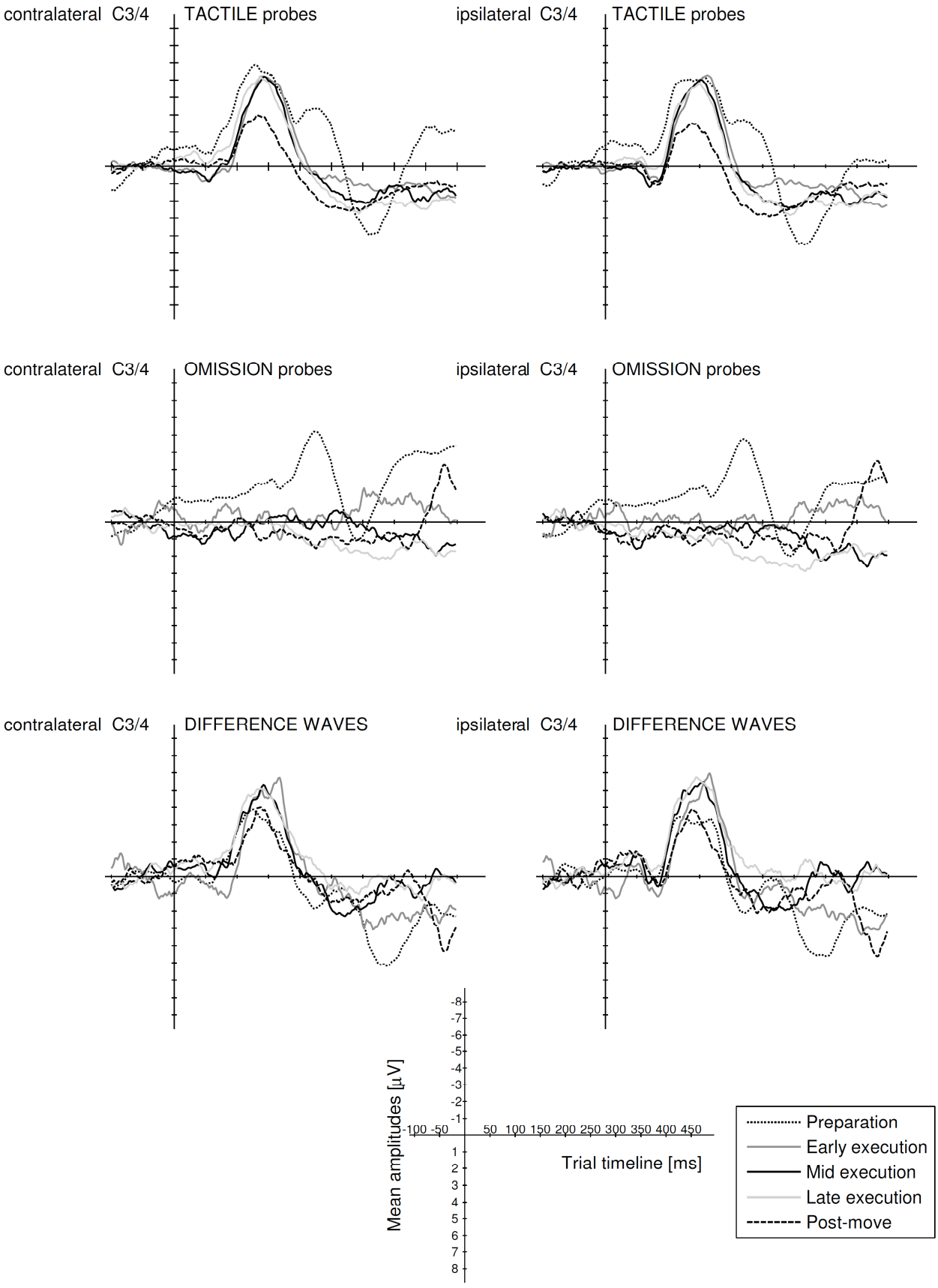


Figure A1.2b. Moving hand tactile ERPs, omission waves, and tactile-omission DWs at the C3/4 electrode location in **Experiment 3.1**.

