THE ANIMATE - INANIMATE DISTINCTION IN VISUOMOTOR COORDINATION

PERCEPTUOMOTOR CROSSTALK IN THE PRESENCE AND ABSENCE OF BIOLOGICAL TOPOGRAPHY AND BIOLOGICAL KINEMATICS

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zur Erlangung des akademischen Grades

Doktor der Philosophie
– Dr. phil. –

genehmigte Dissertation

Berichter: Prof. Dr. Herbert Heuer
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Tag der wissenschaftlichen Aussprache: 16.10.2009

Dortmund 2009

To my parents, Elisabeth & Anton,

To my grandmother, Regina,

To the most wonderful human being, my wife Rebecca,

I gratefully dedicate this thesis.

I would like to thank my advisor Professor Herbert Heuer for his continuous support, and for all the time, effort and thought he invested in my training. I enjoyed every brain storming session we had together and look forward to many more to come.
Thanks to Professor Klaus Roth and Professor Wilfried Kunde for reading this gathering of thoughts and data, and for being so kind about it.
I would like to express my gratitude to the Deutsche Forschungsgemeinschaft for funding my PhD-position within the Priority Program 1184 ”Age-Differentiated Working Systems”.
I would also like to thank all my colleagues and former student research assistants at the Leibniz Research Centre for Working Environment and Human Factors in Dortmund for their support of this work. They are, in no particular order, Sandra Sülzenbrück, Katrin Rapp, Marietta Widynski, Rainer Flöring, Felix Klimmer, Petra Wallmeyer, Jan Delkus, Steven Li, Alexander Fölling, Torsten Klar, Marc Hülsey, Vanessa Schmidt, Helen Schneider and of course Barbara Herbst.

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Chapter 1

Introduction: Sensorimotor Simulation and Cognition

The present study is concerned with the impact of perceived animacy of a stimulus on processes of visuomotor coordination. More specifically, the study aims to investigate the relative impact of static and dynamic stimulus features, which indicate its animacy, on perceptuomotor crosstalk between simultaneous movement observation and execution. Since the present study is limited to the comparison of movements by an object and by a human model, the first part of this introduction is dedicated to the human body and how its understanding has been in constant change in Western thought. The acknowledgement of our bodily existence, it is argued then, gave rise to a whole new way of dealing with purely mental phenomena. Central to this new perspective of embodied cognition is the idea of sensorimotor simulation, which is introduced in the subsequent section.

1.1 A Short Intellectual History of the Body

In the classic view of Aristotle and Plato, the living human was conceived as something *in the world*, by virtue of its body, a thing among other things. Only by the strength of its mind could the human being transcend its existence in the midst of other things and gain access to the ordering unity of the world[1]. In the resulting conflict between a man's mind and his body, to reach this ideal, of course, meant to subdue rather than meet the claims of the body. The body was a hindrance, for the striving mind an object among others, which had to be put aside in an effort to "become pure thought thinking itself beyond the primum mobile" (Todes, 2001).

The body was worthless.

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[1] The unity of the world refers to the ontological belief that there is only one actual world and everything that one can think of is in terms of this one and only world (cf. Todes, 2001).

With Descartes came the discovery of human necessity. From his famous *cogito* argument, which showed that even the effort to dispose of individual human existence presupposes the latter, he deduced that the essence of human existence was to think and that this thinking substance was entirely distinct from the body and would not cease to be what it was even if the body did not exist. Thus, the first consequence of Cartesian philosophy for the body was that it was no longer fixed firmly among other things *in the world*, but denied any essential significance for human existence altogether.

The body was gone[2].

The ambiguous status of the human subject in Cartesian philosophy as being placed somewhere above the things in the world, but below identification with the ordering unity of the world, gave rise to two diverging schools of thought, Continental Rationalism and British Empiricism, culminating in the respective work by Leibniz and Hume. For Leibniz, the rationalist, man's personal identity was given by his unified experience of a godly-created ordered world and no experiential content was special in a sense that it had a privileged relation to this identity. The internal horizon of the monads,which built the body, represented the whole world in its prestabilized harmony, but the way the human subject experienced having his body was no different from the way he experienced being in possession of other things. For Hume, the empiricist, the human subject was a passive spectator detached from his body and reduced to a disembodied point of view. Sensations from the world merely stroke upon him, leaving their trace in his explication of the unity of the world. The body was just an experiential object, a passive receiver of sensations that were perceived by a disembodied spectator.

The body was a thing among things.

Kant combined the rationalist's belief of indubitable truths with the empiricist's idea of factual sense experience in arguing that intelligible sense experience was not immediately given to a Leibnizian monad, but had to be transformed from mere sensation into intelligible conceptual content, leaving no room for veridical sensory appearances apart from the employment of abstract concepts. Though Kant recognized the special status of the body as being the sole source of sense experience to a point at which no mental

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[2] ..., which is not completely correct since Descartes actually did not postulate a dualism but a trialism in that he posited the existence of a third substance in terms of the empirical unity of body and soul. However, he failed to provide a reasonable account of how this third substance integrated into his philosophical system.

activity could be conceived without involvement of the body, all bodily experiences were subject to conceptual judgement.

The body was a concept.

The phenomenology of Merleau-Ponty marked the return to the world which precedes, abandoning the empiricist's objects, which were forced upon a disembodied perceiver, and the rationalist's objects, which were mere constructions of an all-knowing mind. Instead, objects were experienced as actual revelations to our body by our senses, being unintelligible without reference to the fundamental bodily activities that seek, solicit, and maintain their presence. It is the lived, active body that finally provides the unity of the world in that it is the one and only actual world that can be experienced by the subject-body.

The body is being in the world.

1.2 The Idea of Sensorimotor Simulation

During the last 20 years, there has been an ever increasing interest in the complex interaction of the physical body and the surrounding environment within virtually all the branches of cognitive science, e.g. psychology (e.g. Turvey, 2004; Turvey & Carello, 1995; Wilson, 2002), philosophy (e.g. Clark, 1997; Lakoff & Johnson, 1999; Varela, Thompson, & Rosch, 1991), robotics (e.g. Arkin, 1998; Brooks & Stein, 1994; Brooks, Breazeal, Marjanovic, Scasselati, & Williamson, 1998; Lund, Webb, & Hallam, 1998), neuroscience (e.g. Chiel & Beer, 1997; Grafton, 2009), and linguistics (e.g. Boroditsky & Ramscar, 2002; Lakoff & Johnson, 1999). Within the emerging view of what had been termed as *embodied cognition*, discontent was voiced about the fact that traditional cognitive science had only a limited conception of the mind as a central processor of abstract information without giving proper regard to its connections to the outside world (cf. Clark, 1998). While perceptual and motor systems were conceived to be proper areas of scientific inquiry, their relevance for cognition was simply disregarded in that thought was treated separately from perception and action. In contrast to this predominant point of view, there had always been demonstrations of interactions between cognitive and sensorimotor processes.

Paillard (1955), for instance, had participants perform a mental multiplication task and used simultaneously evoked Achilles tendon (T) and Hoffmann (H) reflexes to distinguish activation of the alpha motoneuron and the gamma motoneuron system during mental calculation. He found an increase of the T-reflex amplitudes while participants were performing covert multiplications, but no changes in the H-reflex. He interpreted this as an increased activation of the fusimotor system based on a changed sensitivity of muscle spindles, presumably originating within the brainstem, where the reticular formation (Granit & Kaada, 1952; Eldred & Fujimori, 1958) and the red nucleus (Appelberg & Jeneskog, 1972) were shown to exert a facillatory influence on the gamma motor neuron system. While this finding could be regarded as a rather unspecific effect of general arousal on fusimotor functioning, Davis (1939) demonstrated more specific effects of mental arithmetics on sensorimotor behaviour. He had participants covertly perform various psychological tasks and simultaneously measured their electromyographic responses. The analysis of the EMG recordings revealed that each task was associated with a specific pattern of muscular activity, such that performing mental calculations elicited electromyographic gradients in the right forearm extensor muscles of right-handers. More recent neurophysiological studies reported an increase in regional blood flow in the prefrontal and parieto-temporal association cortices (e.g. Roland & Friberg, 1985), but also in the cerebellar hemisphere (Decety, Sjoeholm, Ryding, Stenberg, & Ingvar, 1990; Ryding, Decety, Sjoeholm, Stenberg, & Ingvar, 1993) while subjects were engaged in arithmetical counting. Modern-day research on the neuronal basis of mental arithmetics implied that the posterior part of the cerebellar cortex belonged to a motor finger representation network, together with the left precentral gyrus, the anterior part of the intraparietal sulcus and the right superior occipital gyrus, which is assumed to underlie numerical knowledge (Zago et al., 2001). The idea of a covert use of finger representations, at least for simple arithmetic tasks such as arithmetic fact retrieval (Zago et al., 2001) suggests that humans might actually think *embodiedly*, i.e. that mental phenomena cannot be conceived without sensorimotor processes that control bodily movement. As a consequence, theoretical models that assign purely motor functions to brain areas such as the cerebellum are unreasonably narrow. Instead, it seems more plausible to assume an elaborate information-processing system, which controls movement but is also bidirectionally connected with parallel systems that subserve ”pure” cognitive functions such as reasoning, language, and emotion (cf. Leiner, Leiner, & Dow, 1993). Accordingly, Ito (1993) suggested that ideas and concepts could in principle be manipulated in the same way as limbs are manipulated in the course of movement execution, and, as a consequence, that thought and movement do not differ in terms of being a controlled object. Once encoded in the brain, they could both be controlled via the same neuronal circuitry, giving rise to the formation of internal models of body dynamics, but also of the dynamics of mental representations in the microstructures of the cerebellum (cf. Ito, 2008).

The idea that *offline*-cognition, i.e. cognitive processes that are detached from current sensory input and motor output, was based on a sensorimotor representation of the body, opened up a new perspective on the cognitive strategies employed by the human agent. Many abstract cognitive abilities might actually employ sensorimotor functions in the way described above. Mental structures that especially developed to subserve perception and action execution might be adopted to augment cognitive processes, giving rise to the idea that sensorimotor resources could be used to run a simulation of particular aspects of the physical world as means of representing information or drawing inferences (e.g. Grush, 1995, 2004; Jeannerod, 2001, 2006). Sensorimotor simulation has indeed been found to be crucial for many functions in human *offline*-cognition such as mental imagery (e.g. Grush, 2004; Kosslyn, Pascual-Leone, Felician, & Camposano, 1999; Jeannerod, 2004), working memory (e.g Wilson, 2001b), and reasoning (e.g. Damasio, 1994).

There is no a priori reason why sensorimotor simulations should be limited to *offline*-cognition and indeed, many theories exist that conceive such simulation processes as the basis for *online* cognitive functions, i.e. cognitive processes that continuously receive input from the senses or generate control signals to move the body in the environment, such as visual discrimination (e.g. Miall et al., 1996; Zwickel, Grosjean, & Prinz, 2007), language comprehension (e.g. Gallese, 2005; Glenberg & Kaschak, 2002; Rizzolatti & Arbib, 1998), action understanding (e.g. Blakemore & Decety, 2001; Jackson & Decety, 2004; Jeannerod, 2001), or the coordination of joint action (e.g. Sebanz, Bekkering, & Knoblich, 2006).

Consequently, based on the idea that particular aspects of *online*- as well as *offline*-cognition are based on a covert simulation of bodily actions, i.e. that simulation is *embodied*, the core theoretical contribution of embodiment to cognition as conceived in this study refers to the existence of a representational system that specifically encodes knowledge of man's bodily existence along with the body's functional capabilities in interacting with the world (for a systematic review of additional postulates of embodied cognition, see Wilson, 2002). Such a representational system is necessarily required as a knowledge base from which sensorimotor simulation can be used to augment the kinds of processes mentioned above (cf. Grafton, 2009).

The existence of such a specific knowledge system dedicated to the representation of the embodied existence of animate agents implicates that the perception of animate agents, especially that of conspecifics, constitutes a special event in the perception of objects in the environment radically different from the perception of inanimate objects. This assumption is supported by two naive notions, that of relevance and that of expertise (cf. Wilson, 2001a). On the one hand, bodies might comprise a special status due to the high evolutionary relevance of processing bodily stimuli. Global form and surface features that indicate animacy of an object, i.e. structural cues such as the availability of parts with biological functions (limbs), or biologically relevant surface textures (hair, faces), might have evolved to automatically attract a perceiver's attention since these features represent the conduits of social interaction. On the other hand, humans by virtue of having a body of themselves possess a high degree of expertise in controlling bodily movements. This expertise can be used to facilitate perception of other bodies by directly matching perceived dynamic information, i.e. kinematic cues such as motion onsets, motion trajectories or velocity profiles, to the configuration and movements of one's own body. Such a kinematic isomorphism based on the biomechanical properties of the body and the physical laws governing its interactions with the world makes it reasonable to assume that coordinated interactions with animate stimuli are achieved in a qualitatively different way than interactions with inanimate objects, which is due to the privileged perceptual status of the former.

The aim of the present study was to elucidate the relative impact of the presence of a human body and the presence of biological kinematics on visuomotor coordination. More specifically, it was examined whether the presence of those two features particularly affects perceptuomotor crosstalk, which is normally observed when perception and action planning/execution rely on a representational system that is responsible for actual movement execution as well as sensorimotor simulation.

1.3 THESIS OUTLINE

The idea that animate and inanimate objects are processed differently by the cognitive system on a quite fundamental level is explored in **chapter 2** with an excursion that depicts behavioural consequences of the animate/inanimate distinction in infancy along with its developmental origins, demonstrating that sensorimotor simulation plays a crucial role in this development. Infants' perceptions are ideally suited to provide insights into how objects in the world are treated differently according to their animacy because they are not yet overformed by internalized constraints based on cultural learning. The chapter ends with the conjecture that an infant's intuitive conception of animacy is based on a process of sensorimotor simulation, which matches observed object motion to the motor properties of the perceiving infant.

Assuming that sensorimotor simulation is the basis for the distinction between animate and inanimate objects, the focus of **chapter 3** is on the neural substrates of sensorimotor simulation. The discovery of mirror neurons in various parts of the monkey brain is discussed, followed by an analysis of a functionally similar system in the human brain, which is referred to as the action-observation-execution-matching system. This denomination was chosen in order to account for the present uncertainty of whether mirror neurons also exist in the human brain and furthermore to express a functional characterization of such a network instead of a mere anatomical reference to the presence of mirror neurons.

Having established the biological reality of a representational system that maps observed actions to executable actions on the part of the observer, and thereby providing the necessary representational basis for sensorimotor simulation, **chapter 4** explores the organization of this action-observation-execution-matching system in terms of specialization of different subsystems, which are related in a hierarchical fashion. Then, a computational model of sensorimotor control is described (MOSAIC Wolpert & Kawato, 1998; Haruno, Wolpert, & Kawato, 2001; Wolpert, Doya, & Kawato, 2003), in which the concept of internal models is introduced. It is proposed that internal models are useful to relate the subsystems within the action-observation-execution matching system to form a sensorimotor simulation loop.

In **chapter 5** reviews empirical evidence in order to characterize the *modus operandi* of the action-observation-execution-matching system with respect to interactions between perception and action, referred to as perceptuomotor crosstalk. Different varieties of perceptuomotor crosstalk are introduced, assimilation and contrast. A theoretical account of perceptuomotor crosstalk, the Theory of Event Coding (Hommel, Müsseler, Aschersleben, & Prinz, 2001), is outlined, which is going to provide the necessary vocabulary to discuss perceptuomotor crosstalk in the following experiments.

In **chapter 6**, the initially described idea of the animate-inanimate distinction is picked up in order to re-review the literature on perceptuomotor crosstalk, but with special regard to the sensitivity of the action-observation-execution-matching system to the animate-inanimate distinction. This leads to the central question of this study of how the presence of a human body and biological kinematics affect perceptuomotor crosstalk within the action-observation-execution-matching-system.

Chapters 7-11 constitute the empirical part of the thesis. After introducing general aspects of the study such as purpose, task, and paradigm, four experiments dealing with individuals' visuomotor coordination performance with regard to animate and inanimate stimuli are described. Experiment 1 investigates perceptuomotor crosstalk during response selection and movement execution in the presence of and absence of perceptual cues indicating animacy within an observed action. Experiment 2 focuses on the nature of the perceptuomotor crosstalk observed in Experiment 1 and the effects of different visuomotor mappings. Experiment 3 explores the interaction of different frames of reference for the observed perceptuomotor crosstalk. Finally, Experiment 4 aims to elucidate the generalizability of the effects found in the first three experiments to the execution of a more complex movement.

Chapter 12 closes the thesis with a general discussion of its empirical findings. Initially, the central findings of the four experiments of this thesis are reviewed. The subsequent discussion centres around the impact of animacy on perceptuomotor crosstalk and touches upon some particularities of the observed effects.

CHAPTER 2

SENSORIMOTOR SIMULATION AND THE ANIMATE-INANIMATE DISTINCTION IN INFANCY

The capacity to categorize things in one's environment as animate beings or as inanimate objects is a fundamental cognitive ability, which develops early in life and presumably corresponds to a domain-specific knowledge system that is subserved by distinct neural mechanisms (Caramazza & Shelton, 1998; Mahon & Caramazza, 2009). With respect to the development of such conceptual knowledge, the ability of infants to discriminate people and objects has been the focus of much research because the person-object differentiation as established during the first two years of life can be conceived as a precursor for the broader distinction between animate and inanimate entities, which in turn has been proposed to form the basis of the more inclusive biological-nonbiological distinction (cf. Poulin-Dubois, Lepage, & Ferland, 1996).

Infants are naive to the world. Neither do they come fully equipped with semantic knowledge about the ways of the world nor do they possess a sophisticated episodic memory system yet. Thus, studying infants can inform us about how animate and inanimate entities are distinguished without reference to interindividual differences in the beliefs regarding the essential properties of biological entities.

It has been shown that in later stages of development, conceptual knowledge can be detached from the domain in which it developed. Thus, features that have been associated with animate objects can transcend the animate-inanimate distinction, for example in ascribing psychological constructs as desires and intentions to the motion of geometrical shapes (Heider, 1944; Heider & Simmel, 1944) or other inanimate entities such as clouds (cf. Piaget, 1976). However, it is assumed that at the initial stages of development, the differential behaviour that is organized along the animate-inanimate distinction is still limited to the domain in which it developed, and thus reflects an intuitive understanding of the concept of animacy. Therefore, the following overview of the role of animacy in infants' interaction with persons and inanimate objects is limited to the first two years of age.

2.1 DIFFERENTIAL RESPONDING TO ANIMATE AND INANIMATE OBJECTS

Infants quickly become sensitive to differences between persons and inanimate objects. Already newborns between two and six days of age show differential patterns of motor responses to people versus objects. Roennqvist and von Hofsten (1994) compared newborns' motor behaviour in the presence of an animate human agent with motor responses to the presentation of an inanimate object. They reported that the observation of a human actor led to an overall increase in finger movement frequency, which was found to be especially pronounced for transitional opening and closing movements of the hands. The presentation of a ball, which triggered only half as many movements, elicited mainly thumb-index finger activity and forward extensions of the arm, movements that had previously been described to be common in the preparation of reaching and grasping (cf. van Hofsten, 1984). It should be noted that these movements do not possess a manipulative function at this age. It is not until around nine months of age that infants start to use the pincer grip to pick up small objects (cf. van Hofsten & Roennqvist, 1988). Since the experiments conducted by Roennqvist and von Hofsten (1994) controlled for unspecific effects of arousal in response to animate and inanimate objects, it seems reasonable to infer that animacy might indeed trigger specific modes of interaction, a social mode for animate and an object mode for inanimate entities (cf. Trevarthen, 1986).

At two months of age, infants have further refined and extended their behavioural repertoire in response to animate and inanimate objects. They attend to persons with eye contact, vocalizations, and social gestures such as pointing, whereas they greet an inanimate object with incipient manipulatory actions such as grasping, showing only little or no communicative behaviour (Brazelton, Koslowski, & Main, 1974; Ellsworth, Muir, & Hains, 1993; Legerstee, Corter, & Kienapple, 1990; Trevarthen, 1977). With respect to communicative actions, Legerstee, Pomerleau, Malcuit, and Feider (1987), for instance, showed that upon presentation of a communicative adult, babies smiled, vocalized and exhibited complex gaze patterns, whereas they continuously fixated inanimate, but responsive objects and engaged in increased arm activity. Furthermore, when being confronted with an unresponsive, still-faced adult, those infants showed signs of distress, which were not found in response to other familiar static objects. However, these pattern of findings is not unequivocally replicated so that, as is the case in many studies dealing with participants at this age, the reliability of those findings is subject to debate (Frye, Rawling, Moore, & Myers, 1983; Sylvester-Bradley, 1985).

With respect to manual actions, it has been shown that two-month-olds produced hand and arm actions in relation to affective states, gaze behaviour and vocalizations (Fogel & Hannan, 1985). Legerstee et al. (1990) demonstrated that these sequential behavioural linkages were differentially organized for animate and inanimate stimuli. They found pointing to be associated with gazing, smiling and vocalization. This was specific for the presence of the communicating mother. To a passive mother, infants responded with closed hands, averted gaze, and distressed facial expressions. A passive doll, on the other hand, led to the co-occurrence of gazing, arm extension, and hand opening, presumably a developmental step towards reaching and grasping in order to explore objects that are currently at the centre of fixation.

Further support for the contention of differential responding of infants towards animate and inanimate objects comes from studies on babies' exploratory behaviour. As infants master independent locomotion, they begin to actively explore their surroundings. In a study by Eckerman and Rheingold (1974) ten-month-old infants viewed either a novel toy or an unfamiliar person. Infants chose to approach and make contact with the toy, but remained at a distance from the person, showing elevated frequencies of regard and smiling, even more so when the person talked and smiled back. Thus, exploratory behaviour also includes social and non-social components, which are activated with respect to the status of animacy of its target. The same pattern of results was found in a study by Poulin-Dubois et al. (1996). Nine-month-olds were found to approach and manipulate a robot, but refrained from approaching a present stranger, again showing increased frequencies of communicative behaviour (smiling, vocalization) toward the unfamiliar person. As a sidenote, it seems as if infants also distinguish between animals and persons in that they show sustained attention towards animals (as compared to inanimate objects), but reserve social behaviour such as smiling and vocalization for people (Ricard & Allard, 1993).

2.2 DIFFERENTIAL REASONING ABOUT ANIMATE AND INANIMATE OBJECTS

At six to seven months of age, infants begin to understand that events unfold in a world where things have to make sense according to certain general principles. Using preferred looking methods[1], it was shown that with respect to inanimate objects, infants knowledge apparently comprises three principles

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[1] The most common paradigm is the habituation-dishabituation of looking technique. Here, infants are repeatedly confronted with a stimulus until the infant begins to lose interest in the stimulus as indicated by the length of succeeding unbroken looks. After this, various slightly modified versions of the stimulus are presented and any renewed interest can be identified based on a comparison with an unchanged baseline stimulus.

that constrain their understanding of object motion.

The principle of cohesion refers to the fact that an object is a separate entity with clear boundaries of its extension, i.e., it does neither disperse into several subparts nor merge with other objects in the course of movement. According to the principle of continuity, objects follow a path of motion that is continuous and does not lead to the occupation of the same spatial location by two different objects at the same time (e.g. Baillargeon, 1986; Spelke, Breinlinger, Macomber, & Jacobson, 1992). Finally, the principle of contact asserts that objects interact only if they come in direct contact with each other (Ball, 1973; Leslie, 1988; Oakes & Cohen, 1995). Despite different methods and stimuli, the convergence of empirical findings corroborate the validity of these principles, thereby supporting the existence of a central system in infant cognition that applies inviolable principles to maintain a model of the world by means of a conceptual identification of sensory input (cf. Leslie, 1988).

However, studies that examined the generality of those principles showed that infants apparently form different expectations about how animate and inanimate entities behave in the world. While the first two principles, cohesion and continuity, seem to apply to the motions of all material objects, the principle of contact does not necessarily apply to human actions. Consequently, it was shown that six-to-seven-month-olds represent successive motions of two inanimate objects as causally related only if those two objects come in direct contact with each other (Ball, 1973; Leslie, 1988; Oakes & Cohen, 1995). A similar causal link is represented for the interaction of animate agents without contact as indicated by longer looking times for a no-contact-event involving inanimate objects as compared to people (Spelke, Phillips, & Woodward, 1995; Woodward, Phillips, & Spelke, 1993). Thus, infants do not apply the principle of contact to people, which apparently supports the assertion that infants reason differently about animate and inanimate entities.

Straightforward support for a development of differential reasoning during the first six months also comes from a recent study by Molina, Walle, Condry, and Spelke (2004), who assessed preferential looking behaviour in four-to-six-month-old infants and experimentally varied the naturalness of observed person-person and person-object interactions. They found that only the six-month-old infants unequivocally preferred to look at videotaped events of a person speaking to another person and a person manipulating an object in contrast to the complementary conditions of person-person-manipulation and person-object-communication. Apparently, six-month-old infants understand that communicative actions such as smiling and talking are more naturally directed to a conspecific, whereas grasping and manipulating are more naturally associated with inanimate objects (cf. Molina et al., 2004). This shows that the animate-inanimate distinction in infancy is a meaningful distinction, which provides a basis for evaluating the interactions that are appropriate for entities in each category.