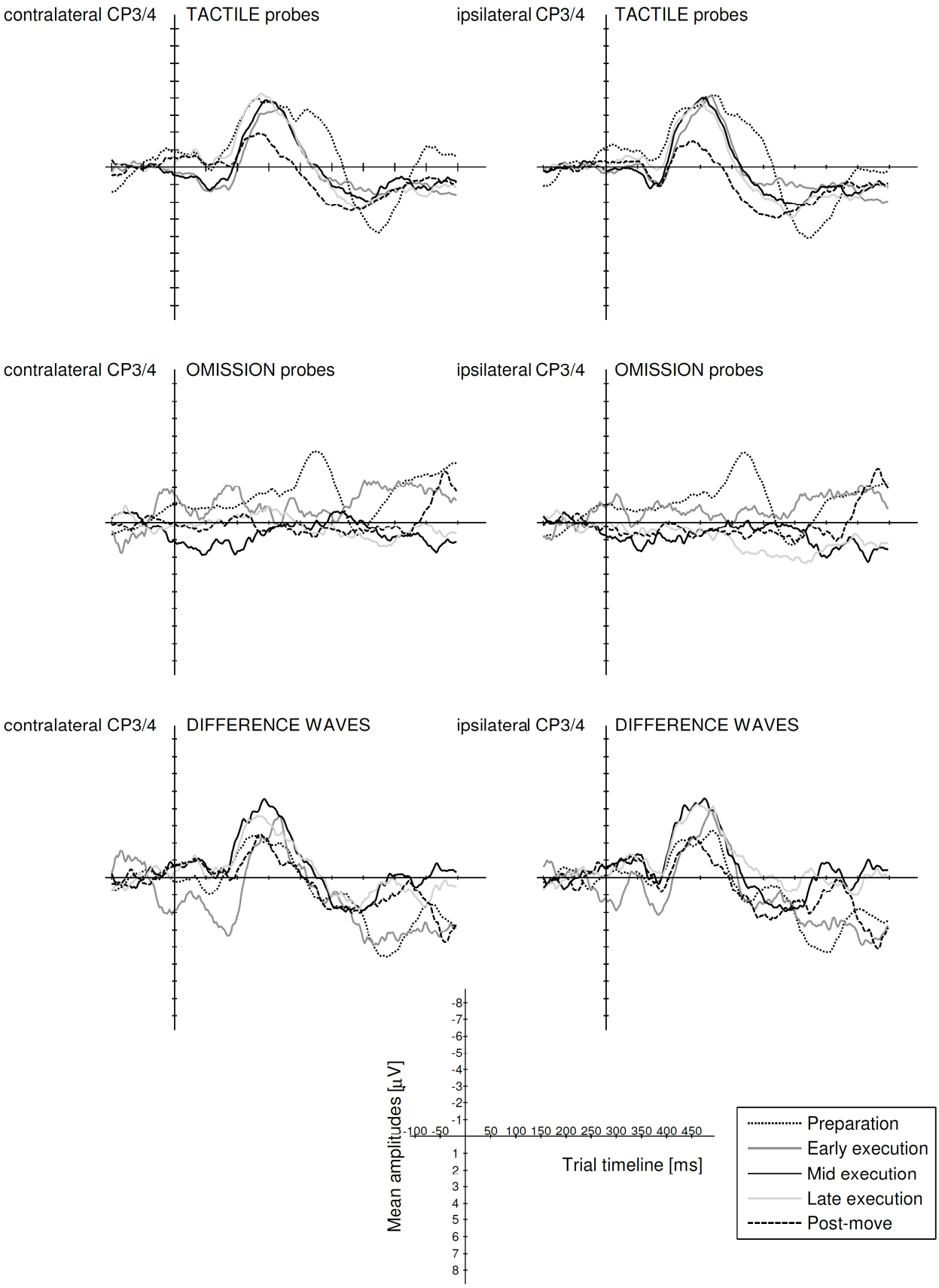


Figure A1.2c. Moving hand tactile ERPs, omission waves, and tactile-omission DWs at the CP3/4 electrode location in **Experiment 3.1**.

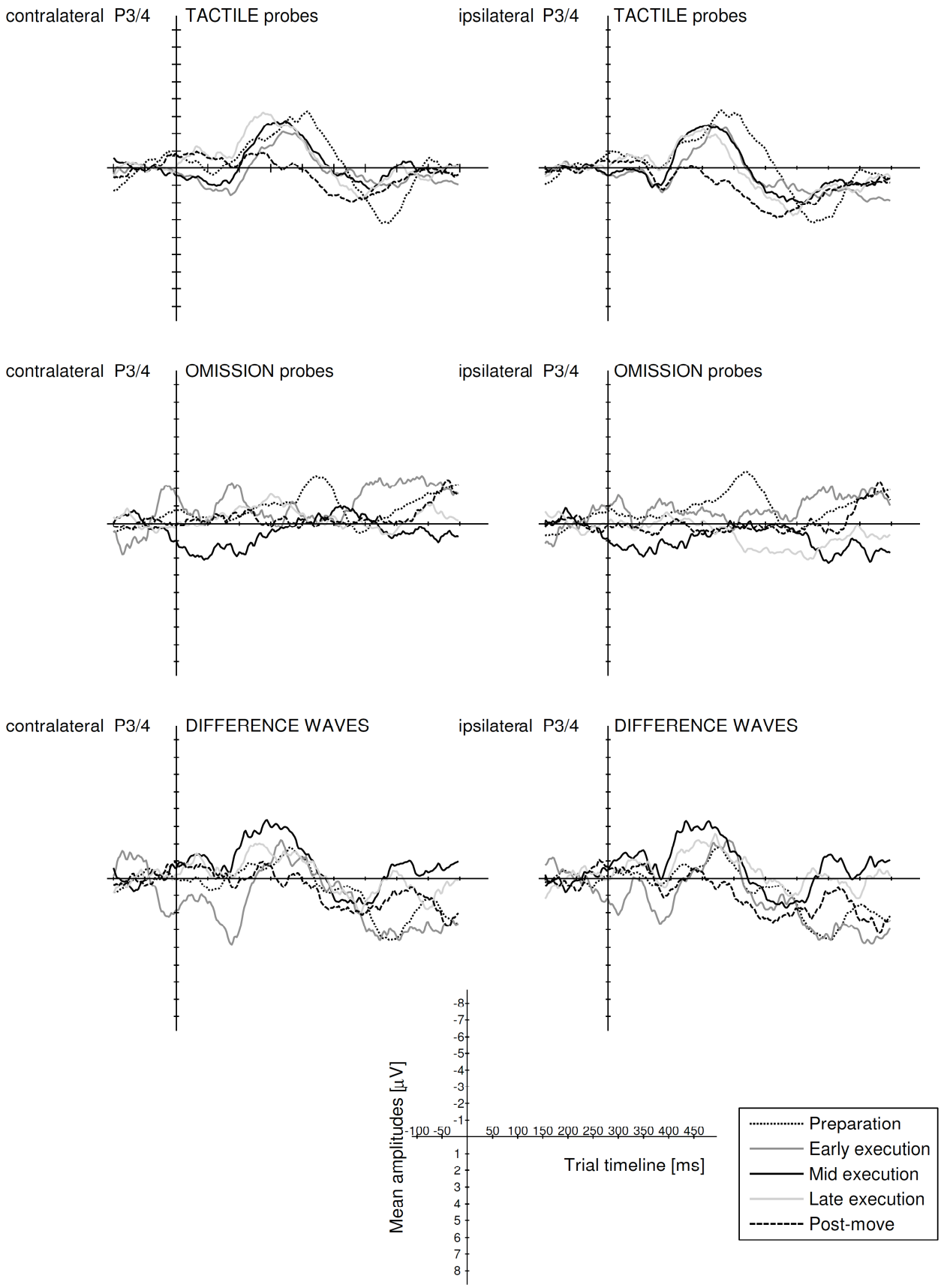


Figure A1.2d. Moving hand tactile ERPs, omission waves, and tactile-omission DWs at the P3/4 electrode location in **Experiment 3.1**.

Another significant three-way interaction between TIMING, HEMISPHERE, and ELECTRODE PAIR [$F(12,180)=2.82$; $p=.040$; $\varepsilon=.292$] was also observed. This interaction was followed with separate ANOVAs with the factors TIMING and HEMISPHERE at each of the electrode pairs (FC3/4, C3/4, CP3/4, P3/4). Nevertheless, none of the interactions between the two factors reached significance at any of the electrode pairs.

A1.2.3. Summary of the results of Analysis A1

The focus of this supplementary analysis reported in **Appendix A1** was on the moving hand. In this respect, the analysis investigated, for the movement effector only, whether a differential pattern of tactile ERPs would be observed for the different phases of the goal-directed movement. For this purpose, a detailed examination of the timing of tactile stimulation delivery was used with the following levels: movement preparation, movement execution (early, mid, and late execution period), and the post-movement period. In order to assess the contribution of the movement itself to the on-going brain electrophysiological responses, ERPs corresponding to movement-only trials were derived with the same levels of the timing factor. In a last step, DWs were calculated by subtracting the movement-only trials from the tactile trials.

The tactile N140 analysis on the moving hand indicated a differential pattern of brain electrophysiological responses to tactile stimulation during movement: The preparatory and early execution phases exhibited a significantly enhanced electronegative activity as compared to the late execution and post-movement phases. One interpretation of these results is that the preparatory and early execution phases receive the highest attentional prioritization relative to the other later movement stages.