Further evidence for differential reasoning was presented by Carlson-Luden (1979), who showed that ten-month-old infants learned to move an object by pushing a lever, but did not learn to make a human model wave and smile via the same action, as well as by Poulin-Dubois et al. (1996), who exposed nine-to-twelve-month-old infants to an independently moving radio-controlled robot. The latter study found that infants in both age groups considered autonomous motion, no matter if it was self-propelled or remotely controlled via verbal commands by the infant's mother, to be anomalous in an inanimate object as indicated by increased negative affect and attentive behaviour towards the moving robot.

2.3 Differential Understanding of Animate and Inanimate Objects

Between 14 and 18 months of age, another step in development that is apparently sensitive to the animate-inanimate distinction takes place. Infants demonstrate that they conceive other people as agents that possess mental states such as goals, intentions, and desires. Until now, the infants' concept of animacy seemed to be limited to a negative notion of what inanimate objects *could not* do. However, at this stage, infants have apparently developed a positive understanding of human action, i.e., an appreciation of what animate agents *can* do.

Older infants' understanding of intentional action has preferentially been studied in imitation tasks, in which infants observed demonstrations of accidental actions (e.g. Carpenter, Akhtar, & Tomasello, 1998; Tilden, Poulin, & Desroches, 1997; Tomasello & Barton, 1994) or actions, whose intended outcome had not been achieved (unfulfilled intentions; e.g. Johnson, Booth, & O'Hearn, 2001; Meltzoff & Moore, 1995). In support of a positive understanding of others' actions, Carpenter et al. (1998) showed that 14-to-18-month-olds were able to discriminate between action outcomes that had been produced intentionally and action outcomes that had been produced accidentally in that they subsequently imitated only observed purposive motor acts but not accidental ones. Furthermore, Tilden et al. (1997) described that infants used inferences about an actor's desires to subsequently evaluate his or her action with respect to the inferred mental state. With respect to unfulfilled intentions, Meltzoff and Moore (1995) reported that 18-month-old infants were able to perform a motor act that they had never seen realised in response to the repeated observation of a failed attempt to complete the respective action by a human model. Most interestingly in the present context was their finding that when infants were confronted with a mechanical device that also failed to perform the same action, they also failed to produce the target action. Meltzoff and Moore (1995) concluded that while infants were apparently able to code observed actions in terms of their goals, they did so with respect to the animacy of the agent, i.e. ascribing goals to persons, but not to inanimate objects.

2.4 SIMULATION AS A BASIS FOR THE ANIMATE-INANIMATE DISTINCTION

With respect to theoretical perspectives on the emergence of conceptual understanding of animacy in infants, the debate has centred around the controversy between nativist accounts versus empiricist accounts. While the former emphasize the importance of innate domain-specific knowledge systems that constrain learning in a top-down fashion, the latter highlight the contribution of early perceptual processes and low-level associative learning mechanisms for the development of the animate-inanimate distinction.

Even though they differ with respect to domain-specificity, both theoretical approaches emphasize features of object motion as crucial for the development of the animate-inanimate distinction. Indeed, motion is an effective visual stimulus for capturing infants' attention (e.g. Girelli & Luck, 1997) and moving stimuli are furthermore preferably attended to as compared to stationary stimuli (e.g. Burnham, 1987; Shaddy & Colombo, 2004; Slater, 1989). Premack (1990), for instance, argued that newborns were innately sensitive to the distinction between self-propelled and non-self-propelled motion, i.e. state changes without assistance from other objects versus state changes because of another object's intervention under conditions of spatial and temporal contiguity. According to his nativist theory of self-propelled objects, infants expected self-moving objects to engage in goal-directed actions, ultimately giving rise to the perception of intentionality for self-propelled and of causality for non-self-propelled motion. The attribution of intentionality based on the observation of self-propelled motion of an object designated this object as an animate entity, whereas the attribution of causality classified moving objects as inanimate. Premack (1990) argued that this process of attribution was not based on repeated experience but on proper stimulation of hard-wired neural circuits.

However, it seems implausible to assume that self-propelled motion is a sufficient condition for identifying an object as animate since this ”would flood our perceptual system with false positives” (Csibra, Gergely, Biro, Koos, & Brockbank, 1999). Accordingly, Mandler (1992) proposed an empirical account of conceptual development according to which young infants acquired *conceptual primitives* based on an innate analysis of the perceptual display. This analysis was conceived to capture abstract characteristics of objects' structure and motion properties. As a result, this gradual development endowed infants with the ability to distinguish animate from inanimate objects. Movement-related conceptual primitives were the primary source of this distinction. More specifically, Mandler (1992) posited three types of movement-related conceptual primitives, which together form the first concept of animacy: (a) motion onset (see above), (b) motion trajectory (linear vs. nonlinear), and, in accordance with the principle of contact, (c) contingency of motion (interaction over a distance vs. interaction via direct contact). It is important to note that only the process of analysis was conceived to be innate and that discrimination performance was based on repeated analyses of perceptual content.

Thus, regardless of their epistemological nature, theories of the animate-inanimate distinction in infancy have explicitly emphasized the role of object movement as a decisive factor for distinguishing between animate and inanimate entities.

However, the above mentioned theoretical approaches remain vague with respect to how motion cues came to be crucial in the first place. They have to resort to postulating innate mechanisms for specific perceptual features, but why those features are concerned with motion remains unexplained. One reason might be that infants are particularly sensitive to moving stimuli. This heightened sensitivity might result from the differential development of cortical and subcortical structures that control visual attention. While cortical control develops during the first several months, subcortical control is present from birth. Here, the superior colliculus receives massive input from the magnocellular visual pathway, which is highly sensitive to motion, and can thus bias subcortical control of visual attention towards moving stimuli (cf. Colombo, 2001). However, there still remains the question why evolution favoured faster development of neural pathways that are concerned with analyzing motion information from the environment.

Meltzoff and Decety (2003) provided an explanation for the importance of motion cues to distinguish animate from inanimate objects by postulating that motor imitation was the functional mechanism that was favoured by evolution and underlies the understanding of animacy in infancy. Animate beings, in this case conspecifics, were conceived to stand out in the perceptual array because they represented a distinct class of imitable stimuli, i.e., stimuli whose configurations and movements could be directly mapped on the infant's own bodily configurations and movements. Consequently, the identification of people was based on their ability to perform biomechanically possible body movements, which the infant could map onto his body scheme (Meltzoff & Moore, 1995; Meltzoff & Decety, 2003). Only movements that could be successfully matched were classified as a human act and became, for instance, endowed with goals. This matching process was thought to be based on what Meltzoff and Moore (1997) conceived to be a foundational body scheme, which provided an innate link between the perception and production of animate actions in terms of shared neural representations (cf. Meltzoff & Decety, 2003).

CHAPTER 3

NEURAL SUBSTRATES OF SENSORIMOTOR SIMULATION

The hypothesis that we are able to recognize and understand the actions of animate others in a privileged way by simulating their actions with our own motor system (e.g. Gallese, Keysers, & Rizzolatti, 2004; Jeannerod, 2004; Wolpert et al., 2003) implies the existence of a neural system that directly matches the visual representation of an observed movement to our own motor representation of the same action by covertly activating the motor programs necessary to perform the observed movement (Rizzolatti, Fogassi, & Gallese, 2001). The general idea is that the production and perception of actions are functionally connected by a system that predicts the expected sensorimotor consequences of one's own and of others' actions relying on common neural networks in the premotor and parietal cortices, which match observed and executed actions within a common representational format. In this chapter, the neural underpinnings of such a matching system are reviewed, starting with the so-called mirror neurons found in the monkey brain and proceeding towards evidence for the existence of a functionally similar action-observation-execution-matching system in the human brain.

3.1 NEUROPHYSIOLOGICAL BASIS

Discoveries in neurophysiology made during the 1990s provided empirical support for concepts emphasizing the close interdependence of perception and action (e.g. Gibson, 1979; James, 1890; Lotze, 1852). Single neuron recordings in area F5 in the ventral premotor cortex of behaving monkeys showed that neurons in this part of the monkey brain specifically code goal-directed motor acts such as grasping, holding, or other object-related motor actions (Rizzolatti et al., 1988). Furthermore, these neurons were found to be highly selective for both the type of action and the specific movement configuration. This indicates that F5 neurons can code movements in abstract terms, such as the goal of a motor act regardless of its endeffector, (Rizzolatti et al., 1988; Fadiga, Fogassi, Gallese, & Rizzolatti, 2000), but can also encode the specific way in which a given goal could be accomplished (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995).

Besides the majority of pure motor neurons in F5, there is a subpopulation of about 20 percent that shares the motor properties of the former, but also responds vigourously to specific visual stimuli. According to the visual stimuli effective for triggering activity of those neurons, two completely different categories of visuomotor neurons are distinguished.

Neurons of the first category respond to the observation of three-dimensional objects whose size and shape are congruent with the motor act coded by the neuron. Those neurons were termed canonical F5 neurons (Rizzolatti et al., 1988; Rizzolatti & Arbib, 1998). For example, canonical grasping neurons were found to be active during a precision grip, but also responded to small objects, whereas neurons that encoded a whole-hand grip also responded to large objects in the absence of any detectable movement (e.g. Jeannerod et al., 1995; Murata et al., 1997; Rizzolatti et al., 1988).

A second category of visuomotor neurons in area F5 was described to respond to the observation of actions performed by another individual as long as those actions were similar to the motor act coded by the neuron. Based on this congruency between motorically coded action and observed actions that evoke the visual discharge, those neurons were named mirror neurons (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996).

The essence of both types of neurons is the transformation of specific sensory information into a motor format. Accordingly, it has been proposed that the visuomotor coupling in canonical neurons could be conceived as the neural substrate of the sensorimotor transformations necessary to adapt the hand to a given object, neurally implementing Gibson's concept of affordances (Gibson, 1979). This is especially plausible since a considerable percentage of canonical neurons shows increased activation during execution of a particular grip and in response to various objects that differed in shape, but all afforded the same grip type. The visuomotor coupling of mirror neurons, on the other hand, has been suggested to embody the basis of imitation and action understanding by neurally implementing a matching system that directly relates observed actions to their execution (e.g. Fadiga & Craighero, 2003).

3.2 The Parieto-Frontal Mirror Neuron System in Monkeys

Within the cytoarchitectonic organization of area F5 in the macaque monkey, canonical neurons are mainly found in the dorsal part of the posterior bank of the arcuate sulcus (area F5p), whereas mirror neurons are located within a sector lying on the cortical convexity (F5c; cf. Belmalih, 2008). A third sector (F5a) located ventrally from F5p also seems to contain neurons with mirror properties, although this is based on fMRI data instead of single-cell-recordings (Nelissen, Luppino, Vanduffel, Rizzolatti, & Orban, 2005). Interestingly, it has been suggested that neurons in F5a and F5c respond to observed motor acts in different ways. While F5c responds to an individual performing a motor act, F5a responds when just the relevant effector is visible, suggesting different representations of different degrees of specificity (Nelissen et al., 2005).

Another distinction between different types of mirror neurons has been drawn according to the degree of congruency between observed and executed actions that is necessary for neurons to respond. While *strictly congruent* mirror neurons are only active when observed and executed motor acts are identical in terms of goal and movement, *broadly congruent* neurons do not require action identity but similarity in that their activity is confined to the goal of an action (Gallese et al., 1996). The latter type of neuron is apparently, at least to some degree, able to recognize the goal of an observed action across many instances of its observed execution. This led to the assumption that mirror neurons in area F5 are functionally related to a network that is responsible for action recognition in that they place the individual in the same internal state as when the observed action was actually performed.

Consistent with this, Umiltà et al. (2001) found that a subset of mirror neurons discharged under conditions when the last, critical part of the observed action was occluded, so that the monkey was unable to observe the actual object manipulation. However, the monkey had to know that there was an object behind the occluder and see how the experimenter's hand moved behind the occluder. This indicates that if there is enough information to build a mental representation of the observed motor act, a subpopulation of mirror neurons can recognize the movement in terms of its outcome. By simulating the action, inferences about the goals of the observed behaviour of others can be drawn based on the activity of motor neurons that code the goal of the same action in the observer's brain.

Another subset of F5 mirror neurons has been shown to respond not only to visual observation or actual execution of a particular action, but also to auditory stimuli that are specifically associated with it. These so-called audiovisual mirror neurons discriminate, for instance, between the sound of breaking a peanut or ripping a piece of paper (Keysers et al., 2003; Kohler et al., 2002). This activation of premotor neural circuitry normally controlling the execution of an action by visual as well as auditory information related to the same action can be conceived as a further piece of evidence in support of the biological reality of action simulation (cf. Gallese, 2005).

Besides area F5 in the ventral premotor cortex, mirror neurons were also found in the inferior parietal lobule (Gallese, Fogassi, Fadiga, & Rizzolatti, 2002). Those parietal mirror neurons are characterized by the fact that they respond differently when the same motor act is part of different actions (e.g. grasp to eat versus grasp to place). This indicates that the parietal mirror system can encode the same motor act in different ways depending on the goal of the action in which the observed motor act is embedded (Fogassi et al., 2005). Because of this it has been suggested that mirror neurons within the inferior parietal lobule can not only infer action goals in terms of an action's outcome, a property commonly assigned to mirror neurons (cf. Gallese et al., 1996), but also facilitate the understanding of the intentions of others during action observation. By taking context and object type into account, an expected course of action based on mirror activity within the inferior parietal lobule is predicted, so that similar motor acts become discriminatable in terms of their anticipated action goal and the underlying intention of the actor.

The studies cited above all examined transitive actions, i.e. they employed experimental tasks that involved actions comprising object manipulation. The presence of manipulatable objects has been conceived to be a necessary requirement for the activation of mirror neurons (e.g. Press, Bird, Walsh, & Heyes, 2008; Umiltà et al., 2001). However, a small subset of mirror neurons in the most lateral part of F5, where mostly mouth-related mirror neurons can be found, were reported to discharge upon observation of intransitive, communicative facial actions such as lip-smacking or tongue-protrusion (*communicative mirror neurons*, Ferrari, Gallese, Rizzolatti, & Fogassi, 2003).

In order to fully characterize the mirror neuron system in the monkey brain, there is another region of the cortex comprising a population of neurons that is similar in function to mirror neurons and is thus closely related to the parieto-frontal mirror system. This population is predominantly located in the region of the superior temporal sulcus, especially in its lower bank. Both neuronal populations respond similarly to the observation of action in that they are able to generalize to different realizations of the same action, do not respond in the absence of a manipulatable object, and are also selective for biological effectors (e.g. Oram & Perrett, 1996; Perrett, Rolls, & Caan, 1982; Perrett et al., 1990). However, only mirror neurons also show movement-related activity, which is lacking in neurons within the superior temporal sulcus.

3.3 The Action-Observation-Execution-Matching System in Humans

Several studies using different methodologies have demonstrated that a matching system similar to the the mirror system found in monkeys also exists in humans. With respect to humans, the term *action-observation-execution-matching system* is used instead of the more common denomination *mirror system* in order to avoid the impression that the existence of mirror neurons in humans is a scientific fact. It is not. All assertions made below reflect the function of a neural network distributed across the brain and it has yet to be proven that mirror neurons are truly a part of it.

3.3.1 TMS

One of the first studies demonstrating mirror-neuron-like activation in humans was conducted by Fadiga, Fogassi, Pavesi, and Rizzolatti (1995). Using transcranial magnetic stimulation (TMS), they observed a significant increase in motor evoked potentials (MEPs) during action observation, which corresponded to the muscle activity recorded during actual movement execution. Further research showed that this facilitation effect originated on the cortical level (Strafella & Paus, 2000) but was counteracted on the spinal level (Baldissera, Cavallari, Craighero, & Fadiga, 2001). Thus, it appears as if action observation triggered a covert simulation process on the cortical level, whose overt execution was inhibited on the spinal level. Other important aspects of the human action-observation-execution-matching system demonstrated by TMS refer to the finding of increased cortical excitability, regardless of whether the observed movements were goal-directed actions or intransitive movements such as meaningless manual gestures (Fadiga et al., 1995; Maeda, Kleiner-Fisman, & Pascual-Leone, 2002), as well as the observation that motor cortical excitability followed the time course of the observed manual movements (Gangitano, Mottaghy, & Pascual-Leone, 2001). Furthermore, Urgesi, Moro, Candidi, and Aglioti (2006) have recently demonstrated that this increased corticospinal excitability can also be found when participants only view still photographs of hands positioned in a pincer grip as compared to pictures of hands in a resting position. This supports the notion that activation of the action-observation-execution system can be triggered by form cues in the absence of any kinematic information.

3.3.2 EEG

Additional support for the existence of a functional homologue of the monkey mirror system in humans was reported by Cochin, Barthelemy, Roux, and Martineau (1999), who employed quantified electroencephalography (qEEG). They had participants repeatedly perform or observe bimanual pincer movements of the thumb and index fingers and found that a specific suppression of the EEG mu-rhythm. The electroencephalographic mu-rhythm is usually found in the alpha frequency band over the sensorimotor cortex. It reaches maximal amplitudes when subjects are at rest and has previously been described as being particularly sensitive to sensorimotor events. Suppression of the resting mu-rhythm indicates that the underlying population of neurons has become desynchronized, which is conceived to reflect an increased processing load in these neurons (e.g. Kuhlmann, 1978; Pfurtscheller, 1989; Pfurtscheller, Neuper, Andrew, & Edlinger, 1997).

Muthukumaraswamy and colleagues subsequently reported that this suppression of the human mu-rhythm during action observation and execution exhibited mirror features that were similar to the findings in monkeys. In contrasting three different hand actions, mu-desynchronization occurred only when participants were observing another hand, which was engaged in a precision grip (as compared to a flat hand movement, cf. Muthukumaraswamy, Johnson, & McNair, 2004). While desynchronization was particularly pronounced when the grip action was directed towards an object, it was also found for the observation of intransitive actions, i.e. in the absence of a graspable object (cf. Muthukumaraswamy & Johnson, 2004).

The finding of desynchronization in response to intransitive actions suggests that the action-observation-execution-matching system in humans has apparently lost the object specificity, which was assumed to be a defining property of the monkey mirror system (cf. Press et al., 2008; Umiltà et al., 2001). Instead, a simpler, somatic matching mechanism has developed, by which movements can be directly mapped onto the observer's motor representations. Just as a speculative, phenomenological interlude, this might correspond to the development of self-consciousness that enables humans to regard their body parts as objects, i.e. to localize them with respect to a disembodied "I" that can, for instance, move an arm just like a stick with the only difference that the arm is miraculously moved by the "I". The detachment of mirror mechanisms from the presence of objects can also be conceived as a huge evolutionary success since it might afford the development of a sign-based language system and of course might, since vocal speech also consists of movements, be crucial for the development of vocal language as well.

Ulloa and Pineda (2007) further refined the pattern of findings by reporting that mu-suppression could also be found while individuals were viewing point-light displays of biological motion (kicks and jumping jacks) as compared to scrambled motion. They localized the effect to sources in the supplementary motor area (Cz) and the primary sensorimotor areas (C3, C4). Their results support the notion that activation of the action-observation-execution-matching system is sensitive to motion cues in the absence of any form cues.

Additional support for the existence of an action-observation-execution-matching system in the human brain comes from MEG experiments. Hari et al. (1998) used median nerve stimulation to quantify rhythmic neuromagnetic oscillations in a frequency range between 15 and 25 Hertz as an indicator for the state of activity of the precentral motor cortex. They found that the cortical rhythmical activity in the human primary motor cortex was strongly suppressed during movement execution, but also observed a significant decrease in activity during action observation, indicating a desynchronization and thus increased activation in the primary motor cortex during movement execution and movement observation.

3.3.3 Neuroimaging

In a recent review of neuroimaging studies, Grafton (2009) has concluded that the observation of another person performing an action engages a widespread, bilateral network of cortical brain regions including the bilateral posterior superior temporal sulcus, the inferior parietal lobule, the inferior frontal gyrus, and the dorsal and ventral premotor cortex. This distributed network for action observation overlapped strongly with areas associated with movement execution, in particular areas within the inferior frontal gyrus and the inferior parietal lobule. This overlapping area in the human cortex has been referred to as a somatotopically organized mirror neuron system (Rizzolatti & Craighero, 2004). However, at present it is unclear whether this designation is a functional or a truly anatomical one as no single-cell recordings from the human brain that unambiguously show the existence of mirror neurons in the human brain exist. Thus, a functional conception of the mirror neuron system as a distributed neural network that subserves both, perception and action, is the current state of the art.

With respect to specific properties of the action-observation-execution-matching system, neuroimaging studies found increased cerebral blood flow when participants observed intransitive mouth actions such as silent speech (Buccino et al., 2004), a finding corresponding to the report of communicative mirror neurons in the monkey (Ferrari et al., 2003). Furthermore, in support of the TMS findings by Urgesi et al. (2006), Johnson-Frey et al. (2003) also found activation of the frontal mirror region in conditions when individuals were viewing only static pictures of an object being grasped or touched by a hand. This indicates that the mere observation of an action goal is sufficient to activate the action-observation-execution-matching system.

3.3.4 Brain Lesions

The few existing lesion studies that allow inferences about the existence of an action-observation-execution-matching system in the human brain corroborate the findings from electrophysiological and neuroimaging studies. For instance, studies of patients with limb apraxia, who also showed impaired comprehension of observed gestures, point towards the existence of an anatomical overlap between the neural structures underlying production and comprehension of gestures (Ferro, Martins, Mariano, & Caldas, 1983; Heilman, Rothi, & Valenstein, 1982; Rothi, Heilman, & Watson, 1985). Efforts to pinpoint the crucial lesion side in these patients also implicated portions of the inferior frontal gyrus (the opercular and triangularis area; Buxbaum, Kyle, & Menon, 2005).

Artificial lesions induced by disrupting the activity in specific brain areas via TMS showed that disrupting activity within the inferior frontal gyrus impaired weight judgements (Pobric & Hamilton, 2006), whereas repeated TMS over the ventral premotor cortex slowed reaction times when observed actions had to be matched (Urgesi, Candidi, Ionta, & Aglioti, 2007).

3.4 Conclusion

Mirror neurons are found in various areas of the monkey brain, where they constitute a multitude of mirror mechanisms that are embedded within various neural networks in the brain. According to their location, those mirror (sub-) systems subserve different cognitive functions. The mirror system, which consists of parts of the inferior parietal lobule and the ventral premotor cortex, translates sensory representations of observed or heard movements into motor representations of the same movements, indicating an immediate, i.e. not cognitively mediated, understanding of sensorily registered motor behaviour (cf. Fabbri-Destro & Rizzolatti, 2008; Gallese, 2005). In addition, neurons within the superior temporal sulcus, which are particularly sensitive to actions performed by animate agents, are closely connected to the parieto-frontal mirror system. Converging findings from studies using a variety of experimental paradigms and methodologies support the existence of an action-observation-execution-matching system in the humans. This system can be conceived as a functional homologue of the mirror system described in the monkey brain.

Chapter 4

Organization of the Action-Observation-Execution-Matching-System

The neurophysiological studies reviewed in the preceding chapter support the notion that the brain comprises specialized neural circuits for matching observed actions to sensorimotor representations of the same action in the observer. Brain areas involved in this neural circuitry were identified within frontal, parietal, and temporal cortices. This network has been conceived to afford the internal simulation of observed actions in order to decode those actions and to assist in inferring or assigning mental states, such as desires, goals or beliefs to an observed actor. In this chapter, it is proposed that the action-observation-execution-matching system is hierarchically organized with different subsystems serving different functions.

4.1 Specialization and Hierarchy

A current prominent idea in cognitive neuroscience is that of a hierarchical organization of the action-observation-execution-matching system (e.g. Hamilton & Grafton, 2007; Kilner, Friston, & Frith, 2007; Kilner & Frith, 2008). Hierarchical organization as such is widely recognized in research on motor control (Keele, Cohen, & Ivry, 1990), perception (Friston & Stephan, 2007; Robertson & Lamb, 1991), executive functions (Dehaene & Changeux, 1997; Marcovitch & Zelazo, 2009) or imitation (Wohlschläger, Gattis, & Bekkering, 2003). With respect to the action-observation-execution-matching system, Hamilton and Grafton (2007), for instance, proposed three broad levels of description of an action: the goal level, which comprises action outcomes and behavioural goals; the kinematic level, which refers to the motion of body parts in space and time; and the muscle level, which describes patterns of muscle activity. These levels were conceived to be relatively independent of each other, but related in a hierarchical fashion.

In a series of fMRI experiments, the repression-suppression method was used to explore the possibility of such a representational hierarchy, which is associated with different levels of functional anatomy within the action-observation-execution network (Hamilton & Grafton, 2006, 2007, 2008). The repression-suppression method is based on the existence of population coding within brain regions (e.g. Georgopoulos, Schwartz, & Kettner, 1986) and the observation of a trialwise reduction in a population's response to repetitions of stimulus features that are encoded by this population (cf. Grill-Spector, Henson, & Martin, 2001).

In the first study (Hamilton & Grafton, 2006), participants observed grasping actions performed by a human actor, in which either the grasped object or the movement trajectory was repeated. A strong repetition-suppression effect showed up in the left anterior intraparietal sulcus when the same goal object was grasped repeatedly irrespective of the movement trajectory but not vice versa. This was taken to support the notion that the goal of another person's action, at least in terms of the object the person is reaching for, is encoded within a neural network in the anterior intraparietal sulcus independent of reach kinematics.

In a follow-up experiment, the type of grasp (precision versus power grip; Hamilton & Grafton, 2007) was varied in addition to the type of object and the trajectory of movement. The repetition of grasp type induced suppression effects in the lateral occipital cortex, which was conceived to provide a visual analysis of the observed grasp action, as well as in the inferior frontal gyrus, which was thought to provide a motor analysis of the observed action. This interpretation of the latter is in line with the involvement of the inferior frontal gyrus in judging the weight of a box lifted by another person (cf. Pobric & Hamilton, 2006). This task has been shown to require the interpretation of movement kinematics rather than goals (Hamilton, Joyce, Flanagan, Frith, & Wolpert, 2007). Goal repetition was again associated with suppression in the anterior intraparietal sulcus. These results clearly demonstrate dissociable repetition-suppression effects for the inferior frontal gyrus and the anterior intraparietal sulcus, two regions that have been described to belong to the action-observation-execution-matching system.

In a second follow-up experiment, movement kinematics and the outcome of the observed action were manipulated (Hamilton & Grafton, 2008). Consistent with previous observations regarding the repetition of goal objects, suppression was found in the anterior intraparietal sulcus, though weaker, for repetitions of action outcomes. The latter mainly induced suppression within prefrontal (inferior frontal gyrus) and parietal (inferior parietal lobule) areas of the brain, with a significantly stronger effect size in the inferior parietal lobule. The repetition of grip kinematics induced changes in lateral occipital areas consistent with the previously described involvement of those areas in a visual analysis of movement kinematics.

Lestou, Pollick, and Kourtzi (2008) have recently used the repression suppression method to explore motor imagery. They had participants mentally imitate actions performed by point light figures and found associations between task goal and parietal activity and task kinematics and premotor activity. Interestingly, the superior temporal sulcus was also selectively affected by repetitions of task goals, which suggests that the processing of biological motion features is crucial to infer action goals from body movement features. Their findings can thus be conceived as support for a hierarchical organization of the action-observation-execution-matching system with a frontal network responsible for directly matching movement kinematics and a parietal system for matching action goals. Activity within those two networks could be modulated based on the presence or absence of an animate agent by inputs from the superior temporal sulcus (cf. Lestou et al., 2008).

In the emerging structure, a neural network comprising areas of the lateral occipital cortex is conceived to be responsible for the visual analysis of observed actions, whereas the inferior frontal gyrus and the ventral premotor cortex are assumed to provide a motor analysis of the action. Both networks constitute subordinate levels to the representation of the action goal associated with parietal areas (anterior intraparietal sulcus, inferior parietal lobule).

4.2 MOSAIC: Modular Selection and Identification for Control

The above mentioned ideas of specialized matching subsystems and a hierarchical organization of the action-observation-execution-matching system nicely relate to computational models of sensorimotor control, which have been proposed to mediate action understanding at different levels of description. Among the most prominent is the Modular Selection and Identification for Control model (MOSAIC; Wolpert & Kawato, 1998; Haruno et al., 2001; Wolpert et al., 2003). Therein, the continuity of perception and action is conceived to be based on perception-action loops, which have been shown to constitute elemental building blocks in the nervous system on all levels of cognitive complexity (cf. Fuster, 2004).

MOSAIC has two core features that are useful in the context of the present thesis. Firstly, while it was originally formulated as a model of motor control (Wolpert & Kawato, 1998), it was subsequently extended to comprise a multilevel control architecture to incorporate aspects of hierarchical motor control (Haruno et al., 2001) as well as to account for social interactions (Wolpert et al., 2003). This multilevel control structure features bidirectional communication between multiple levels of action description. This hierarchical and bidirectional control within a multilevel structure nicely relates to the organization of the action-observation-execution-matching system as described in the previous section. Secondly, the notion of multiple internal models is well suited to describe the functional relation between and within the different subsystems of the action-observation-execution-matching system. Thus, in the remainder of this section, the MOSAIC model is described and the concept of internal models is introduced. The last section aims to illustrate the synergies of combining the concepts of MOSAIC with the idea of a distributed action-observation-execution-matching system.

4.2.1 MOSAIC: The Basics

The MOSAIC model (Wolpert & Kawato, 1998; Haruno et al., 2001; Wolpert et al., 2003) blossomed from a computational approach to motor control. It is based on a conception of the motor system as part of a sensorimotor loop, in which motor commands generate muscle contractions that lead to perceivable sensory feedback, which in turn influences subsequent motor commands (Wolpert & Ghahramani, 2000). Therein, the human actor is viewed as a controller that is continuously faced with two tasks: to compute state variables, which together specify the configuration of the body (e.g., position and velocity of the limbs or muscle activations), and to determine the current context of an action (e.g., object properties or task demands). However, knowledge regarding the state of the body and the current context is not directly available to the controller. Instead, the central nervous system (CNS) has to compute those parameters based on information from the sensory receptors and the centrally represented knowledge of prior experience.

Problems of Motor Control: Time Delays

These computations are problematic, though. First of all, the transduction and transport of sensorimotor signals within the CNS requires time. For the visuomotor loop, Keele and Posner (1968) asserted that the afferent and efferent delays sum up to 190 to 260 ms before visual feedback can influence movement accuracy. Subsequent studies, which, for instance, postulated the existence of an additional fast motion detection system in peripheral regions of the retina (e.g Paillard, 1996), led to a downward adjustment of this estimate. However, the delay has hardly been found to go below 100 ms (for reviews, see Carlton, 1992; Elliott, Binsted, & Heath, 1999). As a consequence, a centrally generated control signal actually refers to a past state of the system through delayed peripheral feedback and might not be suitable within the current state of the system. Such time delays can be critical because they can induce phase-shifts between the actual error signal and the corresponding corrective control signal, which can lead to oscillations in the feedback loop and subsequent dynamic instabilities. If the delay were to remain in the system, only small gains could be applied in the feedback loop, which would considerably slow down learning and adaptation to changes in contexts.

Problems of Motor Control: Noise

A further complication for sensorimotor control is the presence of signal-dependent noise in the system (Harris & Wolpert, 1998; Guigon, Baraduc, & Desmurget, 2008; Todorov, 2005). On the sensory side it has been shown that visual noise depends on the position of the object of interest on the retina in that the standard deviation of that noise is proportional to foveal eccentricity in accordance with Weber's Law (Burbeck & Yap, 1990; Whitaker & Latham, 1997). On the motor side a similar relationship has been observed in that the standard deviation of muscle force linearly increases with the mean force applied in static (Sutton & Sykes, 1967; Todorov & Jordan, 2002) as well as dynamic (Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979) isometric force tasks. However, the assumption that noise is just a property of the musculoskeletal plant or the sensory apparatus is biologically implausible, because signal transduction within the cortex also suffers from internal noise. Synaptic noise, for instance, is based on the fact that the release of neurotransmitters into the synaptic cleft is a stochastic process. While it is possible to achieve reliability of the postsynaptic response in the periphery by averaging over a large number of transmitter release sites because incoming sensory information is highly redundant, those redundant connections are rare in the cortex where synaptic connections comprise only a couple of release sites. This renders communication between cortical neurons unreliable and noisy (cf. Smetters & Zador, 1996).

Two Types of Internal Models

Based on computational studies that tried to account for noise in sensory information input and subsequent signal processing as well as considerable time delays within the sensorimotor loop, it has been proposed that the CNS internally simulates aspects of the sensorimotor loop in planning, control and learning (for reviews, see Jordan, 1995; Kawato, 1999; Wolpert, 1997). Those structures within the CNS have been termed internal models. Those models either mimic the input-output relationship of the controlled object (=body) or their inverses (Kawato, 1999). Thus, they come in two varieties. Forward models have a body-to-world direction of causality and predict the sensory consequences from efference copies of issued motor commands with respect to the current state of the system and the context. Inverse models, on the other hand, have a world-to-body causality, specifying the necessary motor commands to bring about desired sensory consequences. Thus, by daisy-chaining the inverse and the forward model, the system can determine motor commands to achieve a certain effect in the environment through the inverse model and also compute the expected sensory feedback based on the motor commands generated by the inverse model through the forward model.

Modular Organization of Internal Models

However, a single controller would have to be too complex to incorporate all possible contexts in which movements can occur. Such a general-purpose controller would have to adjust each time when the context changes. This would yield large initial performance errors. As an alternative, the MOSAIC model postulates that the brain contains multiple modules of which each comprises a pair of forward (=predictor) and inverse (=controller) models. This modular organization has three advantages (cf. Wolpert & Kawato, 1998; Haruno et al., 2001). Firstly, it affords to organize motor commands with respect to environmental contexts. Secondly, it minimizes temporal crosstalk between different sets of motor commands in the course of learning. Thirdly, it allows to generate novel kinds of behaviour by combining the output of already existing modules. Thus, in a given context, one or a subset of inverse models can actively contribute to the control of movement.

Central to MOSAIC is the conception of the responsibility signal, which, at each point in time, unambiguously specifies to what extent a module contributes to the dynamical behaviour of the sensorimotor system. This signal is driven by two processes: A feedforward selection based on sensory cues and a feedback correction based on the outcome of the movement. In MOSAIC, multiple predictors are thought to provide predictions of the next state of the system based on its current state and an efference copy of the issued motor commands. Those predictions are then compared to the true outcome. The difference between predicted and actual state specifies the extent to which a forward model accurately predicts the sensory consequences of the motor action in the given context. This information is used as a responsibility signal, which can take values between 0 and 1. Thus, it can be conceived as the posterior probability of how well each forward model correctly captures the current dynamics of the system within its present context. Within competitive self-supervised learning, the responsibility signal is used to organize the distribution of error signals among the forward models (Wolpert & Kawato, 1998).

The inverse model associated with a given forward model receives the desired movement outcome as input and generates a set of motor commands as output. Learning and adaptation of inverse models is also achieved via the responsibility signal, which is based on the prediction accuracy of its associated forward model. The relative contributions of the inverse models to the dynamic behaviour of the sensorimotor system are specified in the same way based on the responsibility signal. Thus, if the prediction of a forward model is very accurate, its associated inverse model will contribute significantly to the final motor command and both, inverse and forward model, receive strong error feedback in order to facilitate their adaptation to the current context.

In order to select an adequate module prior to movement initiation solely based on sensory contextual cues, MOSAIC postulates a third type of model. This model is called the responsibility predictor. It predicts which model is most suitable based on prior experience with sensory features of the context, e.g., the size or (estimated) weight of an object. These predicted responsibility signals can then be compared to the actual responsibilities generated during movement execution, whereas as the latter were based on the comparison between predicted and actual sensory consequences. Finally, these two responsibility signals, the feedforward estimate of the responsibility predictor and the feedback signal from the forward model, are combined in a probabilistic (Bayesian) integration of prior and likelihood (cf. Haruno et al., 2001).

4.2.2 HMOSAIC: A Hierarchical Extension

An extension of MOSAIC is HMOSAIC (Hierarchical Modular Selection and Identification for Control; Haruno, Wolpert, & Kawato, 2003). It extends MOSAIC in that it adds superordinate layers to the model in order to explain hierarchically organized information-processing and bidirectional communication between different levels of a hierarchy. The basic structure of the model remains the same. Each layer of HMOSAIC contains a set of modules as described in MOSAIC. Within the modules in the bottom layer, the inverse model generates motor commands, the forward model predicts the sensory consequences of the motor commands, and the responsibility model produces the posterior probabilities, which indicate how well a given forward model predicts those consequences in the current context. This responsibility signal in terms of the posterior probability of the subordinate modules is sent via bottom-up connections to the modules on the higher level.

Modules on the higher levels also contain paired inverse and forward models. Instead of motor commands, these models deal with more abstract aspects of an action, such as the order of sequential elements of an action or the symbolic representation of action goals (cf. Wolpert et al., 2003). As input, modules on a higher layer receive the posterior probabilities from the modules of their subordinate layer and an abstract desired behaviour. As an output, the inverse models of this layer each generate a vector of prior probabilities for the modules on the lower level to achieve the desired behaviour given the current state of the system. Its function is thus to assign priority to those modules on the lower layer whose forward models are deemed to produce the most accurate predictions at the next point in time. Estimating the posterior probabilities of the subordinate forward models is the task of the predictive forward models of this layer. This prediction is, analogously to the lower level, not only used to weigh the output of the higher-level controllers, but also to distribute the learning signals for higher inverse and forward models.

In principle, this architecture can be devised to map any level of complexity. In the previously described organization of the action-observation-execution-matching system, Hamilton and Grafton (2007) suggested three levels of representation within the action-observation-execution-matching system: a muscle level, a kinematic level, and a goal level. The muscle level corresponds to the lowest level in HMOSAIC, where the distribution of activity of elemental modules depends on the specific motor action, but not on the overall task goal. At the kinematic level, which is implemented as an intermediate layer in HMOSAIC, specific features of the task are represented by specific sequences of activation of the modules on the lower level. These features are not specific for the precise details of movement. On the goal level, which would be the highest layer of HMOSAIC, the activations represent the most abstract description of the action, i.e., a specific outcome or an intention by the actor. This level is not tied to any particular patterns of muscle activation, or kinematic details.

Haruno et al. (2003) proposed that these distinct layers of an HMOSAIC architecture are associated with different parts of the cerebellum, which in turn project to different cortical areas via the thalamus. Among those areas are regions within the prefrontal, the ventral premotor, and parietal cortices (cf. Middleton & Strick, 1998), all of which were described to be a part of the action-observation-execution-matching system. This supports the notion that the cerebellum has not only motor functions, but also contains predictive and control modules, which perform computations on various levels of the action-observation-execution-matching system.

4.3 INTERNAL MODELS AND THE ACTION-OBSERVATION-EXECUTION-MATCHING SYSTEM

With respect to a functional hierarchy within the action-observation-execution-matching system, Iacoboni and coworkers (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Iacoboni, 2003) have suggested that mirror-like neurons in the ventral premotor cortex, the posterior parietal cortex and the superior temporal sulcus might constitute a biological implementation of a control scheme such as MOSAIC, which involves forward and inverse models. In their framework, the superior temporal sulcus provides a visual representation of observed actions. This neural network within the STS can be extended to comprise areas within the lateral occipital cortex (cf. Hamilton & Grafton, 2006; Hamilton et al., 2007; Hamilton & Grafton, 2008) and medial temporal structures, which have also been shown to be sensitive to motion as well as to the presence of body parts, i.e., biological effectors (Spiridon, Fischl, & Kanwisher, 2006).

While such an occipito-temporal network is responsible for the visual representation of observed actions, connections to the posterior parietal cortex and onwards to the premotor cortex compose an inverse model, which transforms an (observed) action into a motor plan. This is in line with the findings by Hamilton and colleagues (2006, 2007, 2008) and Lestou et al. (2008), who assigned the motor analysis of observed actions to a frontal network, in particular to the inferior frontal gyrus. Analogously, the backward connection from the inferior frontal gyrus to the posterior parietal cortex and onward to the occipito-temporal network serves as a corticocortical implementation of a forward model that converts the motor plan into a predicted sensory outcome of the action. Iacoboni (2003) conceived this as a basic mechanism of imitation according to which actions are observed, then transformed via the inverse model route into a motor plan, which is subsequently used to perform the observed action. Simultaneously, the forward model route is used to predict the course of action, which can then be compared to the intended action. This two-way process can also be used for tracking hand movements performed by conspecifics (Flanagan & Johansson, 2003).

Miall (2003) extended this neural architecture to comprise the cerebellum, which has been conceived to house internal models in its microstructures (e.g. Ito, 1990, 2008; Wolpert, Miall, & Kawato, 1998), and, as argued above, has been shown to be connected to various cortical areas within the action-observation-execution-matching system. Accordingly (Miall, 2003) suggested to include the projections from the posterior parietal cortex to the cerebellum, which in turn projects to the ventral premotor cortex, in the inverse route. Accordingly, mirror neurons in the inferior frontal gyrus are conceived as motoric representations of observed and executed actions. Those representations are activated by inverse models in the cerebellum. For the forward route, Miall (2003) identifies connections from the premotor and primary motor cortex to the cerebellum, from which connections lead via the thalamus back to the posterior parietal cortex. The function of the forward model that is localized within the cerebellum in this forward route is to update the visuomotor representation in the posterior parietal cortex based on efference copies of the motor commands, which are generated in the inferior frontal gyrus (presumably in the ventral sector of the pars opercularis; cf. Molnar-Szakacs, Iacoboni, Koski, & Mazziotta, 2005).

CHAPTER 5

THE ACTION-OBSERVATION-EXECUTION-MATCHING SYSTEM AND PERCEPTUOMOTOR CROSSTALK

The assertion of a covert sensorimotor simulation process of observed actions has straightforward consequences for overt behaviour in that one would expect systematic crosstalk between perception and action. Accordingly, the simulation hypothesis has traditionally been examined with experimental setups that tried to measure interference effects of another person's limb posture or action on self-generated actions or, vice versa, the impact of self-generated movements on the decoding of another person's actions. At the centre of this endeavour is the idea of perceptuomotor crosstalk, i.e. the unintended interference between perception and action within a common representational substrate. In this chapter, empirical evidence regarding this type of perceptuomotor crosstalk is reviewed and a functional model of how perceptuomotor crosstalk within the action-observation-execution-matching system could work is discussed.

5.1 BEHAVIOURAL EVIDENCE FOR THE ACTION-OBSERVATION-EXECUTION-MATCHING SYSTEM: PERCEPTUOMOTOR CROSSTALK

In principle, crosstalk between perception and action can occur in both directions; from perception to action (*motor resonance*, for a review, see Rizzolatti & Craighero, 2004) and from action to perception (*perceptual resonance*, for a review, see Schütz-Bosbach & Prinz, 2007). Perceptuomotor crosstalk can furthermore manifest in two distinct ways, (a) as assimilation by gearing up the motor system to actually execute the observed movement or facilitating the perception of environmental features related to action planning, and (b) as contrast by inhibiting the observed movement within the motor execution network, or vice versa, by impairing the perception of stimuli related to the planned or executed action.

5.1.1 Perceptuomotor Assimilation

Numerous paradigms have been used to demonstrate facilitative effects of perception on action and vice versa. Kerzel, Bekkering, Wohlschläger, and Prinz (2000), for instance, had participants watch two consecutive object movements and asked them to reproduce the velocity of the first while ignoring the second movement. They found that while participants were able to reproduce an observed velocity, observation of the second movement involuntarily modulated their response in that participants' reproduction of the first movement was faster when the velocity of the second target was higher.

Similarly, Castiello, Lusher, Mari, Edwards, and Humphreys (2002) had participants observe a grasping action directed towards an object, which could either be large or small. They found that when participants were asked to subsequently perform an action towards an object of the same size, variations in cue validity (in terms of the probability that the previously observed action was directed to an object of same size) systematically affected kinematic markers. They found faster reach components (time to peak velocity, time to peak deceleration) and smaller, i.e. more accurate, grasp apertures in valid trials, which comprised identical objects for action observation and execution. Thus, the observation of a matching action facilitated subsequent action execution. In a follow-up study by Edwards, Humphreys, and Castiello (2003), in which the cue validity was decreased to 20 percent, the reach and grasp components of the executed action were found to be primed differentially. Only the reach component was found to exhibit an increased sensitivity to prior observation of a congruent movement. This finding is in line with previously reported dissociations of reach and grasp components of prehensile actions (Jeannerod, 1997). A potential reason for this differential priming effect according to cue validity is the possibility that only the reach component is subject to facilitation by an action-observation-execution-matching system because this component is specified prior to movement initiation during action planning. The grasp component, however, remains largely under online control and is thus not affected by an influence of prime perception on action planning.

Glenberg and Kaschak (2002) studied the interaction of action perception and action execution on a more abstract level. They asked participants to make sensibility judgements to sentences, which implied actions directed either towards or away from the body by making a response that required them to move either towards or away of their bodies. They found what they called an action-sentence compatibility effect, according to which response times were faster in trials in which the direction of the response movement and the movement direction implied in the sentence were compatible. Accordingly, Zwaan and Taylor (2006) found similar facilitation effects. They reported shorter response times when sensibility judgements of sentences, which described manual rotations, were made by same-direction rotations of the hand (experiment 2), as well as when simultaneously observed visual rotations were in the same direction as the one described in the sentence.

Reed and Farah (1995) demonstrated that action execution could also facilitate the perception of action-related visual information. In their study, participants were asked to detect changes in the arm or leg position of a human model. At the same time, they were asked to perform arm or leg movements themselves. Thus, executed and observed motion could refer to the same or to different limbs. Results showed a priming effect in that observers more accurately detected position changes in the corresponding limb condition, which presumably reflected the automatic engagement of embodied knowledge that directed attention to the corresponding parts of other viewed bodies during movement execution.

5.1.2 Perceptuomotor Contrast

In accordance with the bidirectionality of perceptuomotor crosstalk, there have also been numerous demonstrations of decrements in perceptual performance caused by action or vice versa. Müsseler and Hommel (1997a), for instance, found that the identification probability of an arrow pointing left- or rightward was impaired when the arrow was presented during the execution phase of a compatible left- or right-button press (more precisely: briefly before the overt onset of a preplanned response). This action-effect blindness was subsequently reported for a visual detection task as well (Müsseler & Hommel, 1997b). The authors interpreted this effect as a transient inhibition of the features which were used for movement execution, and which accordingly were not available for subsequent perception of stimuli comprising the same features.

Similarly, Hamilton, Wolpert, and Frith (2004) reported a contrastive influence of active movement on perceptual judgements. In their study, participants were required to either lift or hold a box of various weights. Simultaneously, they were asked to judge the weight of a box they watched being lifted by an actor. Results showed that participants systematically judged the observed box to be lighter when they were lifting or holding a heavy box.

That such perceptuomotor contrast is indeed bidirectional has been demonstrated by Schubö, Aschersleben, and Prinz (2001), as well as Zwickel, Grosjean, and Prinz (in press). The former asked participants to draw sinusoidal curves on a graphic tablet while observing unrelated sinusoidal stimulus movements. Besides their finding that observed stimulus motion exerted a contrastive influence on response movements, they also reported a contrast effect in the other direction with movement execution also affecting stimulus encoding in terms of movement amplitude. Amplitudes of stimulus motion were perceived to be smaller when larger movement amplitudes had to be produced. Zwickel et al. (in press) further developed these findings in demonstrating bidirectionality of perceptuomotor contrast not between, but within experiments, i.e. with the same task under identical constraints.

With respect to the specificity of perceptuomotor contrast, Jacobs and Shiffrar (2005) reported that action production interfered with the perception of similar actions in that observers' own walking movements on a treadmill selectively impaired their sensitivity for performing gait speed comparisons of two point-light walkers. This effect was found to be highly specific in terms of the performed movement as it was absent when observers were engaged in other bodily activities such as cycling or standing.

5.2 TEC: The Theory of Event Coding

The Theory of Event Coding (TEC Hommel et al., 2001) is a psychological (meta-)theory that integrates conceptual and empirical work inspired by the ideomotor principle (James, 1890; Greenwald, 1970), the idea of common coding (Prinz, 1990, 1992, 1997) and the feature-based organization of visual perception (Singer, 1994) and attention (Treisman & Gelade, 1980) to account for the bidirectional interactions between perception and action planning that were described in the previous section. In the following, its characteristic properties are outlined.

5.2.1 Common Coding

The anatomical separation of afferent and efferent information in the spinal cord in an ascending dorsal root, which transports sensory signals from the periphery to the brain, and a descending ventral root, which transports motor signals from the brain to the periphery, along with the prevalent Cartesian conception of the reflex arc as the elementary unit of behaviour gave rise the conception of sensory and motor processes as two distinct properties of mental life. However, in phenomenal experience, this separation simply does not exist, as already pointed out by Dewey (1896), who emphasized the inseparability of sensory stimulus and motor response. He argued that both constitute necessary parts of a continually reconstituting coordination cycle, in which perception presupposes and affords active behaviour, and acting both relies on and generates perceptual information.