A decision on the true cause of this enhancement in electronegativity found in this experiment for the moving hand needs nevertheless first to consider the difference waves analysis. Since in the tactile ERPs were derived from stimulation delivered during the various phases of a goal-directed movement, by subtracting the movement-only activity from these and obtaining the DWs, one can discuss how tactile information is affected in a moving hand. When considering the DWs results, the previously found differences in the brain responses to tactile events for the various phases of the goal-directed movement did not reach significance. In fact, the only effect that survived the correction for multiple comparisons was that of electrode pair: The DWs analysis indicated a significantly less negative activity at posterior electrodes as compared to the more anterior tested sites. This effect could signal that even once the movement-related activity (i.e., the omission trials) has been discarded from the tactile data, some 'reminiscences of movement' are still detected in the frontal-central brain regions concerned with motor planning and execution.

To summarize, the results of this supplementary analysis that considered the moving hand only data (i.e., with a finer temporal tuning of the movement execution phase) demonstrated that the timing of tactile stimulation delivery did not affect the electrophysiological responses to tactile events. Such results point to the fact that in order to assess the mechanisms of tactile perception during goal-directed movement in man, one needs to consider both moving and resting effectors.

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Appendix A2

Supplementary material to Chapter 4

A2.0. Questionnaire used in Experiments 4.4-4.8

Age:

Sex:

Handedness:

Have you played any of these ball sports before?

- Basketball
- American football
- Baseball
- Cricket
- Rugby
- Volleyball
- Netball
- Handball
- Throwers (discus, javelin, shot put, hammer)

For how many years?

……

Were you part of an organized sports club? If yes, which kind?

……

If you played at university level, then which level was it?

……

Have you received any monetary benefits for playing sports (e.g., sports scholarships)?