According to the idea of common-coding (Prinz, 1990, 1997), this continuity is not only phenomenal and introspective, but also functional reality in that late perceptual products and early action precursors share a common representational medium. Prinz (1992) argued that proximal internal representations of perceptual objects and action plans, such as patterns of retinal excitation or of muscular innervation, are not related to each other in a meaningful way, as sensory excitation is incommensurable with muscular activation. However, since both refer to events in the environment that are either perceived by the senses or generated by actions, cognitive representations for perception and action can be related on a more abstract level with reference to the informational content of a distal event, which is independent of the modality-specific encoding of proximal representations. As a consequence, commensurability in the coding of perception and action planning is achieved by their common reference to perceivable events in the environment.

5.2.2 Ideomotor Principle

While it is easy to see why perceptual codes refer to perceivable events, Hommel et al. (2001) employed the ideomotor principle to establish this association for action planning as well. According to the ideomotor principle, actions are not caused by stimuli in the environment but by internally represented goal states and an intention to achieve them (James, 1890; Lotze, 1852). Each time a movement is performed, this movement is necessarily associated with reafferent consequences of its execution. These consequences may be resident feelings of the movement itself or remote changes in the environment that a movement brought about. Through an individual's continuous active interaction with the environment, sensorimotor contingencies are established, which integrate the perceptual consequences of a movement with the motor neuron activity that generates the movement. Thus, the mere memory of a resident or remote effect, e.g. a goal state, can trigger the movement that brought about the effect in the past. With repeated execution of a movement, the remoteness of its contingent effects can be increased, which affords effect coding in terms of distal events as postulated by the common-coding view (Prinz, 1992, 1997). Accordingly, those event codes, the core concepts of TEC (Hommel et al., 2001), are cognitive representations that do not differentiate between processes of perception or action planning, which act upon them.

5.2.3 Three Types of Codes

Representations in general have been conceived to be composites of single features so that a given representation requires binding, i.e. activation and integration of features that are distributed across the brain (Singer, 1994; Treisman & Gelade, 1980). Analogously, TEC postulates that event codes are composites of feature codes, which represent single aspects of a distal event. Thus, TEC distinguishes three types of codes. Proximal codes comprise sensory and motor codes, which either specify a particular pattern of sensory stimulation or of motor activation. In contrast, distally defined feature codes are not specifically tied to a single stimulus or response pattern. Instead, feature codes comprise abstract information such as the direction of (stimulus or response) movement. This information can be derived from sensory codes, i.e. patterns of proximal sensory excitation in different modalities, or can be used to activate various motor codes. Thus, feature codes are conceived to receive and spread their activation from and to sensory and motor sources. Feature codes whose activation overlap in time are automatically integrated into event codes. This process of integration is insensitive to the temporal succession of distal events, which means that there is no differentiation between cause and effect but blind coactivation. In accordance with the ideomotor principle, action-effect learning can thus afford effect-action retrieval.

Furthermore, the idea of feature codes gives rise to the notion of similarity in terms of the degree to which two event codes share the same feature codes. This similarity is thus based on an overlapping activation of feature codes that refer to properties of the stimulus and the action as they occur in the external world. This overlapping activation can give rise to perceptuomotor crosstalk, i.e. interactions between the distal internal representations of perceived and produced events. As described in the preceding section, perceptuomotor crosstalk can manifest in terms of assimilation and contrast. In TEC, this division corresponds to the distinction between activation and integration of feature codes (Hommel et al., 2001). The activation of a feature code primes all event codes that comprise this particular feature. Thus, the activation of a feature code during the planning of an action, for instance, automatically facilitates the perception and the production of other actions that also contain this particular feature code. Once the active feature codes are integrated in an event code, assimilation turns into contrast because the integrated feature codes are no longer available for the formation of another event code.

As actions are controlled by their distal to-be-perceived events, the idea of an action, no matter if it is due to reading a sentence that describes it, or due to its mere observation, activates the feature codes that represent the perceivable effects of that action. Those effects are integrated into neural networks event codes that serve to register and to produce the coded effects. Because these event codes possess sensorimotor components, activation within the event code also spreads out to motor codes. As a consequence, each thought of an action or its observation yields a tendency to execute the action.

5.2.4 Intentional Weighting

According to TEC, event coding is adaptive. In order to afford flexible behaviour, which is attuned to a particular situation and the respective goals of an agent, he or she can adjust the degree to which a particular feature code contributes to the resulting event code. Thus, preparation to react to a stimulus, for instance, invokes the preactivation of task-relevant feature dimensions such as colour, direction or higher-order abstract features. For the case of spatial direction, Memelink and Hommel (2005) showed that performing a task that required stimulus coding in either the horizontal or vertical direction specifically modulated performance in a subsequent two-dimensional Simon task by increasing the effects of stimulus-response compatibility for the direction that had been coded previously and decreasing the effects along the other direction. In another experiment, Wykowska, Schubö, and Hommel (in press) had participants perform grasping or reaching actions and found that the type of action selectively increased discrimination performance when the discriminative cue corresponded to a feature dimension that was activated in the previously executed hand action. Thus, while stimulus observation can activate feature codes and thereby prime a certain response (as is the case in many paradigms investigating compatibility effects such as the Simon- or the Stroop-task), there is also intentional weighting of features codes in that high-level processes of action planning can affect low-level perceptual processes to selectively attend to particular features of the stimulus, which in turn can affect the specification of action parameters.

Chapter 6

The Action-Observation-Execution-Matching System and the Animate-Inanimate Distinction

6.1 An Argument Based on Relevance and Expertise

With respect to functional specialization within the action-observation-execution-matching system, Jacob and Jeannerod (2005) postulated a two-systems-model, which comprised a non-social mirror system in the ventral premotor and the parietal cortex, and a social perception system including the superior temporal sulcus, the amygdala and the orbito-frontal cortex. While the task of the former is to detect motor intentions, i.e., intentions directed towards inanimate objects, the task of the latter is the detection of social intentions directed towards animate agents, especially conspecifics. Recently, Pierno, Ansuini, and Castiello (2007) have suggested that this separation might be too strict and have instead argued in favour of a unified system that codes both motor and social intentions. However, regardless of whether one postulates a common or two distinct subsystems serving sensorimotor simulation, what can be retained from Jacob and Jeannerod (2005) is the idea that sensorimotor simulation within the action-observation-execution-matching-system could be particularly sensitive to the observation of actions performed by animate agents.

There are several good reasons why activity of the action-observation-execution-matching system should be specifically sensitive to biological, i.e., animate movements. In support of this, the two naive notions of relevance and expertise, which were already mentioned in the introduction, are reconsidered.

With reference to the notion of relevance, according to which the action-observation-execution-matching system is particularly sensitive to bodily actions since bodies of animate beings are the conduit of social interaction, it is generally accepted that humans and animals have mental states, such as desires or goals. Even though mentalizing can easily be transferred to the perception of object motion (e.g Heider, 1944; Heider & Simmel, 1944), it is generally assumed that machines and inanimate objects do not possess those states. If a function of the action-observation-execution-matching system, amongst other things, is to support inferences about mental states to allow for social interaction, activation of the action-observation-execution-matching system by inanimate motion could be maladaptive in that it leads to false attributions of mental states (cf. Press, Bird, Flach, & Heyes, 2005) and therefore should be sensitive to the animacy of objects of interaction.

According to the notion of expertise, animate actions are specifically potent in activating the action-observation-execution-matching system because observed and produced kinematics can directly be mapped onto each other. It has been shown that activation of the action-observation-execution-matching system is stronger during the observation and presumably during the simulation of movements that are physically familiar. Aglioti, Cesari, Romani, and Urgesi (2008), for instance, have recently reported increased accuracy in predicting the outcome of basketball throws by professional basketball players as compared to sports journalists, who were conceived to possess visual expertise on judging free throws, but not the motor competence the players possessed. Moreover, TMS application in the basketball players showed sensorimotor involvement in action observation. Since humans are experts in performing biological actions, observation of these should lead to stronger activations in the action-observation-execution-matching system.

Thus, in the following, neurophysiological and behavioural studies that specifically compared the responsiveness of the action-observation-execution-matching system for actions performed by animate agents and inanimate objects are reviewed.

6.2 EMPIRICAL EVIDENCE FOR BIOLOGICAL TUNING OF THE ACTION-OBSERVATION-EXECUTION-MATCHING SYSTEM

6.2.1 Neurophysiological Studies

First evidence for biological tuning of the action-observation-execution-matching system comes from the seminal paper by Gallese et al. (1996). They reported that the matching of observed and executed actions in mirror neurons is highly specific, in that it not only refers to the action but also to how it is executed. In their taxonomy of mirror neurons, they grouped mirror neurons according to the hand action effective in activating them. One of those subgroups called manipulating neurons was found to discharge when an experimenter touched and retrieved an object, but only if he did so with his fingers. The neurons remained silent when the experimenter obtained the object with a tool. Additionally, efforts to elicit discharges in other subgroups by using objects or tools to imitate the respective actions also failed. This has been taken to suggest that manipulating mirror neurons are sensitive for the presence of a biological effector.

Studying humans, Cochin, Barthelemy, Lejeune, Roux, and Martineau (1998) used quantified electroencephalography (qEEG) to compare cortical activity during the observation of human and object motion. They discovered a desynchronization of the EEG pattern in the precentral motor cortex specifically during the observation of human motion. A subsequent study by Martineau and Cochin (2003) with children (two to eight years of age) who watched human, animal, and virtual movements confirmed the differential activation according to the observed movement. Most interestingly, they incorporated an additional distinction between real and virtual body movements in their experimental design (observing a young person performing scissor movement with his/her legs while lying on the back versus a snippet of a Walt Disney cartoon showing Cinderella dancing with the prince). They identified a network within centro-parietal areas of the left hemisphere during the perception of the young person and Cinderella, which was absent during the perception of animal motion. Based on their findings, Martineau and Cochin (2003) concluded that the observation of human action, regardless of being performed by a real person or a comic character, elicited activation within a cortical network specifically tuned to movements performed by human agents.

This assumption of an equivalence of virtual and real human actions is implicitly assumed in many studies of visuomotor coordination (e.g Decety et al., 1994; Ghahramani & Wolpert, 1997). Perani et al. (2001) examined this assumption of equivalence in adults. They had participants watch object-grasping actions performed by a real right hand compared to a virtual-reality reconstruction with either high (with biological texture and shape) or low (only biological shape) virtual-reality level. While they found common activations in areas specialized in the processing of motion information (early visual areas and area MT; e.g. Buchel & Friston, 1997; Watson et al., 1993), and sensorimotor control (posterior parietal cortex; e.g. Andersen, Snyder, Bradley, & Xing, 1997; Milner & Goodale, 1995), they found selective activations for the observation of real actions in the right inferior parietal cortex. Perani et al. (2001) concluded that only real actions activate parietal areas that provide nonretinocentric coordinates in an egocentric frame of reference, which can be used for motor planning (cf. Willingham, 1998). This egocentric visuospatial representation might be a prerequisite for a direct-matching mechanisms mediating the internal simulation of observed actions within the action-observation-execution-matching system. This suggests that only perception of actions by a real hand can be mapped onto existing action representations, whereas virtual-reality conditions do not access the full-motor knowledge available to the central nervous system.

Tai, Scherfler, Brooks, Sawamoto, and Castiello (2004) conducted the first neuroimaging study that demonstrated a similar preference for biological agents of a neuronal population within the human premotor cortex. In showing grasping actions to participants placed in a PET scanner, they compared grasping performed by a human to a robot model performing the same actions. They found activation in the left ventral premotor cortex only in the presence of the human model. They concluded that only observing a biological effector activates a matching mechanism that maps the observed action to the observer's motor representations. While in the monkey study by Gallese et al. (1996), the action of a tool grasping an object might simply not be a part of the behavioural repertoire of the monkey and might account for the absence of cortical matching in the premotor cortex between the observed action and the internal motor commands, this reasoning is difficult to uphold for a human model observing a robot arm, since grasping is definitely part of a human's motor repertoire. Alternatively, Tai et al. (2004) suggested that the mismatch of perceptual information in terms of movement kinematics explained the differential pattern of activation because movements performed by the robot arm lacked the typical smoothness of human motion.

However, the idea of biological tuning of the action-observation-execution-matching system is controversially discussed in neuroscience. One of the experiments in study by Nelissen et al. (2005), which was described in chapter 3.2, did also comprise a comparison of fMRI scans of monkeys who were watching videos of grasping actions performed by a human to the same actions performed by a robot hand (experiment 3). Similar to the results by Tai et al. (2004), they found a significantly larger increase in cerebral bloodflow in the anterior sector of the ventral premotor cortex during the observation of grasping actions performed by the human model in comparison to grasping actions performed by the robot. However, with respect to a neutral baseline, the observation of the robot action also led to a significant increase in activation. This indicates that even though activation of the monkey mirror system is apparently more pronounced during the observation of a human model, actions performed by a robot model also have the ability to trigger activation of the monkey mirror system.

A study by Oberman, McCleery, Ramachandran, and Pineda (2007) examined human participants in a similar task. They used EEG to measure mu-suppression during the observation of transitive and intransitive grasping actions performed by a robot hand with human form characteristics, i.e., four fingers and an opposable thumb. They found mu-suppression, which has been conceived to reflect activation of the action-observation-execution-matching system in humans, during the observation of both transitive and intransitive grasping actions by the robot.

Gazzola, Rizzolatti, Wicker, and Keysers (2007) criticized the study by Tai et al. (2004) by arguing that the authors did not properly control the amount of movement variability between robot and human motion, which rendered it impossible to attribute the results on differences in movement kinematics and action variability. Of course, it could be argued that these two explanations are by no means exclusive since movement variability is an essential feature of biological kinematics. In their study, Gazzola et al. (2007) used fMRI to measure brain activation during the observation of four different stimulus displays, which depicted a rest condition, an intransitive motion, a simple grasping action (picking up an object), and a complex action (placing a lid on a jar). Their results revealed equivalent neural responses to the observation of goal-directed human as well as robotic grasping actions in brain regions involved in the execution of similar actions, i.e. in temporal, premotor and parietal brain regions. Gazzola et al. (2007) argued that the diverging results reported by Tai et al. (2004) were due to the repeated presentation of identical stimuli of the robotic movement, which led to habituation within the action-observation-execution-matching system (see also chapter 4.1, on the repetition-suppression effects reported by Hamilton & Grafton, 2006; Hamilton et al., 2007; Hamilton & Grafton, 2008). However, contrary to the findings by Nelissen et al. (2005) and Oberman et al. (2007), they only found a weak activation of the action-observation-execution-matching system during the observation of intransitive actions, as compared to actions that involved object manipulation. However, they reported that, while no differential activation of the action-observation-execution-matching system was found during the observation of a complex action, there was a larger activation in response to simple actions that were performed by the human model.

6.2.2 Behavioural Studies

That the presence of a human body might be functionally relevant for the influence of action execution on action perception has been shown by Flanagan and Johansson (2003). In their study, participants had to perform and observe a block-stacking task. Their eye movements were recorded simultaneously. Flanagan and Johansson (2003) found that almost all gaze fixations in the execution condition were directed towards the grasp locations of the blocks that had to be lifted and the landing location where the blocks had to be placed. Subsequent timing analysis revealed that gaze behaviour was predictive rather than reactive in that gaze preceded the actual hand movement towards the respective location by 150 ms. In the observation condition, the coordination between participants' gaze and the observed actor's hand was highly similar to the pattern observed in gaze-hand coordination when they were required to perform the task themselves. Again, gaze behaviour was found to be anticipatory as it preceded the hand movements of the actor. The authors also employed an additional experimental condition, in which participants observed block-stacking movements without actually seeing the actor who performed the movements. While the pattern of gaze behaviour was found to be similar to actual movement execution and observation with the human model present, the anticipatory nature of gaze control vanished in the absence of the human model. This indicates that the mere presence of the object manipulation is not sufficient to trigger the action-observation-execution-matching system, but requires the presence of the human actor. Thus, the human body had to be present for prediction to occur.

In the study by Castiello et al. (2002), which showed a priming effect of observed grasping actions to subsequent action execution (see chapter 5.1), this effect was not found when subjects were viewing a robotic hand/arm model performing the grasping movement. This supports the notion of biological specificity of the action-observation-execution-matching system. However, visuomotor priming was also absent when the observed model was blindfolded during movement production and thus its movement kinematics for large and small objects did not differ. The differential effect of visuomotor priming for a human as compared to a robotic hand reported by Castiello et al. (2002) might not truly reflect biological tuning of the action-observation-execution-matching system, but rather be the result of the presence of discriminative kinematic cues, which allow the preactivation of different grasping actions without reference to biological features of the observed actions.

Other studies provided more direct evidence with respect to the animate-inanimate distinction within the action-observation-execution-matching system. In a series of experiments, Brass and colleagues (Brass, Bekkering, Wohlschläger, & Prinz, 2000; Brass, Bekkering, & Prinz, 2001) used a stimulus-response-compatibility paradigm to assess the influence of observed finger movements as compared to symbolic and spatial cues on visuomotor priming of manual actions. Observation of a finger movement strongly affected subsequent movement execution, irrespective of whether the finger movement was the relevant or irrelevant stimulus dimension (cf. Brass et al., 2000). Reaction times to observed finger movements were faster than reaction times in response to symbolic or spatial stimuli. In the latter two conditions, in which observed finger movements were task-irrelevant, they nevertheless significantly interfered with movement execution in incongruent and facilitated movement execution in congruent trials as compared to a baseline condition. A similar interference was not observed when spatial or symbolic cues were used as irrelevant stimuli. Similarly, Brass et al. (2001) also reported a compatibility effect that was found to depend on the type of moving object. While the observation of finger movements elicited significant compatibility effects on pre-instructed finger movements, compatibility effects were only marginally significant when responses were triggered by moving squares. The squares represented the position of the finger tip and thus did not differ in terms of kinematics or amplitude from the finger movements.

However, analogous to the neurophysiological findings by Gazzola et al. (2007) and Oberman et al. (2007), there also exist behavioural studies that propose that the action-observation-execution-matching system can also be activated by artificial stimuli. Press et al. (2005), for instance, reported response compatibility effects for observing both human and robot hands. In their study, they showed participants either naturalistic or schematic photographic images of a human or a robot hand in a terminal posture, either depicting an open or a closed hand. Those images could be compatible or incompatible with the subsequent response. Results showed that both stimulus types could elicit automatic priming supporting the notion of stimulus generalization as postulated by associative learning accounts (e.g. Heyes, 2001; Heyes, Bird, Johnson, & Haggard, 2005; Keysers & Perrett, 2004). However, the finding that human stimuli, naturalistic and schematic, are more powerful visuomotor primes than the respective robot hand stimuli indicates that the observation of animate stimuli is more closely related to action execution and affords a more direct matching. Since the schematic stimuli differed only in shape, the observed stronger activation of a human hand implies that other cues such as kinematics, texture, or size is not necessary to produce differential activation of the action-observation-execution-matching system. Accordingly, the compatibility effect was further pronounced when the robotic hand was visually more similar to the human hand stimuli (Press, Gillmeister, & Heyes, 2006).

The above mentioned examples all used discrete responses to show that the observation of actions performed by an animate agent specifically affected response execution. However, Kilner, Paulignan, and Blakemore (2003) employed a continuous movement execution and observation paradigm, which showed that perceptuomotor crosstalk is apparently sensitive to the animate-inanimate distinction. In their study, they found specific interference in movement production while participants were simultaneously observing incongruent movements made by a human model in contrast to movements by a robot model. The observation of continuous oscillatory arm movements by a human model led to significantly greater variance in the position of the participants' fingertip Ñ i.e. greater vertical position variance for horizontal movements and vice versa Ñ in incongruent trials, in which the movement plane of the participant was perpendicular to the movement plane of the observed model. Later, Blakemore and Frith (2005) argued that this was due to the assimilation of the observed model motion into the ongoing movement via an automatically induced activation of the observed movement.

6.3 What Triggers Activation of the Action-Observation-Execution-Matching System in Response to Animate Action?

The preceding review of the literature suggests that there exist specific responses to animate stimuli in terms of an increased activation of brain areas that are conceived to be part of the action-observation-execution-matching system. Similar results were found in terms of perceptuomotor crosstalk in overt behaviour. The finding that in some studies artificial effectors such as robot hands or moving dots were also able to elicit crosstalk on both the neural and the behavioural level does not necessarily invalidate the claim of a particular sensitivity of the action-observation-execution-matching system to animate actions, especially if one assumes a hierarchically organized system, in which movement kinematics, goals, and even more abstract features such as intentions can be mapped.

Accordingly, recent theoretical work on imitation and social cognition has converged on an associative account of an action-observation-execution-matching system, in which perceptuomotor crosstalk and ultimately sensorimotor simulation is based on individual experience of contingencies between perception and action and possesses the potential for generalization (e.g. Heyes, 2001; Heyes et al., 2005; Keysers & Perrett, 2004). If actions performed by inanimate objects such as a robot hand closely resembled human movements, e.g., by way of shared surface/form features or movement kinematics, activation within the action-observation-execution-matching system would occur in terms of overt perceptuomotor crosstalk. Thus, the appropriate question to ask is not *if* the action-observation-execution-matching system is particularly sensitive to the animacy of a stimulus, but rather which stimulus features define animacy as a trigger for the action-observation-execution-matching system.

According to Cutting (1981), one of the most fruitful ideas in cognitive psychology has been the idea of underlying structures. Structures contain two types of elements: variants and invariants. While variants are inconstant across multiple situations, invariants remain constant across every instantiation of an event. Although variants are mainly the source of the experiential diversion in a wide range of events, the invariants will certainly be most useful for propagating advances in the scientific study of perception and action. The invariants in an event structure were classified by Köhler (1947). He distinguished between topographic and dynamic invariants. While the former refer to structural relations in space, i.e., the structural properties in static images of an event, the latter are conceived as structural relations in time, i.e., as the rules that govern the nature of change over the course of an event.

An important invariant in biological movement trajectories is the two-thirds-power law (Lacquaniti, Terzuolo, & Viviani, 1983). It is an empirical law, which governs voluntary upper-limb movements. It postulates an inverse non-linear relationship between the tangential velocity of the hand and the curvature of its trajectory. Within an elliptic movement trajectory, for instance, there are segments with low curvature in the middle of the ellipse, and, segments with large curvature at the turning points of the trajectory. While performing such a movement, one has to slow down as curvature increases and can speed up as curvature decreases. The amount of deceleration and acceleration is proportional to the change in curvature raised to the 2/3 power. Viviani and Monoud (1990) showed that individuals are unable to generate hand movements that violated the velocity-curvature covariation specified in the two-thirds power law even after extensive training under visual guidance. Furthermore, the power law has been demonstrated to hold for perception as well. Viviani and Stucchi (1992) showed that people judge the observed motion of a single light-point stimulus to move with constant velocity when it actually accelerated and decelerated on an elliptical movement trajectory in accordance with the power law. Moreover, Kandel, Orliaguet, and Viviani (2000) showed that people's ability to predict a letter that is about to be traced critically depends on whether the movement of the previous letter corresponded to the two-thirds-power law. Based on these observations, Viviani (2002) argued that the velocity-curvature covariation specified in the two-thirds power law ”is a kind of signature that can be used to tell rather reliably what is biological and what is not” (p. 416).

With respect to the topographical invariants of biological motion, evidence for a particular sensitivity of the action-observation-execution-matching system for animate action comes from research on apparent motion (e.g. Shiffrar & Freyd, 1990, 1993; Heptulla-Chatterjee, Freyd, & Shiffrar, 1996). Apparent motion refers to the perception of movement when two spatially separated, stationary objects are presented in close temporal succession. When those two objects are simple light points and have identical shapes, apparent motion follows the shortest path possible (Korte, 1915; Wertheimer, 1912). Shiffrar and Freyd (1990), however, showed that when participants saw pictures of different body postures instead of inanimate objects, the perception of the apparent path of motion was modulated by the presence of a human body. When the time interval between the presentation of two successive pictures was small, the shortest path between two postures is perceived, even though it might be physiologically impossible. With longer time intervals, however, only biomechanically possible paths of motion are perceived. It was concluded that observers are apparently sensitive to the biomechanical properties of the human body and that knowledge about these properties is automatically activated in the presence of human bodies in the stimulus display.

Consequently, it should be possible to discriminate biological from non-biological motion based on the kinematics of a single-point light, whose motion is mapped on one's own motor apparatus, as well as based on the presence of a human body, which automatically activates embodied knowledge regarding the observed course of action. In principle, both kinds of stimulus features should be able to trigger activation of the action-observation-execution-matching system, given that it is particularly sensitive to animate actions.

Such a dual activation of the action-observation-execution-matching system based on topographic and dynamic stimulus properties corresponds to a differentiation within the occipito-temporal network, which was previously distinguished as a part of the action-observation-execution-matching system, whose task is to provide a purely visual analysis of observed actions (see chapter 4.1). This network comprises areas that are particularly responsive to the observation of biological motion (superior temporal sulcus, e.g. Grossman et al., 2000; Grossman & Blake, 2001) as well as to the presence of features of biological form (lateral fusiform gyrus, e.g. Spiridon et al., 2006). The contributions of these areas are integrated within the network to achieve a unified representation of the visual stimulus with respect to its animacy. This provides neurophysiological support for the notion that the distinction between animate and inanimate stimuli can be made based on the presence of both topographic and dynamic invariants in the visual signal.