……

Thank you! If you would like to have further info about the study please leave your e-mail address below:

Appendix A3

Summary of experiments presented in Chapters 2-4

Experiment	Movement task type	Perceptual task type	Tactile stimulus location	Trial sequence	Dependent variable(s)	Independent variable(s)	Outcomes
Experiment 2.1	Speeded reach-to-grasp movement	Non-speeded tactile discrimination	Ventral part of middle fingers of right and left hands	Prepare signal – go signal – end signal	Tactile discrimination thresholds	Timing of tactile stimulation delivery (preparation, start, execution, grasp, post-movement)	Significantly elevated thresholds (i.e., poorer performance) during movement execution.
Experiment 2.2	Speeded reach-to-grasp movement	Non-speeded tactile discrimination	Ventral part of middle fingers of right and left hands	Prepare signal – go signal – end signal	Tactile discrimination thresholds	Timing of tactile stimulation delivery (preparation, early-, mid-, and late-execution, post-movement)	Significantly elevated thresholds during movement execution. Comparable tactile attenuation for the right and left hands
Experiment 2.3	Rest	Non-speeded tactile discrimination	Ventral part of middle fingers of right and left hands	Start signal – end signal	Tactile discrimination thresholds	Left hand – Right hand time difference in stimulation (short, medium, long)	Significantly elevated thresholds for the shortest time interval (100 ms)
Experiment 2.4	Speeded reach-to-grasp movement Rest	Non-speeded tactile discrimination	Ventral part of left hand wrist and forearm	Prepare signal – go signal	Tactile discrimination thresholds	Condition (both hands at rest, right hand moving)	Comparable sensitivity measured at the left hand under conditions of both hands at rest and right hand moving
Experiment 2.5	Speeded reach-to-grasp movement	Non-speeded tactile discrimination	Ventral part of index fingers of right and left hands	Start signal – prepare & go signals – end signal	Tactile discrimination thresholds	Timing of tactile stimulation delivery (preparation-unknown hand, preparation-known hand, execution, stopped execution) Movement hand (left hand, right hand)	Significantly elevated thresholds during movement preparation and execution as compared to the stopped execution condition. Comparable tactile sensitivity between the two hands.

Experiment 2.6	Speeded reach-to-grasp movement	Speeded tactile detection	Ventral part of index fingers of right and left hands	Prepare & go signals	Tactile RTs	Probability of tactile stimulus (higher at resting hand, equal, higher at moving hand) Stimulated hand (moving, resting) Timing of tactile stimulation delivery (preparation, execution, post-movement) Movement hand (left hand, right hand)	Significantly faster RTs for higher probabilities of stimulation delivery to both resting and moving hand, as compared to the equal probability condition. Significantly slower RTs over the preparatory phase of the movement, as compared to preparation and post-movement phases.
Experiment 2.7	Speeded reach-to-grasp movement	Non-speeded tactile discrimination	Ventral part of middle fingers of right and left hands	Start signal – prepare & go signal – end signal	Tactile discrimination thresholds	Attention allocation time (short, medium, long)	Comparable sensitivity across short, medium, and long preparation periods of a reach-to-grasp movement.
Experiment 2.8	Speeded reach-to-grasp movement	Non-speeded tactile discrimination (TD) Non-speeded surface discrimination (SD)	Ventral part of right and left hands wrists Index, middle, ring, and little fingers fingertips	Experimenter's vocal instruction of trial start – go signal	Tactile discrimination thresholds Tactile accuracy	Condition (rest, active exploration, active reaching); Task type (TD at rest, TD at rest plus passive exploration, TD at rest plus passive reaching); Movement type (exploration, reaching) Movement type (exploration, reaching); Execution mode (passive, active); Task type (single, dual)	Significantly elevated thresholds during movement execution, as compared to rest. Significantly higher SD performance under conditions of active movement, single tasking, and under conditions of exploration, as compared to reaching.
Experiment 3.1	Speeded reach-to-grasp movement	None	Ventral part of index fingers of right and left hands	Prepare signal – go signal – end signal	Tactile & visual ERPs mean amplitudes	Hand (moving, resting) Timing of tactile stimulation (preparation, execution, post-movement) Hemisphere (contralateral, ipsilateral) Electrode pair (FC3/4, C3/4, CP3/4, P3/4)	Significantly enhanced tactile ERPs for the moving hand, as compared to the resting hand. Significantly enhanced tactile and visual ERPs while moving, as compared to the preparation and post-movement phases.
Experiment 4.1	3-ball juggling Rest	Non-speeded tactile gap detection	Ventral part of left hand wrist	Start signal – go signal – end signal	Tactile sensitivity (d') Response bias (c & c')	Timing of the temporal gap in tactile stimulation delivery (1000, 1500, 2000, 2500 ms) Type of hand movement (up, down) Session (juggling, rest)	No significant change in tactile sensitivity and response bias depending on the temporal location of the gap, or the type of hand movement. Sensitivity decrement while juggling as compared to rest.
Experiment 4.2	3-ball juggling Rest	Non-speeded auditory gap detection	Headphones	Start vibratory pulse – go pulse – end pulse	Auditory sensitivity (d') Response bias (c & c')	Timing of the temporal gap in auditory stimulation delivery (1000, 1500, 2000, 2500 ms) Type of hand movement (up, down) Session (juggling, rest)	No significant change in auditory sensitivity and response bias depending on the temporal location of the gap, or the type of hand movement. Sensitivity decrement at rest as compared to juggling.