With reference to the findings of a specific interference effect for biological motion by Kilner et al. (2003), a couple of studies were conducted that aimed to elucidate how this effect is generated. In such a follow-up study, Kilner, Hamilton, and Blakemore (2007) used a paradigm similar to the first study, but this time, participants were shown human and object motion that could either follow a biological (acceleration and deceleration phases according to minimum-jerk) or a non-biological (constant velocity) velocity profile. They found larger orthogonal variability in incongruent trials than in congruent trials when participants performed oscillatory linear movements during the observation of movements with a biological velocity profile. The effect was independent of the type of stimulus (object vs. human model). They concluded that biological kinematics in terms of the velocity profile were crucial for specific perceptuomotor crosstalk in response to animate stimuli to occur.

A study by Bouquet, Gaurier, Shipley, Toussaint, and Blandin (2007) aimed to replicate the original effect reported by Kilner et al. (2003) and also compared biological and non-biological velocity profiles of dot motion with respect to the effect. In their first experiment, in which they tested whether a video display of a human model yielded the same effects as the observation of an actual human model, they did indeed find a congruency effect with increased variance along the orthogonal spatial axis for incongruent movements. However, this effect cannot unambiguously be attributed to the observation of a human model, since they did not include a control condition that depicted an inanimate stimulus. In their second experiment, they showed participants dot movements that either moved with biological or non-biological kinematics. Here, they found a specific increase in movement variance when participants simultaneously observed dot motion with a biological velocity profile. They also found a significant main effect of congruency with observation of incongruent perpendicular movements, which led to higher orthogonal variance. However, the interaction between type of motion and congruency did not approach significance at all, $F < 1$, so that the observed effects cannot be taken as evidence for specific perceptuomotor crosstalk due to the observation of biological movements (only).

By using a similar paradigm, Stanley, Gowen, and Miall (2007) also compared perceptuomotor crosstalk during the execution of linear oscillatory movements and simultaneous observation of dot movements. Similar to the studies by Kilner et al. (2003) and Bouquet et al. (2007), both stimulus and response movements were either horizontal or vertical. Furthermore, dot movements either followed a biologically plausible or implausible velocity profile. They found that the presentation of an incongruent dot stimulus did not produce specific effects of perceptuomotor crosstalk when participants had been told that the dot motion was computer generated. Crosstalk in terms of increased orthogonal variance was observed only when participants were told that dot motion represented the movement trajectory of a human agent, irrespective of the motion's velocity profile. Based on these effects, the relevance of inferred agency and the lack of impact of the velocity profile, Stanley et al. (2007) concluded that the interference effect reflected a top-down modulation of perceptual input without reference to the actual movement kinematics.

Thus, at present it is unclear which stimulus features actually trigger perceptuomotor crosstalk, which is specific to the observation of actions performed by animate agents. Based on the conceptual distinctions by Cutting (1981) and Köhler (1947), and the empirical work described in the previous chapter, the general purpose of the present study was to explore the effects of the presence of topographic and dynamic invariants that indicate animacy of an observed action on perceptuomotor crosstalk during the simultaneous observation and execution of intransitive actions. Therefore, biological kinematics (= dynamic invariants) and surface/form features of a human body (= topographic invariants) were either present or absent in the stimulus display in order to measure their relative contribution to interactions between simultaneous perception and action.

Chapter 7

The Experiments: General Aspects

7.1 Task

For the present study, intransitive continuous oscillatory right-left and up-down movements were selected as actions that should be observed and simultaneously executed by the participants. It was assumed that the presence of an object would not be necessary to activate the human action-observation-execution-matching system. While this assumption is firmly grounded on empirical evidence regarding intransitive actions as described in previous chapters (e.g. Fadiga et al., 1995; Press et al., 2008), there are several methodological reasons not to use transitive, object-directed actions in the context of the present study.

Firstly, it has was shown that the mere presentation of an object can induce a motor response that is afforded by the object (Castiello, 2003; Craighero, Fadiga, Umiltà, & Rizzolatti, 1996; Tucker & Ellis, 1998). Castiello (2003), for instance, showed that the prior observation of a graspable object can prime its respective goal representation, which in turn activates features of the associated action. Consequently, if one is interested in investigating the properties of the action-observation-execution-matching system, one will have to use intransitive actions in order to avoid confounding activity from an affordance-based canonical network (cf. 3.1).

Secondly, the action-observation-execution-matching system was shown to be particularly sensitive to intransitive actions. Buccino et al. (2004) compared cerebral blood flow when participants were watching mouth actions performed by a human, a monkey or a dog. These actions were either object-oriented (= transitive), such as biting a piece of food, or communicative (= intransitive), such as human silent speech, dog barking, or lip smacking by the monkey. They found activation of the action-observation-execution-matching system within the posterior parietal and ventral premotor cortex during all biting (= transitive) actions, but activation within the premotor sector of Broca's area only for intransitive actions that belonged to the human motor repertoire, i.e., silent speech and lip-smacking.

Besides its intransitivity, the present task has two additional advantages.

First, to perform oscillatory back-and-forth-movements should be easy for the participants. This is important since previous research implicated that perceptuomotor crosstalk depends on the level of expertise at performing the observed action (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Repp & Knoblich, 2004; Aglioti et al., 2008). The use of simple continuous arm movements with no novel demands to sensorimotor expertise should minimize interindividual differences in activation of the action-observation-execution-matching system due to differences in sensorimotor competence.

Furthermore, the present task comprised no particularly salient action goal. Goals as such do not exist in the objective world. There are only internally represented goal states, the external world, and the individual's relation to the world, which all possess a certain value for the organism (cf. Gallese & Metzinger, 2003). As such, action goals are always subject to interpretations on the part of the actor. These interpretations might differ between individuals. As a consequence, it was tried to minimize the influence of interindividual differences in the interpretation of an action goal on the activity within the action-observation-execution-matching system.

Consequently, the usage of intransitive, simple actions, such as oscillatory back-and-forth-movements, should prevent differential value assignments with respect to the task goal as well as confounding activation of an object-related canonical neural network outside the action-observation-execution-matching system. Furthermore, no expertise effects should be expected to emerge from such a task.

7.2 PARADIGM

In the present set of experiments, movement direction was chosen as the feature that stimulus (observed motion) and response (executed movement) shared, i.e., that was a feature of both stimulus and response. This was done because, on the one hand, movement direction has been shown to be an important movement parameter that is encoded in the central nervous system as a major determinant in both movement execution (e.g. Georgopoulos, Kalaska, Caminiti, & Massey, 1982; Schwartz, Kettner, & Georgopoulos, 1988; Vindras & Viviani, 2002) and motion perception (e.g. Camisa, Blake, & Levinson, 1977; Dobkins & Teller, 1996; Levinson & Sekuler, 1975). On the other hand, it has frequently been employed as the overlapping stimulus/response dimension in studies investigating perception-perception (e.g. Jazayeri & Movshon, 2007; Marshak & Sekuler, 1979; Raymond & Isaak, 1998), perception-action (Bouquet et al., 2007; Grosjean, Zwickel, & Prinz, 2008; Kilner et al., 2007, 2003; Zwickel et al., 2007), and action-action in-

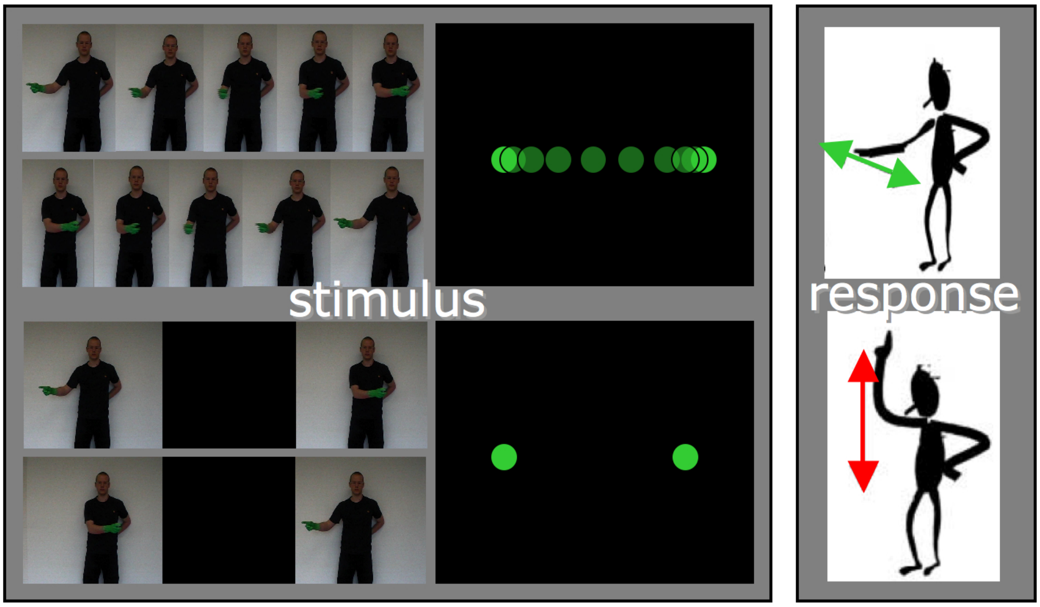

Figure 7.1: The experimental paradigm employed in Experiment 1 and with slight modifications also in the subsequent Experiments 2-4. For a more detailed description, see the Methods section of Experiment 1.

teractions (Heuer & Klein, 2006; Heuer, Kleinsorge, & Klein, 2007; Swinnen et al., 1998).

The basic structure of the experimental paradigm is illustrated in Figure 7.1. Based on the aforementioned consideration, the task of the participants was to perform continuous oscillatory movements in temporal synchrony with the stimulus' motion, but to ignore the orientation of motion presented on the screen. Thus, the orientation of motion was the dimension that could give rise to perceptuomotor crosstalk, but was not the dimension critical for task performance. More specifically, stimulus orientation in space was irrelevant for response execution, whereas the timing of the observed stimulus was the only relevant stimulus features. Thus, as far as the participants' understanding of the task was concerned, there was no reason for the movement orientation of the stimulus to influence the movement orientation of the participants' response.

The experimental manipulations comprised four factors:

1. Biological topography: type of stimulus. In order to assess the impact of biological surface/form features on interactions between perception and action, the observed oscillatory movements were either performed by a human model or a ball-like object.

2. Biological kinematics: mode of presentation. Biological kinematics could either be present or absent in the stimulus display. In the dynamic display condition, participants saw a film depicting actual movements. In the static display condition, participants only saw still pictures that represented the positions of the hand or the object at the turning points of their oscillatory movements. Even though the static display did not comprise actual motion, both displays are referred to as motion displays in the following chapters.

3. Response orientation. Participants were required to perform oscillatory movements that could either be horizontally or vertically oriented.

4. Congruency of stimulus motion. The observed orientation of continuous or implied motion could either be the same (= congruent) as or orthogonal (= incongruent) to the orientation of the required response movement.

CHAPTER 8

EXPERIMENT 1: SELECTION AND EXECUTION

8.1 INTRODUCTION

The purpose of the first experiment was twofold. Firstly, it should be examined whether perceptuomotor crosstalk is differentially sensitive to static and dynamic perceptual cues that indicate animacy of the stimulus. Secondly, it was sought to determine if and how such crosstalk affects response selection and movement execution.

To this end, various stimulus displays were generated that did or did not comprise biological kinematics and bodily topographics. In order to examine how the orientation of an observed stimulus affects processes of response selection, a two-alternative forced-choice procedure was employed. Choice-reaction times have previously been used to show that response selection depends on the spatial relationship between stimulus and response, even in cases, in which this relationship is irrelevant to the task at hand. This so-called Simon effect has mostly been studied with stationary stimuli that were mapped to discrete motor responses (for reviews, see Simon, 1990; Lu & Proctor, 1995), but has also been extended to dynamic stimuli (Ehrenstein, 1994; Michaels, 1988; Proctor, Zandt, Lu, & Weeks, 1993; Stürmer, Aschersleben, & Prinz, 2000).

After the initial choice-reaction-time task, participants had to continuously perform cyclical oscillatory movements in temporal synchrony with the stimulus display. During this phase, visuomotor performance was measured in order to assess emerging perceptuomotor crosstalk during movement execution.

8.2 METHODS

8.2.1 Participants

Sixteen students of the University of Dortmund, nine men and seven women, participated in the experiment. They were 18 to 28 years old (mean: 23.1 years; SD: 3.3 years). In this experiment as well as in all subsequent ones, all participants reported normal or corrected-to-normal vision with normal colour vision according to the Ishihara test (Ishihara, 2005). Each individual had given informed consent prior to the start of the experiment, which was done in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. The participants received 10 euros or course credit for their participation.

8.2.2 Apparatus

The experiment was conducted in a completely darkened room. Participants stood upright facing a 20-inch LCD monitor, which was positioned in front of them on eye level at a distance of about 100 cm. In order to record finger movement trajectories, a sensor of a miniBIRD system (miniBIRD 800, Ascension Technology Corporation) was attached to their right index finger directly above their finger nail. The position of the sensor was recorded at 103.6 Hz (spatial resolution: 0.11 mm) in three dimensions (x,y,z) with the x dimension corresponding to horizontal movements of the participants and the z dimension corresponding to vertical movements. Stimulus presentation was controlled by an IBM-compatible microcomputer using MATLAB and the Psychophysics Toolbox extension (Brainard, 1997; Pelli, 1997). Data collection via the miniBIRD was controlled by a separate computer. The computers were synchronized using the TCP/UDP protocol implemented in MATLAB via the TCP/UDP/IP Toolbox extension (Rydesaeter, 2001).

8.2.3 Stimuli

For the animate stimuli, a male human model (the author), dressed in black and standing upright in front of a neutral, white background, was filmed with a digital video camera (JVC GR-DVL100E, frame rate 25 Hz). Facing the camera, the model performed cyclical oscillatory movements with the whole right arm for about 30 seconds in either the vertical or the horizontal. During the recording of the films, movement frequency was synchronized with a metronome pacing at 1 Hz, so that each unidirectional movement had a duration of approximately one second. The resulting hand displacement covered approximately 750 mm in the horizontal and 700 mm in the vertical movements respectively. Positional data of the fingertip of these movements were recorded with a miniBIRD system at 103.6 Hz in three dimensions. Recordings of the x and z coordinates of these movements were subsequently used to create motion trajectories of a filled circle that served as the object stimulus. Thus, all movements comprised biological motion in terms of natural kinematics, which rendered them comparable in this respect. The size of the circle with a radius of 20 pixel was chosen so that it approximately corresponded to the area covered by the hand of the human model on the screen. Images covered an area of 720 x 576 pixel centred in the middle of the screen.

Films and animated object motion were used as stimuli in the dynamic display condition. In the static display condition, static images of the turning points of the oscillatory movements were presented for 400 ms, separated by a black blank screen. The interstimulus interval was set to 600 ms to avoid the perception of apparent motion.

The object as well as the right hand of the human model were coloured red or green. This colour cue served as the imperative stimulus for the participants and thus indicated the orientation of the required response movement.

8.2.4 Task

In each condition, participants had to produce cyclical oscillatory movements in response to various stimulus displays. Those response movements could either be horizontally or vertically oriented. The orientation of movement was cued by the colour of the model's hand or the colour of the object respectively. Participants were instructed to respond accurately and as fast as possible with horizontal movements in response to a red coloured stimulus and vertical movements when hand or object were green. In addition, they were told to subsequently synchronize their movement with the observed movement rate of the model/object at a rate of about 0.5 Hz.

8.2.5 Design and procedure

The experiment started with three blocks of familiarization, in which participants received their instructions and were introduced to the experimental setup and conditions.

In the first block of familiarization, participants perceived either a red or a green ball-like object appearing in the middle of the screen and had to perform horizontal or vertical movements according to a colour-orientation-mapping rule, which was attached to the apparatus just below the screen and remained there throughout the experiment. This initial block served to establish the mapping between colour stimulus and response orientation and to give participants the opportunity to find a comfortable and stable oscillatory movement pattern. Participants were told to realize an unconstrained arm movement that comprised wrist, elbow, and shoulder joints without artificially freezing any degrees of freedom. More specifically, painting movements were used as a metaphor in the instruction. They were also told to choose a comfortable movement amplitude approximately in the range between 400 and 700 mm.

In the second and third block of familiarization, participants were introduced to the stimuli that corresponded to each experimental conditions, i.e. stimulus type (human model versus ball-like object), mode of presentation (static versus dynamic display), response orientation (green hand/ball versus red hand/ball), and orientation congruency (stimulus motion within the same plane versus stimulus motion in the plane perpendicular to response orientation). These blocks were also used to familiarize participants with the task ("React as fast as possible to the colour cue and subsequently synchronize your movement frequency with the frequency of the stimulus without considering its direction of movement"). Accordingly, they experienced each condition once. While the second familiarization block comprised the static display stimuli, the third block served to introduce the continuous motion stimuli in the dynamic display condition.

The actual experiment consisted of three blocks, which each comprised 16 trials. Each movement trial started with the presentation of a blank screen. Subjects positioned their right hand in a neutral position in front of their body, from where horizontal and vertical movements could be rapidly initiated, and were told to be ready to respond. After a randomly chosen foreperiod of 500, 700, 900, 1100 or 1300 ms, the stimulus appeared on the screen and subjects initiated their movement in the direction indicated by the colour cue as fast as possible. The foreperiod was randomly varied between trials to prevent participants from knowing the precise time at which the stimulus would appear.

For the static display condition, a trial started with one of the two stimulus pictures depicting a turning point of either a horizontal (rightward position) or a vertical movement (upward position). The picture was presented for 400 ms. No neutral middle position was shown beforehand to prevent the perception of apparent motion. The dynamic display condition began with a continuous rightward or upward movement, which started from a neutral middle position. Thus, information regarding the model's direction of movement was presented either statically or dynamically at approximately the same time.

In both display condition, each trial lasted 20 seconds and comprised ten back-and-forth movements. After 20 seconds, the screen turned black and participants were told to prepare for the next trial. Intertrial intervals were fixed at five seconds to prevent fatigue. However, rest breaks were allowed when necessary. The whole experiment took approximately 45 minutes. The order of experimental conditions was counterbalanced across participants and across blocks by using a Latin square (1 2 16 3 15...), which yielded 16 possible block structures. Three of those block structures were assigned to each participant. Thus, each experimental condition as well as each possible transition from one conditions to another occurred equally frequent across the whole experiment. In this and all subsequent experiments, an experimenter monitored each participant throughout the entire testing session in order to make sure that all procedures were carried out correctly.

8.2.6 Data reduction and analysis

For each trial, the x, y, and z positions of the finger were recorded, but only x and z data were analyzed. The resulting time series were low-pass filtered (fourth-order Butterworth filter, 10 Hz, dual pass) and differentiated (two-point central difference algorithm). Separate velocities along the x and z axes were calculated. Movements were analyzed in terms of three parameters: reaction time, main movement orientation and movement variability in terms of the variance of the positional data orthogonal to the main movement orientation.

Reaction time was defined as the time it took participants to initiate their response with the required orientation. It was determined based on movement onset along the orientation required by the colour cue. Therefore, velocity along the z-axis was subtracted from velocity along the x-axis for horizontally oriented movements and vice versa for vertically oriented movements. Accordingly, negative velocity values of the resulting difference curve indicated movements with the wrong orientation. Using this difference curve, a forward search, which started at stimulus onset, determined those samples that exceeded five percent of peak velocity along the movement orientation required by the colour stimulus for the first time, and remained larger for 200 ms thereafter. Due to the continuous character of the response, there were no response errors. Even though participants might have initiated movements along the wrong orientation, they had enough time to correct this once they became aware of their error. Those trials were included in the analysis.

For the kinematical analysis of individual movements (sample trajectories can be seen in Figure 8.1), the continuous oscillatory movements were segmented into single movements from right to left and from left to right for horizontal conditions, and from top to bottom and from bottom to top for the vertical movements. Segmentation was based on the velocity of the finger along the x-axis for horizontal and along the z-axis for vertical movements. Movement segments with extremely short durations ($<$ 200 ms) or short distances travelled (< 5 cm) were discarded as stationary phases at the turning points of the oscillatory movements and not included in subsequent analyses. So were movements that strongly deviated from the response direction as cued by the colour of the stimulus (directional error >= 45°). Thus, only the actual movement phases were included in the analysis.

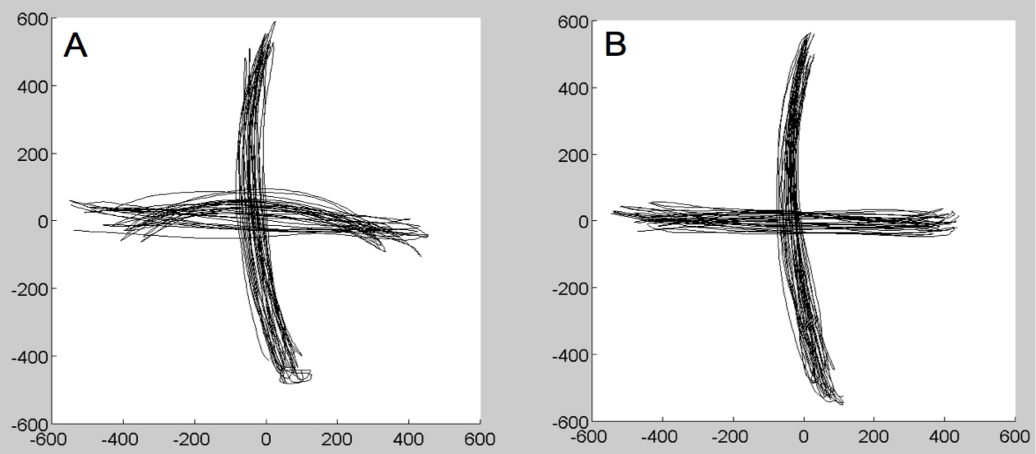

Figure 8.1: Example movement trajectories made in the XZ plane by a single participant. For the purpose of demonstration, movements were normalized so that their mean along the x- and z-axis is equal to zero. The plots show horizontal and vertical movements during the observation of (A) congruent stimulus motion and (B) incongruent stimulus motion performed by a human model in the dynamic display condition. The Figure shows displacement in mm on both axes.

Previous studies used orthogonal variance of oscillatory movements with respect to an extrinsic Cartesian reference system (e.g. Bouquet et al., 2007; Kilner et al., 2003, 2007; Stanley et al., 2007). In the present study, individual submovements were represented by the 95 percent confidence ellipse of the distribution of the sampled data points for each trajectory by using principal component analysis; the length of the semi-axes of this ellipse are the square roots of the eigenvalues of the variance-covariance matrix of the individual point distribution scaled to contain 95 percent of the theoretical point population (Johnson & Wichern, 1982). For the kinematical analysis, the movement confidence ellipse is characterized by (a) its orientation, defined as the angle between the major axis of the ellipse and the x-axis; and (b) its orthogonal variability, defined as the length of the minor axis of the confidence ellipses. Note that this requires a multiplication of the length of the semi-axes by the factor 2. This multiplication with a constant factor does not affect statistical analyses. This procedure affords a decomposition of orthogonal variance as used in previous studies into two components, a directional component in terms of main movement orientation, and a variability component in terms of variance orthogonal to the main movement direction. Finally, a change in movement orientation of orthogonal variance in incongruent trials is conceived to reflect perceptuomotor assimilation, whereas a change in either of the two variables in congruent trials is conceived to represent perceptuomotor contrast.

In this analysis as well as in the following ones, the first four movements, i.e., two cycles, were omitted to prevent the data from being affected by the surprise of the visual stimulus appearing on the screen. From the remaining movements, means were computed for each stimulus condition and each block of trials. Each mean was thus based on approximately sixteen movements. These individual means were analyzed in a five-way analysis of variance (ANOVA) with the within-participant factors stimulus type (human actor versus object), mode of presentation (static versus dynamic display), response orientation (horizontal versus vertical), congruency (same orientation versus orthogonal orientation), and block of trials.

In this as well as in all subsequent experiments, the Greenhouse-Geisser epsilon (Greenhouse & Geisser, 1959) was evaluated to determine whether the repeated measures data met the assumption of sphericity ($\epsilon > 0.75$). In cases where sphericity was not met, the F statistic was evaluated for significance by using the Greenhouse-Geisser adjusted degrees of freedom, though the uncorrected degrees of freedom are reported. In all subsequent analyses, the significance level was set to .05. For the effects that were not significant, p values are only reported for analyses in which $F > 1$.

8.3 Results

Results are first reported in terms of reaction times and second in terms of movement kinematics. Data are presented averaged across blocks.