Experiment 4.3	Rest	Non-speeded tactile & auditory gap detection tasks	Ventral part of left hand wrist	Start signal – go signal – end signal	Tactile sensitivity (d') Response bias (c & c')	Gap duration (20, 40, 60 ms) Condition (auditory, tactile, tactile-ball interference)	Comparable tactile sensitivity and response bias across gap durations. Sensitivity decrement in the tactile-ball interference condition.
Experiment 4.4	Ball-catching movement	Speeded tactile detection task	Ventral part of left hand wrist	Go signal (for the experimenter)	Tactile RTs	Timing of tactile stimulation delivery (preparation, execution, catch) Expertise (novices, intermediate, experts)	Faster tactile RTs while executing the movement, as compared to preparing and catching the ball. Novices slower than both intermediate and expert athletes; no difference in speed of responding between intermediate and expert groups.
Experiment 4.5	Ball-catching movement	Speeded auditory detection task	Headphones	Go vibratory pulse (for the experimenter)	Auditory RTs	Timing of tactile stimulation delivery (preparation, execution, catch)	Faster auditory RTs while executing the movement, as compared to preparing and catching the ball.
Experiment 4.6	Rest	Speeded tactile detection task	Ventral part of left hand wrist	Start signal	Tactile RTs	Timing of tactile stimulation delivery (time 1, time 2, time 3)	Comparable RTs across the three timings of stimulation delivery in the absence of movement.
Experiment 4.7	Ball-throwing movement	Speeded tactile detection task	Ventral part of left hand wrist	Prepare – go signal	Tactile RTs	Timing of tactile stimulation delivery (preparation, execution, throw)	Slower tactile RTs while preparing the ball-throwing movement, as compared to the executio period; no difference in RTs between execution and throw periods.
Experiment 4.8	Ball-catching Ball-throwing Rest	Non-speeded tactile gap detection	Ventral part of right hand wrist	Start signal – go signal	Tactile sensitivity (d') Response bias (c & c')	Condition (rest, catch, throw) Timing of tactile stimulation delivery (preparation, execution, catch)	Significant decrement in tactile sensitivity while executing the movements, as compared to rest. Significant decrement in tactile sensitivity while preparing the ball-throw, as compared to rest and ball-catching preparation conditions. Criterion shift in the preparation period of externally-initiated movements, as compared to rest.