8.3.1 Reaction time

The most important result with respect to reaction times is shown in Figure 8.2. For the dynamic display condition, in which participants were watching continuously moving stimuli, reaction times were significantly slower in incongruent trials than in congruent trials, regardless of the type of stimulus (791 ms vs. 677 ms for the human model, and 766 ms vs. 607 ms for the object). For the static display of movement turning points that merely implied motion, such slowing only emerged in trials in which the human model was part of the stimulus display (857 ms vs. 738 ms for the human model, and 724 ms vs. 701 ms for the object). This pattern of results gave rise to a significant three-way-interaction involving the factors stimulus type, mode of presentation and congruency, $F(1{,}15) = 5.6$, $p < .05$, $\eta^2 = .27$.

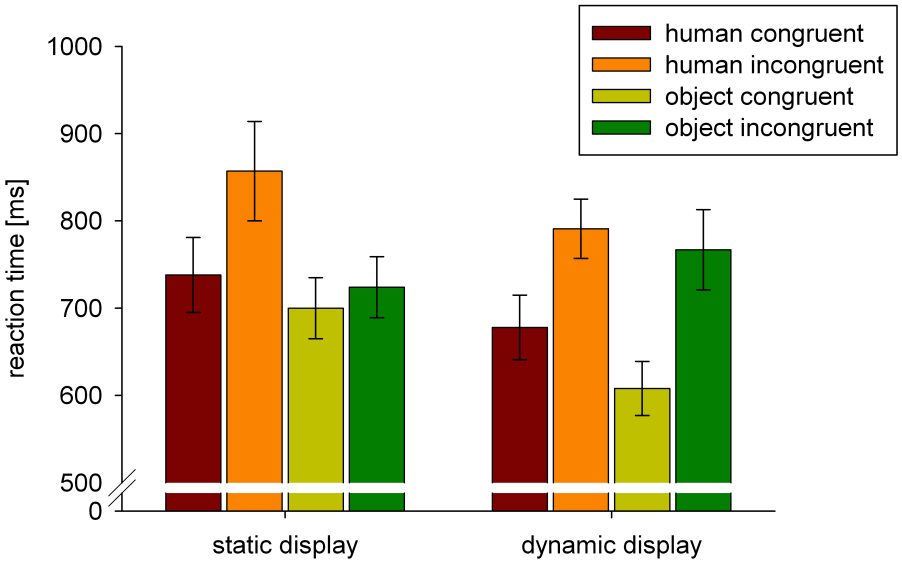

Figure 8.2: Mean reaction times in response to human (red) and object (green) stimuli, displayed separately for each mode of presentation (static versus dynamic), and for congruent and incongruent trials. Error bars represent standard errors of the mean.

Furthermore, reaction times were generally higher in incongruent, 785 ms, than in congruent trials, 681 ms, giving rise to a significant main effect of congruency, $F(1{,}15) = 10.7$, $p < .01$, $\eta^2 = .42$. Participants also responded faster to moving than to static stimuli, 711 vs. 755 ms, and were also significantly faster in responding to the object with a mean reaction time of 700 ms, whereas it took them 766 ms to respond to stimulus displays that involved the human actor, $F(1{,}15) = 4.8$, $p < .05$, $\eta^2 = .24$, and $F(1{,}15) = 14.1$, $p < .01$, $\eta^2 = .50$ respectively.

8.3.2 Kinematics

Movement Variability

The most conspicuous finding with regard to movement variability was a significant four-way-interaction of stimulus motion, stimulus type, congruency, and response orientation, $F(1{,}15) = 5.7$, $p < .05$, $\eta^2 = .28$. As can be seen in Figure 8.3, while virtually no effects of the stimulus display were found for vertical response movements, a significant difference between congruent and incongruent trials appeared only when participants had to respond to a human model in the dynamic display condition, in which continuous movements were shown. In contrast, no significant differences were found regarding the comparisons of congruent and incongruent trials in the remaining conditions.

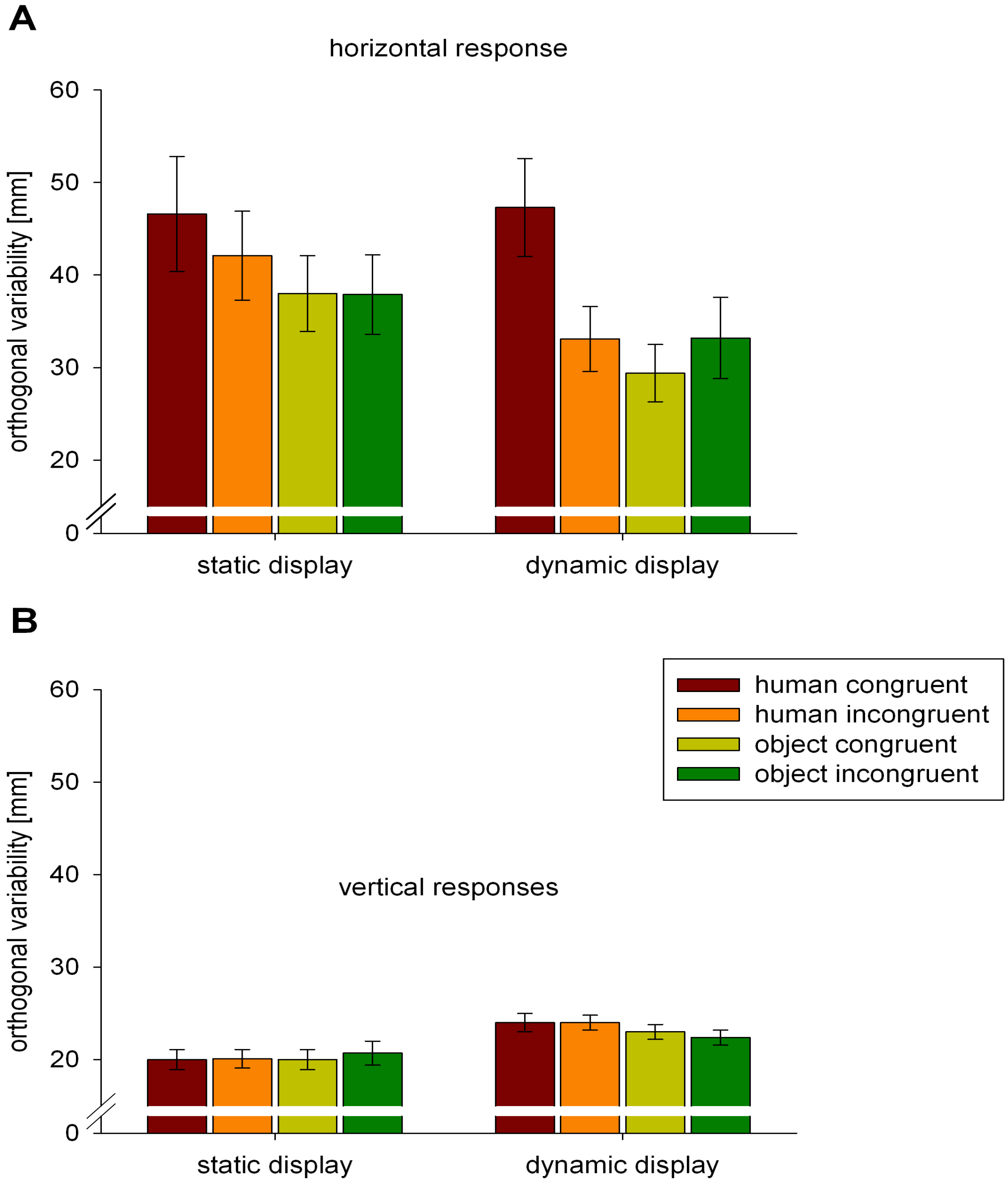

Figure 8.3: Mean movement variability orthogonal to main movement direction for horizontally (A) and vertically (B) oriented response movements shown separately for static and dynamic displays. Bars represent performance in congruent and incongruent trials in response to human (red) and to object stimuli (green).

This four-way-interaction gave rise to a multitude of other significant effects. Accordingly, the difference in orthogonal variance between congruent and incongruent trials was especially pronounced during the observation a continuously moving human model, 14.2 mm, as compared to static depictions of movement turning points, 4.5 mm, giving rise to a significant interaction of stimulus type, mode of presentation, and congruency, $F(1{,}15) = 5.7$, $p < .05$, $\eta^2 = .28$, which together formed the basis for a significant main effect of stimulus type, $F(1{,}15) = 15.2$, $p < .01$, $\eta^2 = .50$, and a marginally significant main effect of congruency, $F(1{,}15) = 4.4$, $p < .1$, $\eta^2 = .23$, as well as a significant interaction of those two factors, $F(1{,}15) = 10.4$, $p < .01$, $\eta^2 = .41$.

The statistical analysis also showed that horizontal movements were significantly more variable than vertical movements, $F(1{,}15) = 22.5$, $p < .01$, $\eta^2 = .62$. Within vertically oriented response movements, experimental variations of the stimulus display did not affect movement variability. Together with the interaction effect described above, this gave rise to significant interactions of response orientation and congruency, $F(1{,}15) = 5.9$, $p < .05$, $\eta^2 = .28$, response orientation and type of stimulus, $F(1{,}15) = 13.4$, $p < .01$, $\eta^2 = .47$, response orientation and mode of presentation, $F(1{,}15) = 7.8$, $p < .05$, $\eta^2 = .34$, and finally response orientation, type of stimulus, and congruency, $F(1{,}15) = 10.9$, $p < .01$, $\eta^2 = .42$.

Movement Orientation

For the main movement orientation, the ANOVA revealed ï£¡ besides the highly significant, but trivial main effect of response orientation, $F(1{,}15) = 32167.9$, $p < .0$, $\eta^2 = 1$ - a significant interaction of congruency and response orientation, which indicated a systematic difference of movement orientation between congruent and incongruent trials when participants had to perform horizontally oriented movements, $F(1{,}15) = 4.8$, $p < .05$, $\eta^2 = .24$. However, the mean difference amounted to only 0.3°.

8.4 DISCUSSION

The purpose of the first experiment was to assess whether perceptuomotor crosstalk is sensitive to the presence of biological surface features and biological kinematics and whether this differentially affects the response selection and the online control of action. Results revealed effects of perceptuomotor crosstalk during both response selection and movement execution, which are discussed separately in the following sections.

8.4.1 Perceptuomotor Crosstalk during Response Selection

Results showed that for response selection, the presence of dynamic motion served as a strong cue, albeit being irrelevant for the current task, which primed movement execution in the direction of observed movement. Short reaction times were obtained when the orientation of stimulus and response movement were congruent, whereas longer reaction times were obtained under conditions in which orientations of stimulus and response were perpendicular to each other. In the absence of dynamical motion information, this priming occurred only in the presence of a human model depicting imitable body postures. Obviously, only the human posture was perceived to provide an orientation of (implied) movement, whereas the spatial position of the object did not affect response selection.

These results are in line with previous empirical work by Stürmer et al. (2000), who also used a two-choice-reaction-time paradigm to explore perceptuomotor crosstalk. In their study, participants had to execute a particular hand gesture in response to a symbolic imperative stimulus while observing corresponding or non-corresponding hand stimuli. They found that observation of both static (= hand posture) and dynamic (= hand gesture) displays affected reaction times as movement initiation in corresponding conditions was found to be faster compared to the non-corresponding conditions. The usage of different stimulus onset asynchronies (SOA; the time between onset of the relevant and the irrelevant stimulus feature) revealed that reactions to static and dynamic stimuli differed with respect to their time course. While the dynamic information inherent in the irrelevant hand gesture always induced a tendency to imitate the observed motion irrespective of the SOA, the influence of the irrelevant static hand posture was greatest for a SOA of 0 ms and decayed with increasing SOAs. Based on this, the authors concluded that perceptuomotor crosstalk for static and dynamic stimuli does not rely on the same functional basis. Accordingly, they distinguished between two mechanisms mediating this correspondence effect, i.e., a state-based mechanism, which accounts for the correspondence effects observed upon the presentation of static hand postures, and a movement-based mechanism, which mediates correspondence based on stimulus inherent movement kinematics.

The potency of the state-based mechanism is based on the notion that actions are specified in terms of their goal-state (e.g. Rosenbaum, Cohen, Jax, Weiss, & Wel, 2007). This idea is also present in the Theory of Event Coding. Within TEC, the ideomotor principle asserts that actions are controlled by action codes that comprise representations of their perceived effects in the environment (cf. Hommel et al., 2001). Thus, whenever a stimulus depicts the goal state of an action, this should automatically gear up the motor system to perform the movement associated with this goal state, which in turn would lead to the observed interference in response selection. This is in line with previous studies by Brass et al. (2000, 2001) who reported similar effects for the comparison of hand postures versus symbolic cues (see chapter 6.2). Accordingly, Stürmer et al. (2000) showed that the presentation of intermediate postures instead of movement end states abolished the correspondence effect. This type of perceptuomotor crosstalk has been referred to as ideomotor compatibility, i.e., "the extent to which a stimulus corresponds to the sensory feedback from its required response" (p. 52; Greenwald, 1972). In line with the notion of ideomotor compatibility, only imitable body postures were found to induce perceptuomotor crosstalk in the present study, whereas the position of the object did not affect reaction times, even though it comprised the same spatial information. This indicates that the state-based mechanism is selectively sensitive to the presence of specific biological features of stimulus topography in the present task.

The movement-based mechanisms active in the dynamic condition led to perceptuomotor crosstalk irrespective of the topographic features of the stimulus. This result, too, can be reconciled within the Theory of Event Coding. The necessity to specify the orientation of the response movement upon stimulus presentation automatically primes the perception of the orientation of the stimulus movement, even though orientation of the stimulus is irrelevant for the response (cf. Hommel, 2009; Wykowska et al., in press). The finding that the effect of stimulus orientation in the presence of dynamic motion information was not sensitive to biological topographics indicates that movement orientation is indeed a feature code involved in action planning and perception (cf. Zwickel et al., in press).

Lastly, some remarks on the conjecture that the present reaction time effects reflect perceptuomotor crosstalk at the level of response selection are necessary. In the dynamic display condition, the onset of the imperative stimulus and the onset of irrelevant stimulus motion coincided. Previous research has suggested a longer latency for the detection of motion direction as compared to the detection of stimulus onset because the detection of movement direction requires at least a minimal extent of stimulus motion (Tynan & Sekuler, 1982; Carl & Gellman, 1987), whereas the imperative colour cue is immediately perceived upon its onset. In combination with the continuous nature of the present response and the way reaction times were determined as the time it took participants to initiate *appropriately oriented* movements, it might be argued that response selection based on the colour cue had already been finished and a response had already been initiated as the incongruent direction information became available. The latter might then have caused a deflection of the orientation of an already selected, and presumably correct response that was shorter than the required 200 ms and thus remained undetected by the algorithm. The response had to be corrected subsequently, which led to longer reaction times. Thus, the observed reaction time differences would not be localized within the stage of response selection, but would rather reflect perceptuomotor crosstalk during movement execution.

While this argument cannot definitely be eliminated based on the current data and setup, there is reason to assume that the reaction time differences in the dynamic display condition indeed reflect perceptuomotor crosstalk at response selection. The time required to identify the direction of a movement with a velocity of 1°/s has been reported to be 200-250 ms (Tynan & Sekuler, 1982), and to drop with higher stimulus velocity (Ehrenstein, 1993; cited in Ehrenstein, 1994). Given that the stimulus in the current study moved approximately with a velocity of 6°/s, it seems reasonable to assume that motion orientation was processed fast enough to interfere with response selection before the selection process is finished in the current task.

8.4.2 Perceptuomotor Crosstalk during Movement Execution

With respect to movement variability, results revealed perceptuomotor crosstalk, which was specifically tied to stimulus type, mode of presentation and response orientation: When participants observed horizontal movements by the human model in the dynamic display condition, movement variability was found to be larger in congruent trials than in incongruent trials.

With respect to the movement orientation, there was a systematic difference between congruent and incongruent trials. Analogously to the results for movement variability, this effect was also limited to horizontal response movements. However, it was neither modulated by the type of stimulus nor the mode of presentation.

At present it is difficult to interpret these results since Experiment 1 did not comprise a proper baseline measure. Thus, it is impossible to discern if the observation of congruent stimuli actually led to an increase in movement variability or if the observation of incongruent stimuli led to a decrease in movement variability, i.e., to determine the nature of perceptuomotor crosstalk in terms of assimilation or contrast. A similar reasoning can be applied to the observed difference in movement orientation. It might reflect assimilation based on a counterclockwise shift of movement orientation in incongruent trials, but also imply contrast caused by congruent stimulus motion. In order to clarify this issue, Experiment 2 aimed to replicate these findings with the inclusion of a baseline and a slightly modified experimental procedure.

Chapter 9

Experiment 2: Of Baselines and Directions

9.1 Introduction

The purpose of the second experiment was threefold. Firstly, the reliability of the results of Experiment 1 should be tested by replicating the specific crosstalk effects during movement execution observed previously, especially with regard to the rather particular modulation of crosstalk by response orientation, stimulus type and presentation mode.

Secondly, it was sought to determine if the perceptuomotor crosstalk effects observed during movement execution in Experiment 1 originated from interference during incongruent or congruent trials and should thus be conceived in terms of assimilation or contrast. To this end, the two-choice-reaction-time-task was abandoned and a continuously assessed baseline was added to the experiment. Participants were informed about the required response at the beginning of each trial. This involved the presentation of arrows that signalled the direction of response movement within the first two cycles (= four movements) of each trial. Those movements were used as a baseline, relative to which movement orientation and variability were then assessed later in the trial when the display switched from arrows to the presentation of the stimuli used in Experiment 1.

Thirdly, Experiment 2 aimed to control for another shortcoming of Experiment 1, namely the potential influence of intra- and interindividual differences in the relationship between the direction of stimulus motion and response movements. This feature, in the following referred to as directional mapping, was not controlled for in Experiment 1 and could potentially distort the effects. With respect to movement orientation, for instance, the observed difference between congruent and incongruent trials, in which horizontal response movements had to be performed, might actually be an underestimation of the true effect because some participants in some trials might have chosen to move rightward as the model moved upward (= 90° directional mapping), whereas others decided to move downward (= 270° directional mapping).

Since participants should already be moving in a stable way at a movement frequency of 0.5 Hz, the initial direction of movement in the dynamic display and the first posture following the initiation phase in the static display were manipulated to generate four different directional mappings between stimulus movements and the participant, i.e., 0°, 90°, 180°, and 270°. Directional mappings refer to the counterclockwise angle between the direction of stimulus and the direction of response motion. Accordingly, in the 0° condition, the directions of stimulus and response movements were identical, whereas they were opposite to each other in the 180° condition. In conditions with directional shifts of 90° and 270°, the response direction was rotated 90° and 270° counterclockwise to the stimulus direction on the screen.

9.2 METHOD

Basically, the same setup was used as in the first experiment. However, some features of the setup were changed in order to accommodate the specific aims and manipulations of Experiment 2. Those are detailed below.

9.2.1 Participants

Sixteen students of the University of Dortmund, eight men and eight women, participated in the experiment. They were 20 to 30 years old (mean: 24.7 years; SD: 2.6 years). Each individual had given informed consent prior to the start of the experiment. They received 10 euros or course credit for their participation.

9.2.2 Apparatus

Increased computational performance allowed that stimulus presentation and data collection could be controlled by a single computer. The LCD monitor was replaced by a CRT display. This was done to improve the quality of motion depiction by an increase in the refresh rate of the screen and to achieve a more accurate synchronization of data collection and stimulus presentation within one refresh cycle. In consideration of the increased duration of the experiment, participants were seated in front of the computer screen.

9.2.3 Task

The task was essentially the same as in the previous experiment. This time however, no speeded reaction to a colour stimulus was required. Participants were only told to synchronize their movements to the stimulus motion as accurately as possible.

9.2.4 Stimuli

The same stimuli were used as in Experiment 1. Even though there was no need for a discriminative colour stimulus, the right hand of the human model remained coloured green to maintain its visual saliency. The colour of the object, which moved on a black background, was set accordingly.

9.2.5 Design and Procedure

Experimental manipulations comprised the type of stimulus (human model versus object), the mode of presentation (static versus dynamic), the orientation of response movement (horizontal versus vertical), and the directional mapping (0° versus 90° versus 180° versus 270°), which yielded a four-factorial 2x2x2x4 within-subject design. The resulting 32 experimental conditions were counterbalanced across participants according to the following schemes: Experimental chunks were generated from the combination of response orientation and mode of presentation. This yielded four experimental chunks, each of which comprised the combination of type of stimulus and directional mapping. Those eight trials within a chunk were presented in a randomized order in each block. The order to chunks was counterbalanced across participants based on a Latin square. The order to chunks within a block was constant within participants.

The experiment comprised three blocks. Each block consisted of 32 (4x8) consecutive trials lasting 21 seconds each. The general procedure of an experimental trial is depicted in Figure 9.1. At the beginning of each trial (preparation phase), a counter counted down from 3 at a pace of 1 Hz. This way, participants could already pick up the pace for the subsequent movement. At the count of zero, an arrow that indicated the initial direction of movement appeared in the centre of the screen. It remained visible for 400 ms, then the screen turned black. After 600 ms, a second arrow that pointed in the opposite direction from the first one appeared on the screen. After 400 ms, the screen turned black again. Anther 600 ms later, this procedure was repeated once for a total of two baseline cycles of four seconds duration. Movements during these two cycles were taken as the baseline for each trial. After the baseline phase, the screen immediately changed to the respective stimulus presentation of continuous or implied model motion. Participants were explicitly told not to stop, but to continue their movement in the same direction, and to temporally synchronize with the stimulus' motion in order to maintain one of four possible directional mappings (Fig. 9.1). Each trial continued for fourteen seconds and thus comprised seven cycles of oscillatory movements under the respective experimental condition.

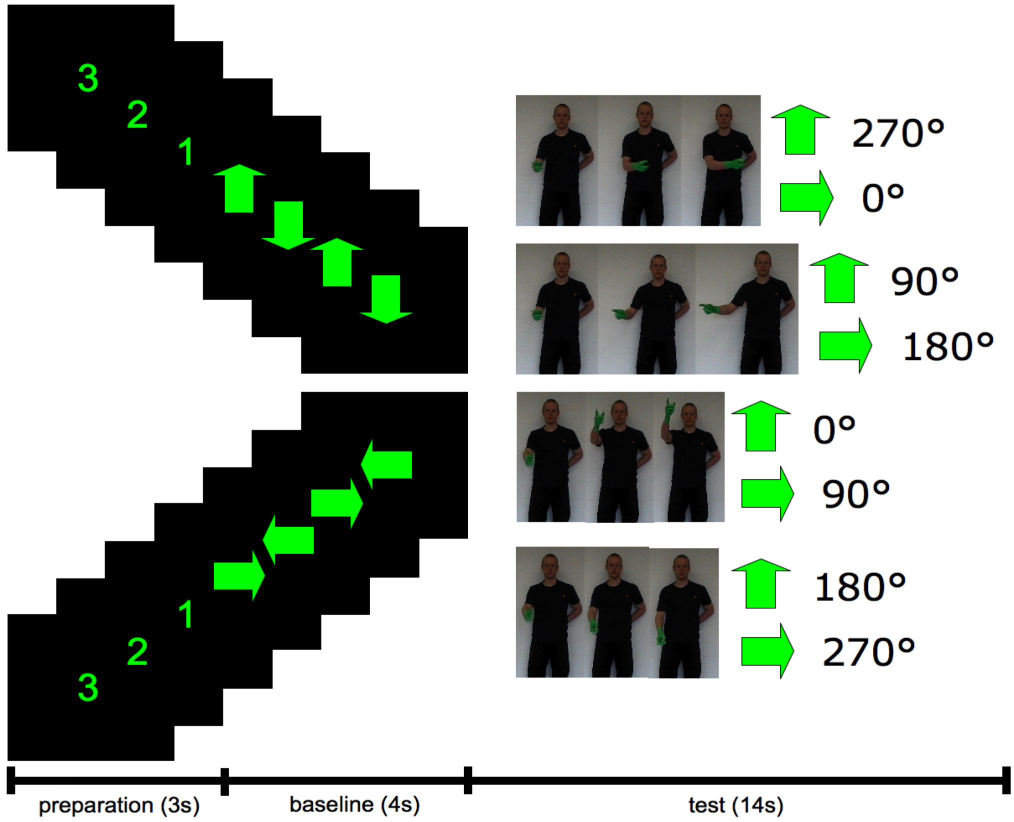

Figure 9.1: Modified experimental paradigm for Experiment 2. For detailed description of the procedure of a trial see text. Arrows behind the stimulus display indicate the required response movement direction at stimulus onset. Accordingly, directional mappings, which describe the angle between stimulus and response motion (counterclockwise), are provided. Note that even though only the human model in the dynamic display condition is depicted in the Figure, the same procedure applied to the object model as well. Stimuli in the static display condition were presented accordingly.

As can be seen in Figure 9.1, explicitly instructing the participants' movement direction in the baseline phase allowed to establish different directional mappings between stimulus and response by varying the initial direction of the stimulus at stimulus onset. Stimulus motion was rotated counterclockwise according to the size of the directional shift. Directional mappings of 0° and 180° imply that stimulus and response take place in the same movement plane, with 0° indicating identical directions and 180° movements in opposite directions. For directional mappings of 90° and 270°, stimulus motion was rotated counterclockwise to the respective response movement. For a rightward movement, for instance, a directional mapping of 90° implies a simultaneous upward motion of the stimulus, and 270° implies concurrent downward motion of the stimulus. In case of a participant not responding in the correct directional relation, the trial was aborted by the experimenter and repeated by the participant.

9.2.6 Data analysis

Data analysis was carried out in the same way as described in Experiment 1. However, only movement kinematics were analyzed.

9.3 RESULTS

For the kinematic analysis, the oscillatory movements were segmented again and the same criteria to determine incorrect movements were used as in the first experiment (duration < 200 ms, distance travelled < 5 cm, directional error $< 45°$). Main movement orientation and orthogonal variance were computed separately for baseline and test phases within each trial. The first four movements of each test phase were discarded. Again, there were no significant interactions involving the factor block so that data are presented averaged across blocks.

9.3.1 Movement Variability

Overall, the observed pattern of results was similar to Experiment 1. Virtually no effects of the stimulus display were found for vertical response movements. As can be seen in Figure 9.2, orthogonal variance was only systematically modulated by the directional mappings when participants had to respond to a human model in the dynamic display condition. Such systematic modulation was absent in the presence of the object stimulus. Accordingly, post-hoc comparisons of horizontal response movements revealed significant differences in orthogonal variance between dynamic displays of the human and the object stimulus when participants performed oscillatory movements in the same movement plane regardless of whether the model moved in the same or the opposite direction, i.e., for directional mappings of 0° and 180°, but not for 90° and 270°. Similar to Experiment 1, this gave rise to a significant four-way-interaction of stimulus type, presentation mode, response orientation, and directional mapping, $F(3,45) = 5.4$, $p < .01$, $\eta^2 = .27$.

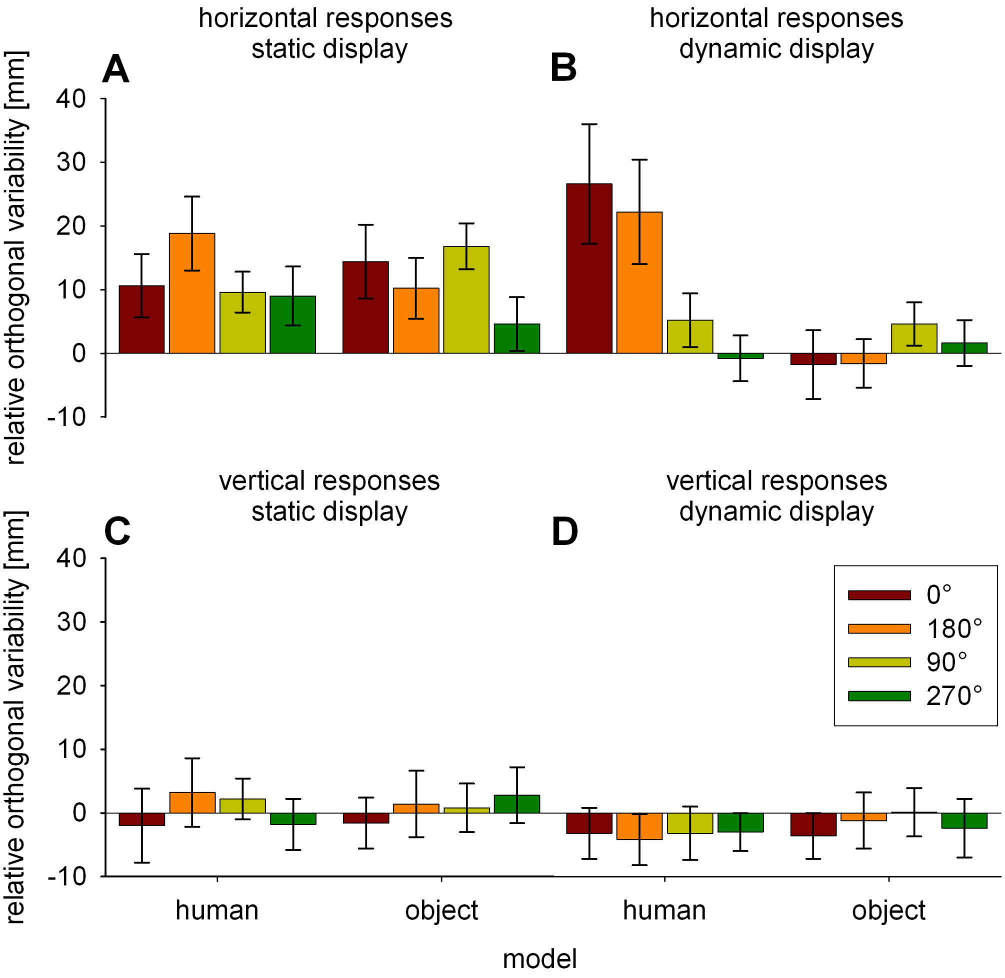

Figure 9.2: Mean shift of movement variability orthogonal to main movement direction relative to baseline as a function of directional mapping, shown separately for (A) horizontal and (C) vertical movements in response to static displays of stimuli, and horizontal (B) and vertical (D) movements in response to dynamic displays of stimulus motions. Lines denote human (red) and object (green) stimuli, along with standard errors of the mean.

Accordingly, based on the four-way-interaction, the following effects also reached significance: A three-way-interaction of type of stimulus, directional mapping, and response orientation, $F(3{,}45) = 3.0$, $p < .05$, $\eta^2 = .17$, two-way-interactions of type of stimulus and directional mapping, as well as type of stimulus and response orientation, $F(3{,}45) = 3.9$, $p < .05$, $\eta^2 = .21$ and $F(1{,}15) = 9.6$, $p < .01$, $\eta^2 = .39$ respectively, and finally the main effects of type of stimulus $F(1{,}15) = 9.6$, $p < .01$, $\eta^2 = .39$, response orientation $F(1{,}15) = 5.5$, $p < .05$, $\eta^2 = .27$, and directional mapping, $F(3{,}45) = 4.7$, $p < .01$, $\eta^2 = .24$.

9.3.2 Movement Orientation

In Figure 9.3, relative orientations of response movement are shown. Relative orientation refers to the difference between the main movement orientation in the two baseline cycles and the main orientation in the subsequent test cycles. A positive value indicates a counterclockwise shift in movement orientation. As can be seen, results showed a significant positive bias when stimulus motion was rotated 90° counterclockwise with reference to the response movement direction. This was supported by the statistical analysis with a significant main effect of directional mapping, $F(1{,}15) = 4.1$, $p < .05$, $\eta^2 = .21$. However, this positive shift was only significantly different from zero for horizontal response movements, 0.8°, $F(1{,}15) = 8.5$, $p < .05$, but not for vertical ones, 0.3°, $F(1{,}15) = 1.3$, $p > .2$, giving rise to a highly significant interaction of directional mapping and response orientation, $F(3{,}45) = 9.0$, $p < .01$, $\eta^2 = .37$.

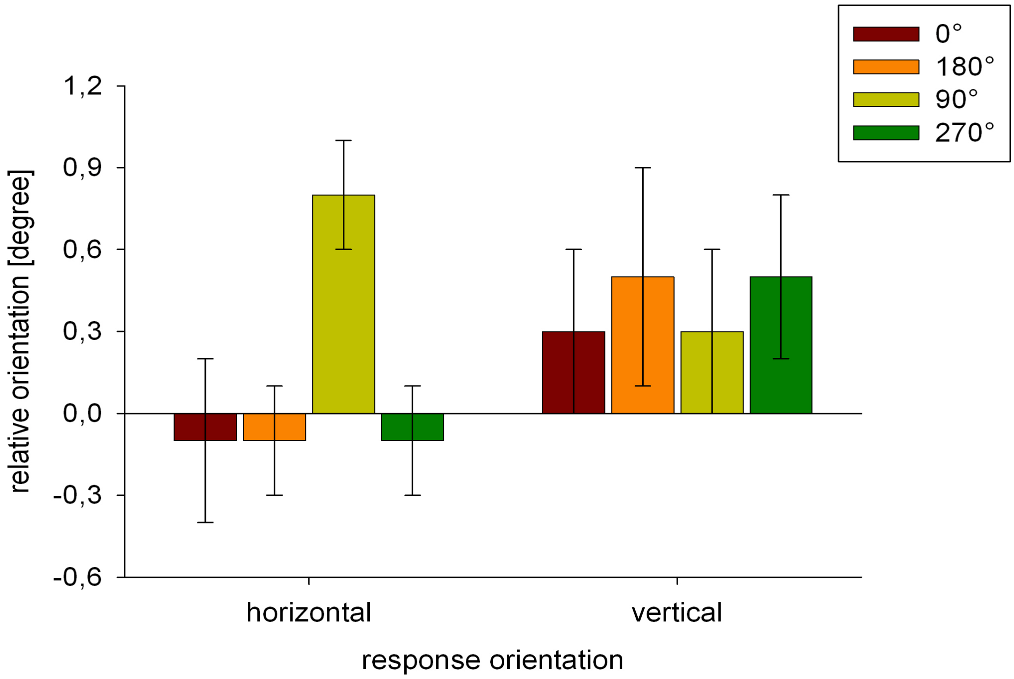

Figure 9.3: Mean orientation of response movements relative to baseline shown separately for horizontal and vertical response movements. Coloured bars represent the four directional mappings between stimulus and response, error bars represent standard errors of the mean. Positive values indicate a counterclockwise shift.

9.4 Discussion

The purpose of the second experiment was to assess whether perceptuomotor crosstalk during movement execution was due to a modulation of movement orientation and movement variability by congruent or incongruent stimulus motion. Results revealed an effect of perceptuomotor crosstalk, which was due to the observation of incongruent stimulus motion and an effect of perceptuomotor contrast during the observation of congruent stimulus motion. These effects are discussed separately in the following sections.

9.4.1 Perceptuomotor Contrast of Response Variability

The results of Experiment 2 on movement variability, on the one hand, confirm, and, on the other hand, extend the findings of Experiment 1. An increase in movement variability relative to baseline performance was found when observed and executed movements both occurred within the horizontal plane. Perceptuomotor crosstalk between simultaneous action execution and observation indeed manifested as a contrast effect. Perceptuomotor contrast effects have previously been reported in a variety of tasks such as weight judgements (Hamilton et al., 2004), stimulus detection and identification (Müsseler & Hommel, 1997a, 1997b), and visuomotor coordination (Schubö et al., 2001; Schubö, Prinz, & Aschersleben, 2004; Zwickel et al., in press). Zwickel et al. (in press), for instance, had participants perform discrete linear hand movements of a certain direction while, at the same time, encoding the direction of an unrelated stimulus motion. They found that perceived directions were repelled by produced directions and vice versa.

Importantly, the perceptuomotor contrast effect during movement execution in the present experiment emerged only in the presence of both a biological topography of the stimulus and biological kinematics of its motion; neither a biological velocity profile nor surface features alone were able to elicit this effect. Instead, it appears that both constitute necessary, but not sufficient preconditions for the activation of the action-observation-execution-matching system.

Furthermore, the contrast effect was found to be limited to horizontal response movements. While this is a rather strange result in itself, it has been described previously. Kilner et al. (2003) used a similar experimental paradigm. As described in chapter six, they also found specific interference effects for the observation of biological motion. Furthermore, they reported a significant main effect of response direction, according to which orthogonal variance of horizontal movements had been found to be significantly greater than orthogonal variance in the vertical direction. They attributed this to a natural tendency to perform more arching movements in the horizontal plane. Even though the interaction of response direction and congruency, as well as the three-way interaction with the additional factor of animacy of the stimulus (robot arm vs. human actor) exhibited a significant trend, $F(1,7) = 5.2$, $p < .1$, and $F(1,7) = 4.0$, $p < .1$, respectively, the authors rejected a modulatory influence of response orientation on the observed interference effect. However, Stanley et al. (2007) also reported modulatory effects of response orientation on perceptuomotor crosstalk. In their study, the observation of specific effects of perceptuomotor crosstalk was limited to the horizontal movement plane as well.

Being cautious with between-experiment comparisons, it nevertheless seems reasonable to assume that the modulatory effect of response orientation on the specific interference effect of biological motion described by Kilner et al. (2003) and Stanley et al. (2007) is analogous to the one found in Experiments 1 and 2 of the present study. Thus, it might not be a simple chance result, which could be attributed to the small sample sizes used in their studies (cf. Stanley et al., 2007). Consequently, the nature and the reliability of this modulatory effect of response orientation was taken up and more closely examined in Experiment 3.

With respect to the study by (Zwickel et al., in press), who reported a contrast effect for concurrent execution and observation of discrete linear movements, it is noteworthy that they did not find a systematic relationship between the size of the contrast effect and the amount of angular separation between stimulus and response movements (except for the angular separation of 100°, in which contrast switched to assimilation). They argued that perceptuomotor crosstalk occurred at a categorical level, where movement directions are encoded in terms of up-down or left-right, and that this type of coding is the preferred coding of movement direction. The present results of a support such a categorical coding of movement orientation. In terms of the amount of movement variability, there was no difference between the directional mappings of 0° and 180°. Similarly, no difference was found between mappings of 90° and 270°. This indicates that the overlapping codes that presumably caused the observed contrast effect do not encode a particular movement direction, but rather an orientation of movement.

9.4.2 Perceptuomotor Assimilation of Response Orientation

As the directional mappings between response and stimulus movements were pre-established, a significant positive (= counterclockwise) bias of response direction appeared for the 90°-mapping whenever participants were performing horizontal movements. The effect was not sensitive to the mode of presentation or the type of stimulus. Contrary to the findings on movement variability, this systematic shift towards the observed movement reflects assimilation rather than contrast. This corresponds to findings by Zwickel et al. (in press), who examined the limits of the observed contrast effect mentioned in the preceding paragraph by increasing the angular separation between stimulus and response movement up to 100°. In this condition, participants observed a vertical stimulus motion, while they performed an approximately horizontal movements (10° below the horizontal). Zwickel et al. (in press) found that the previously observed contrast effect turned into an assimilation effect in this condition, i.e. the perceived orientation of vertical stimulus motion was systematically biased towards movements performed by the participants. Moreover, their results show an asymmetry for left- and rightward responses in that only a combination of rightward response and upward stimulus motion led to a significant deviation of the perceived motion orientation from the vertical towards the produced movement (assimilation effect). This directional mapping of stimulus and response is similar to the 90° mapping of horizontal response movements in the present experiment. However, one cannot definitely rule out the possibility that this asymmetry was due to an inherent bias in the perception of verticality as no control condition assessed the participants' perception in the absence of movement.

On a speculative note, this effect, especially its particular association of up- and downward stimulus motion with right- and leftward response movements respectively, is somewhat reminiscent of a reaction time effect known as the orthogonal stimulus-response-compatibility-effect (e.g. Weeks & Proctor, 1990). According to this type of compatibility effect, reaction times are often shorter for the stimulus-response mappings of up to right and down to left than for alternative mappings. Recently, Nishimura and Yokosawa (2006) has demonstrated that orthogonal stimulus-response-compatibility effects emerge even when the stimulus position is task-irrelevant, as it was the case with the orientation of the stimulus in the current experiment.

As an explanation, Weeks and Proctor (1990) drew upon the *salient features coding principle* introduced by Proctor and Reeve (1985). It states that stimulus and response sets are coded with respect to their salient features. Hence faster reaction times should be observed when the respective S-R mapping maintains correspondence of the salient stimulus and the salient response features. With respect to the structural correspondence of vertically arranged stimuli and horizontally arranged responses, they used word-picture-verification tasks to demonstrate that up and right are the salient polar referents along their respective spatial dimension. This would explain the observed orthogonal compatibility effect based on asymmetrical coding of up-down and left-right dimensions. Nowadays, salience has been replaced by polarity to avoid the implication that different values along a given dimension vary with respect to identification time (cf. Proctor & Cho, 2006), but the argument of the *polarity correspondence principle* remains the same.

Orthogonal stimulus-response-compatibility has mainly been reported for speeded binary classification tasks in terms of reaction times and was thus associated with processes of response selection. The analogy drawn here is rather far-fetched and not sufficiently backed by the present data. However, if the correspondence of the polarities of stimulus and response codes is such ”a fundamental aspect of human information processing” (p. 426; Proctor & Cho, 2006), there seems to be no apriori reason that precludes a polarity-based explanation of the effect of movement orientation in the present study.

If one accepts that a theory gains in power by explaining seemingly unrelated facts, the present association of a perceptuomotor assimilation effect in terms of a counterclockwise shift of horizontal response towards vertically oriented stimuli with orthogonal stimulus-response-compatibility effects certainly has the potential to add to the credibility of polarity correspondence beyond the performance of speeded binary classification tasks.

Chapter 10

Experiment 3: On Horizontality

10.1 Introduction

The purpose of Experiment 3 was to further investigate the boundary conditions of the previously found reliable modulation of the perceptuomotor contrast effect by response orientation. Perceptuomotor contrast was found to be limited to response movements performed within the horizontal plane, whereas there were virtually no effects for vertical response movements. For the present experiment, it is important to note that the modulatory influence of movement plane occurred irrespective of whether perceptuomotor assimilation (Kilner et al., 2003; Stanley et al., 2007) or contrast (Experiments 1 and 2 of the present study) was observed. Thus, it is unlikely that it is a pure stimulus artefact or a result of particular properties of the horizontal model movement in the present study. Instead, it seems as if horizontal response movements are generally more susceptible to effects of perceptuomotor crosstalk.

Given that horizontal movements are more variable in general and also more susceptible to perceptuomotor crosstalk, Experiment 3 aimed to determine what "‘horizontal’" actually means, or, more specifically, which reference system actually defines the horizontal movement plane that affects perceptuomotor crosstalk in terms of movement variability. Three relevant frames of reference were distinguished. Each of them defined a horizontal and vertical axis in space: the gravitational reference frame (GRF), the person reference frame (PRF), and the stimulus reference frame (SRF). In order to test how these reference frames interact in generating the modulatory effect of response orientation on the observed contrast effect, the spatial orientation of the stimulus as well as the orientation of the participants were systematically varied as shown in Figure 10.1. While the GRF remained unchanged, the SRF was varied by rotating the stimulus display, and the PRF was manipulated by putting the participants in either a sitting or a lying posture. Subsequently, horizontal and vertical are always used with the respect to the GRF, which remained constant in all condition.

With respect to the rotation of the SRF, two additional display conditions that showed the human model rotated about 90° and 180° counterclockwise with reference to the GRF were added. In addition, the spatial orientation of the PRF was manipulated as well. For that purpose, participants had to respond while sitting on a chair or lying on their left side on an examination table, i.e., the PRF was rotated about 90° with respect to the GRF.

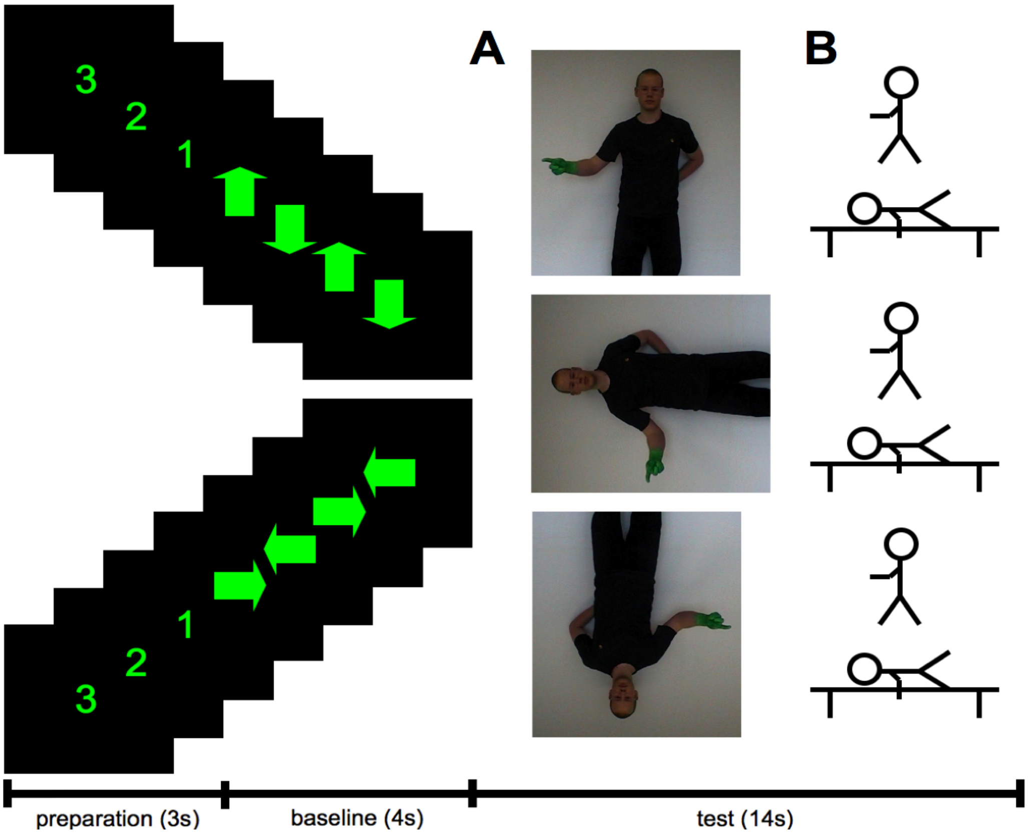

Figure 10.1: Central experimental manipulations in Experiment 3. Preparation and baseline were identical to Experiment 2. Additional experimental manipulations comprised (A) a rotation of stimulus orientation (0° vs. 90° vs. 180°), as well as (B) a rotation of the participant (upright vs. reclined) relative to gravity. Note that even though the different directional mappings between instructed and observed motion are not depicted, the same mappings as in Experiment 2 were used.

10.2 METHODS

10.2.1 Participants

Twelve students of the University of Dortmund, three men and nine women participated in this study. They were 20 to 29 years old (mean: 24.2 years;

SD: 2.1 years). Each individual had given informed consent prior to the start of the experiment. They received 10 euros or course credit for their participation.

10.2.2 Apparatus

The experiment was conducted in a completely darkened room. According to the experimental conditions, participants were either sitting on a height-adjustable chair or lying on their left side on an examination couch. In both conditions, the computer screen was placed at a distance of about 100 cm in front of them and was positioned on eye level. Data were collected in the same way as described in the previous experiments.

10.2.3 Task

The task was the same as in Experiment 2.

10.2.4 Stimuli

In this experiment, only continuous motion of the human model was used as a stimulus. This was the condition for which perceptuomotor contrast modulated by response direction was found in the previous experiment.

10.2.5 Design and Procedure

The experiment consisted of twelve blocks, which were organized in four experimental phases. Each phase was associated with the participant sitting upright or lying on their left side. The order of the phases was either sit-lie-sit-lie or lie-sit-lie-sit. Each phase comprised three blocks, each of them containing one of the three possible stimulus orientations (0°, 90°, 180°). The order of the posture of the participant and the rotation of the stimulus was counterbalanced across participants. Each block comprised eight trials, in which all possible combinations of response orientation and directional mapping (cf. Experiment 2) occurred once in a randomized order. Experimental procedure within a trial was the same as in Experiment 2.

10.2.6 Data reduction and analysis

Data analysis was conducted in the same way as in Experiment 2, except that, due to larger variances of the baseline trials, especially when participants were lying, baseline measures were averaged across trials for the sitting and lying position respectively. Furthermore, separate ANOVAs were conducted for the sitting and the lying position.

10.3 RESULTS

As in the previous experiments, no differences between blocks of trials were significant according to the statistical analysis. Thus, data are presented averaged across blocks.

10.3.1 Sitting

Results in terms of movement variability are shown in Figure 10.2. As can be seen in Figure 10.2A, the observation of a normally oriented (0°) or inverted (180°) human model led to an increase in movement variability for directional mappings of 0° and 180°. Similar to the results of Experiment 2, this variation of movement variability across directional mappings was only present for horizontal movements and absent for vertical movements.

This pattern of results was supported by a significant interaction of stimulus rotation and directional mapping, $F(6,66) = 2.3$, $p < .05$, $\eta^2 = .17$, as well as a significant three-way interaction of stimulus rotation, directional mapping, and response orientation, $F(6,66) = 2.4$, $p < .05$, $\eta^2 = .18$. These effects also gave rise to a significant main effect of directional mapping, $F(3,33) = 5.8$, $p < .01$, $\eta^2 = .35$. Furthermore, horizontal response movements were again found to be more variable than vertical ones, $F(1,11) = 3.4$, $p < .1$, $\eta^2 = .24$,

10.3.2 Lying

The ANOVA on movement variability for the blocks in which participants were lying on the examination table during movement observation and execution revealed no significant main effects or interactions.

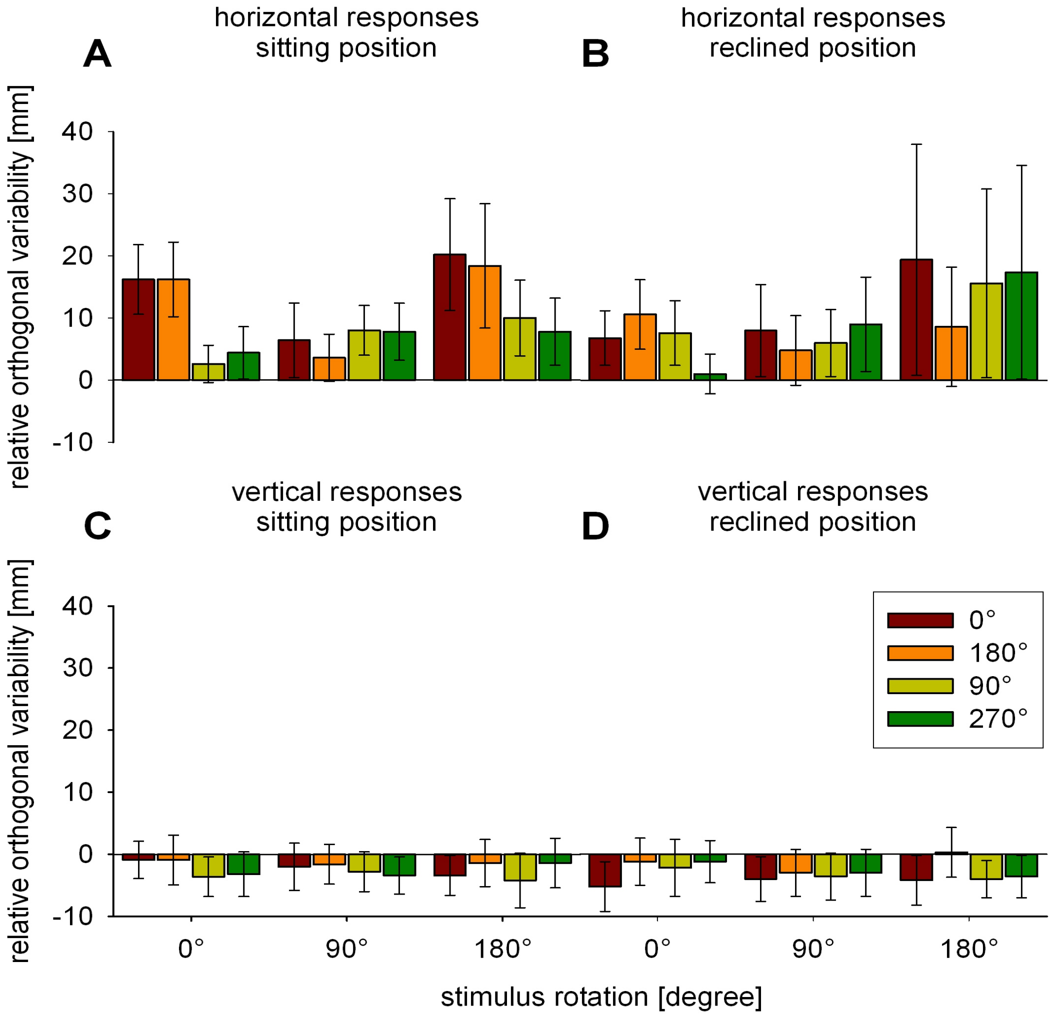

Figure 10.2: Mean relative variability orthogonal to main movement direction (with standard errors of the mean), shown separately for sitting participants performing horizontal (A) and vertical (C) response movements, and for lying participants performing horizontal (B) and vertical (D) response movements. Coloured bars represent performance under different directional mappings. Response and stimulus motion could either occur within the same plane (red bars) or in movement planes that were perpendicular to each other (green bars).

10.4 Discussion

The purpose of the third experiment was to replicate the previously observed modulatory influence of response direction on perceptuomotor contrast in terms of movement variability and to explore the relative contribution of horizontality as defined in different frame of reference. Results from the model orientation of 0°, which corresponded to the observation of continuous motion by a human model as employed in Experiment 2, replicate the previously observed pattern of results across directional mappings. This further corroborates the reliability of both the observed perceptuomotor contrast effect in congruent trials and the modulation of perceptuomotor contrast by response orientation.

Furthermore, perceptuomotor contrast was also found in the 180° (=inverted) model orientation, with a pattern across directional mappings that was similar to the pattern observed in Experiment 2 and in the 0° condition of the present experiment.

The results clearly show that perceptuomotor contrast observed within the horizontal movement plane is not tied to a particular frame of reference. All three reference frames need to be aligned for perceptuomotor contrast to emerge, Furthermore, the finding of similar effects for the 0° and the 180° stimulus display supports the abstract coding of movement orientation, which was proposed in Experiment 2. In the 180° display, the horizontal and the vertical axes of the SRF, though being inverted, have the same orientation as the horizontal and the vertical in the 0° display of the SRF, i.e., they are both aligned to the GRF. Analogous to this equivalence of 0° and the 180°, Grossman and Blake (2001) measured BOLD response during the observation of scrambled motion, and point-light displays of human movements, which were either shown with an upright or inverted stimulus orientation. They found that inverted biological motion activated posterior superior temporal sulcus more than scrambled motion, but less than upright biological motion. This suggests that for a stimulus to be classified as animate, at least in terms of the visual analysis of an observed action, it does not matter whether the human motion is depicted upright or inverted.

The present findings provide an analogous finding with a visuomotor coordination task by demonstrating that a specifically biological effect of perceptuomotor contrast is also still present, when an inverted version of a human model is presented. However, no systematic effects of perceptuomotor crosstalk emerged neither for the 90° condition, not for any experimental condition that involved a lying position of the participants, which indicates that the effect disappears as soon as the PRF or the SRF are not aligned with the GRF anymore (note that for the inverted stimulus display, the axes of SRF, PRF and GRF are aligned, the SRF is just rotated about 180°).

CHAPTER 11

EXPERIMENT 4: GENERALIZABILITY TO CIRCULAR MOVEMENTS

11.1 INTRODUCTION

In the previous experiments, response as well as stimulus movements were linear, i.e., they could be defined by a one-dimensional movement vector, which either described motion along the x- or the z-axis. In congruent trials, or rather in trials with directional mappings of 0° and 180°, there was a full orientational overlap between stimulus and response motion (overlap means that both referred to the same one-dimensional vector). In those trials, perceptuomotor contrast emerged as an increase in movement variability. In incongruent trials (directional mappings of 90° and 270°), no overlap at all was present as orientations, and thus the one-dimensional movement vectors of the stimulus and the response were perpendicular to each other. Accordingly, no perceptuomotor contrast effect showed up. The purpose of Experiment 4 was to explore the generalizability of this pattern of results to a case, in which response movements did comprise both an overlapping and a perpendicular, non-overlapping orientation.

To this end, circle drawing was chosen as the new experimental task. A continuous circular motion can be conceived as a superposition of a sine-wave and a cosine-wave, or as a two-dimensional movement vector that describes motion along orthogonal spatial dimensions. It thus comprises both, an x- and a z-component, whereas the observed movements still comprised only motion along the x- or the z-axis.

Accordingly, participants in this experiment were asked to continuously produce circles while simultaneously observing the linear movements of experiment one and two performed by the human actor or the object in either a horizontal or a vertical orientation. As in the previous two experiments, as well as in many studies on circle drawing (e.g. Franz, Zelaznik, & McCabe, 1991; Franz, 1997), movements were performed at a preferred, self-selected circle size and thus, given the task constraint of synchronizing movements with the stimuli at approximately 0.5 Hz, at a preferred velocity.

11.2 METHOD

11.2.1 Participants

Sixteen students of the University of Dortmund, nine men and seven women, participated in the experiment. They were 18 to 30 years old (mean: 23.1 years; SD: 3.5 years). Each individual had given informed consent prior to the start of the experiment. They received 10 euros or course credit for their participation.

11.2.2 Apparatus

The same apparatus as in the previous experiments was used.

11.2.3 Task

Participants had to perform continuous circular movements with their right arm while observing the same dynamic and static displays of a human model or an object as presented in Experiment 2. Stimulus motion (continuous in case of dynamic and implied in case of static displays) was again linear. The orientation of stimulus motion was either vertical or horizontal. Participants were instructed to temporally synchronize their circular movements with the reversal points of the stimulus' movement.

11.2.4 Stimuli

The same stimuli as in Experiments 2 were used.

11.2.5 Design and Procedure

With respect to presentation mode, a control condition was added to check for unspecific effects of directing attention towards either the x- or the z-axis by the initially presented arrows (see description below). This control condition corresponded to a static display of the human model or the object in a neutral position, i.e., the end effector positioned in the centre of the screen. Thus, experimental manipulations comprised the type of stimulus (human model versus object), the mode of presentation (static versus dynamic versus control), and the orientation of stimulus motion (horizontal versus vertical), which yielded a three-factorial 2x3x2 within-subject design. The resulting twelve experimental conditions were divided into two experimental chunks according to the factor response orientation. Each chunk comprised a combination of the remaining factors stimulus type and presentation mode, which are arranged in a randomized order. Two chunks formed one block of twelve trials and the experiment consisted of six blocks. The order of blocks were counterbalanced across participants (ABABAB or BABABA).

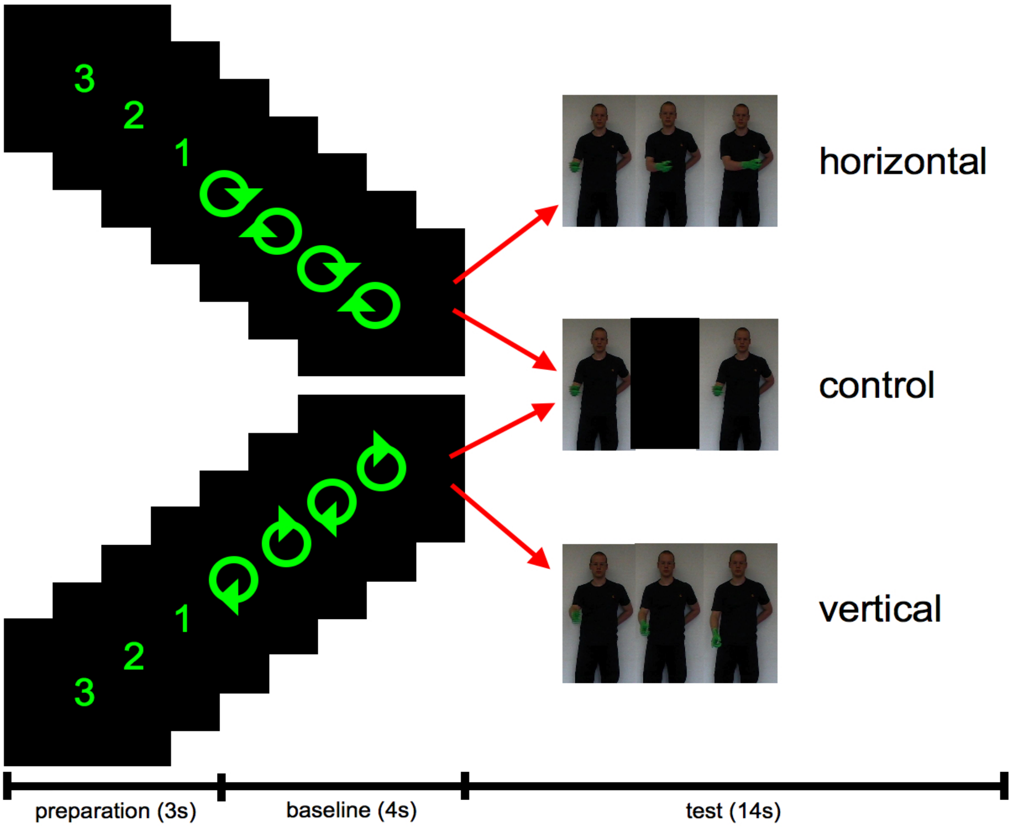

Figure 11.1: Modified experimental paradigm for Experiment 4. This time, arrowheads were presented within a circle template and participants were instructed to synchronize their circular movement in space and time with the circle-arrows. Only the human model in the dynamic display condition is depicted. The dynamic display of the object and the static displays were set accordingly.

After the initial countdown, an arrow within a circle template appeared, indicating both, the direction of movement, which was always clockwise, and the starting point of the circular motion. The initial starting point of the circular movement corresponded to the direction of stimulus movement or the direction connecting the two stimulus postures, i.e., it was on the top of the circles (90°) in trials, in which subsequent stimuli showed vertical movement or up-down-postures, or at the circles' rightmost location (0°) for trials with horizontal motion or right-left postures. The arrow remained onscreen for 400 ms, then the screen turned black for 600 ms and then, the circular template reappeared, but this time with the arrow on the opposite side of the circle, i.e., at 270° for vertical and 180° for horizontal motion. This was repeated once so that participants had enough time to initiate the circular movement at the respective pace.

As in Experiments 2 and 3, the initiation phase was followed by the respective stimulus display. Stimulus presentation was constrained. Arrowheads that appeared at 0° and 180° were always associated with subsequent horizontal stimulus motion or the control condition. Accordingly, arrowheads that appeared at 90° and 270° were always followed by vertical stimulus motion or the control condition. For the control condition, which depicted either the human model or the object in a neutral position, static displays were used with the exact same timing as employed in the other static displays.

Intertrial intervals were set to ten seconds and additional rest breaks were given as needed to avoid fatigue. Between blocks three and four, a three-minute rest break was given filled with irrelevant conversation. Each testing session lasted approximately 45 minutes.

11.2.6 Data Reduction and Analysis

For the subsequent kinematic analysis of individual movements, the first two circles after the stimulus onset were discarded as in the previous experiments. The remaining circles were centred around their respective barycentre and displacement of the circular movements along the x- and z-axis was calculated based on the zero crossings on the x- and z-axis. Means of each dependent variable along with one measure of variability (standard deviation, SD) were computed for each trial and each subject. In the next step, difference scores were computed by subtracting the mean displacement along the x- and z-axis respectively in both dynamic and static displays of model motion, from the control condition. Those difference scores, in the following referred to as x-deflection or z-deflection respectively, were each analyzed in a three-factorial analysis of variance (ANOVA) for repeated measures with the relevant within-subject factors type of stimulus, mode of presentation, and stimulus orientation.

11.3 Results

Mean x- and z-deflections are shown in Figure 11.2. X-deflection (Fig. 11.2A and 11.2B) was found to differ significantly from zero when participants observed horizontal human stimulus motion in both static and dynamic displays, 7.7 mm, $F(1{,}15) = 19.6$, $p < .0005$, and 19.9 mm, $F(1{,}15) = 43.7$, $p < .0005$, respectively. All other tests against zero failed to approach the Bonferroni-adjusted level of significance.

Accordingly, the analysis of variance revealed that x-deflection was particularly pronounced during the observation of continuous horizontal movements by the human model. The respective three-way interaction of stimulus type, mode of presentation, and stimulus orientation was significant, $F(1{,}15) = 5.7$, $p < .05$, $\eta^2 = .27$. This interaction gave rise to other significant effects. X-deflection was also found to be larger during the observation of the dynamic display of continuous stimulus motion as compared to the static display of movement turning points, 9.1 mm vs. 2.2 mm, $F(1{,}15) = 18.6$, $p < .01$, $\eta^2 = .61$, and it was also larger in trials, in which participants observed stimulus motion along the x-axis, 10.5 mm, as compared to motion along the z-axis, 0.8 mm, $F(1{,}15) = 6.6$, $p < .05$, $\eta^2 = .31$.

For movement deflection along the z-axis, a similar pattern of specific interference emerged. Z-deflection was only significantly different from zero, 23.9 mm, $F(1{,}15) = 40.4$, $p < .0005$, during the observation of vertically oriented continuous motion by a human model. This nicely corresponds to the findings for x-deflection and horizontal stimulus motion. The respective three-way interaction of stimulus type, mode of presentation, and stimulus orientation was marginally significant, $F(1{,}15) = 3.6$, $p < .1$, $\eta^2 = .19$.

Again, this pattern of z-deflection across stimulus conditions gave rise to several significant main effects and interaction effects. Whereas the main effect stimulus orientation was only marginally significant, $F(1{,}15) = 3.1$, $p = .1$, $\eta^2 = .17$, it pointed in the expected direction since it was larger for vertical than for horizontal stimulus motion, 10.0 mm vs. 5.4 mm. Furthermore, larger deflections were found for dynamic displays, 11.2 mm, as compared to static displays, 4.2 mm, $F(1{,}15) = 21.1$, $p < .01$, $\eta^2 = .58$, as well as for the observation of human as compared to object stimuli, 10.6 mm vs. 4.7 mm, $F(1{,}15) = 4.6$, $p < .05$, $\eta^2 = .24$.

Lastly, the ANOVAs on the standard deviations of x- and z-deflection revealed no significant main effects or interactions.

11.4 DISCUSSION

The purpose of Experiment 4 was to examine perceptuomotor crosstalk with movement orientation as the overlapping feature of stimulus and response in a situation, in which the orientation of stimulus movements did overlap with the orientation of one component of a circular movement.

Therefore, the paradigm was slightly modified by using a task that had

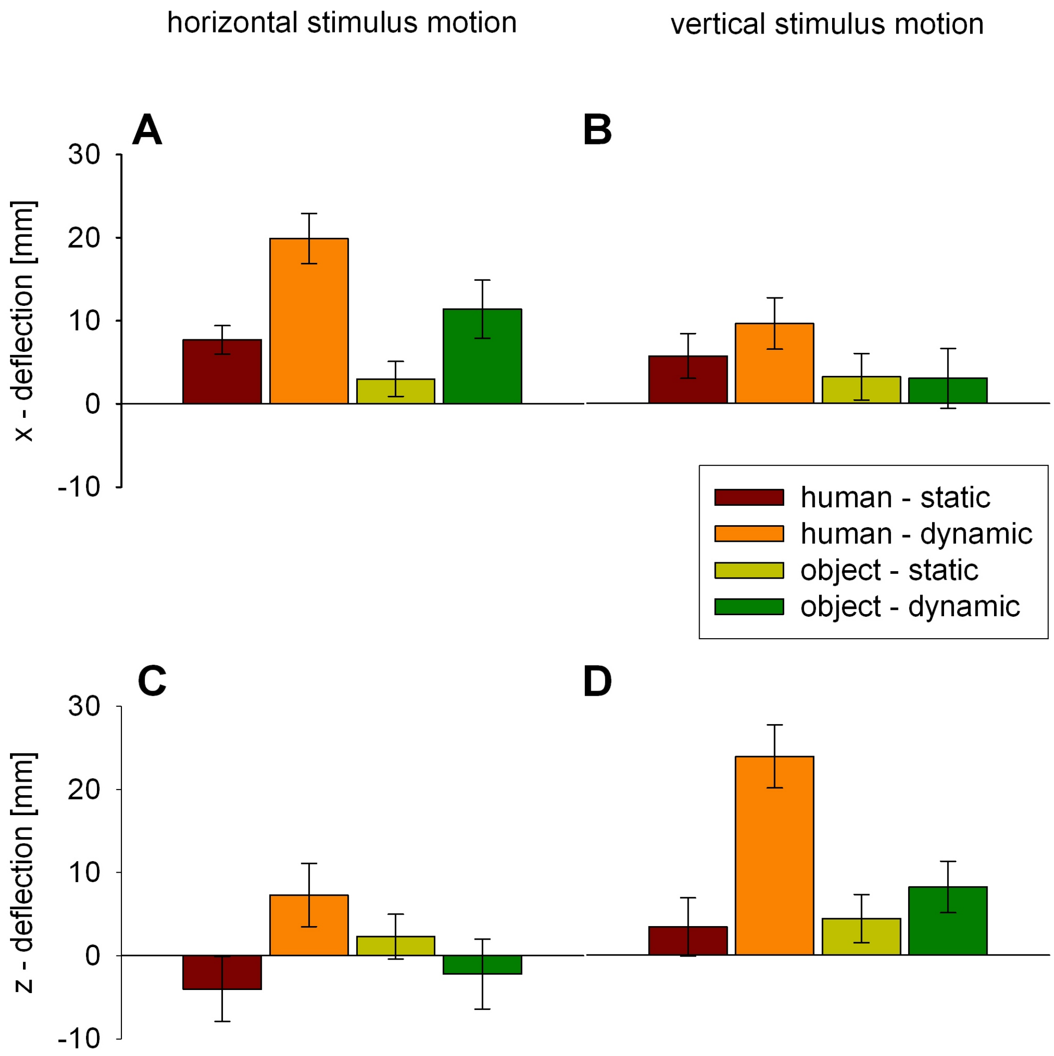

Figure 11.2: Mean deflection along the x-(A-B) and z-axis (C-D) shown separately for horizontal (A,C) and vertical (B,D) stimulus motion. Coloured bars represent mean deflection as a function of type of stimulus and mode of presentation. Errors bars indicate standard errors of the mean. Deflection is defined as the change in displacement along the respective axis in an extrinsic Cartesian coordinate system relative to the control condition, which showed a neutral stimulus without orientation information present in the display.

previously been shown to produce interlimb crosstalk, i.e., circle drawing. In contrast to Experiments 1, 2, and 3, the circular response movements required by the participants in this experiment comprised motion along two spatial axes. This way, the coupling between observed and generated movements comprised a partial overlap within one of the two spatial dimensions used in movement execution as compared to full overlap in the congruent and nill overlap in the incongruent trials of the previous three experiments with one-dimensional movements.

Results revealed that when the circular trajectories were decomposed in orthogonal directional component vectors along the x- and z-axis, spatial coupling was observed for motions in the dominant dimension of the observed movement. This effect was found to be specific for the observation of a human model. Object motion did not affect either component vector. Furthermore, only continuous model motion in the dynamic display condition yielded the effect.

Circle drawing has previously been used to investigate spatial as well as temporal coupling of two movements (e.g. Franz et al., 1991; Franz, 1997; Semjen, Summers, & Cattaert, 1995). The present results correspond to studies on bimanual coordination that had demonstrated specific patterns of perceptuomotor crosstalk, when the two hands were assigned to perform different movements. Franz et al. (1991), for instance, asked their participants to continuously draw circles with the one hand while simultaneously performing repeated cycles of lines with the other hand. Aside from temporal coupling of the two limbs characterized by a 1:1 frequency ratio, they also found spatial coupling that made the trajectories of the circular movements become more linear and the trajectory of the lines become more circular.

However, in these studies, movement parameters were thought to be channelled to two different effectors both part of the same body and thus controlled by the same brain. More specifically, it was argued that spatial coupling in bimanual coordination was mediated by cortical interactions via the corpus callosum. Accordingly, spatial coupling was found to be absent in callosotomy patients (Franz, Eliassen, Ivry, & Gazzaniga, 1996).

In the present experiment, no cortical interactions between the two end effectors were present. However, perceptuomotor crosstalk reminiscent of spatial coupling was observed. This is in line with previous research, which showed that principles governing interlimb coordination such as the Haken-Kelso-Bunz equation (Haken, Kelso, & Bunz, 1985; Kelso, 1995) also applies to rhythmic coordination between persons, regardless of whether this interpersonal coordination is achieved intentionally or developed spontaneously (e.g. Richardson, Marsh, Isenhower, Goodman, & Schmidt, 2997; Schmidt & O'Brien, 1997). The present results are in line with this as they extend findings from *intra*individual to *inter*individual bimanual coordination. However, the specificity of the perceptuomotor assimilation to the observation of an animate agent also supports the notion of a difference between interpersonal coordination patterns, which presumably rely on a biologically tuned action-observation-execution-matching system, and person-object coordination, which would not require or cannot use such a system.

Chapter 12

General Discussion

The starting point of the study was the notion of a hierarchically organized action-observation-execution-matching system that augments cognitive functions based on a covert simulation of observed actions. Due to the embodied nature of sensorimotor simulation within the action-observation-execution-matching system, it has been argued that the latter is particularly sensitive to animate as compared to inanimate stimuli. The purpose of the present study was to investigate the impact of dynamic and static features that cued the animacy of an observed stimulus. Accordingly, it was distinguished between biological topography in terms of surface and form features of a human body and biological kinematics of stimulus motion. Interactions between simultaneous perception and execution of intransitive actions were examined in the presence and absence of these static and dynamic animacy cues.

In four experiments, participants were required to perform continuous oscillatory movements with their right arm during the observation of static or dynamic displays of a human model or an object, both of which were performing movements of either same or orthogonal orientation. Experimental manipulations comprised a differentiation between discrete and continuous measures of perceptuomotor crosstalk during response selection and response execution (Exp. 1), the directional mapping between stimulus and response motion (Exp. 2), variations of reference frames for visuomotor coordination (Exp. 3), and the complexity of executed actions (Exp. 4).

All in all, the present study reveals various effects of perceptuomotor crosstalk. Some of the observed effects were specifically tied to the presence of animacy, whereas others were found to be insensitive to the presence of animacy features in the stimulus display.

12.1 Summary of Experimental Findings

In Experiment 1, perceptuomotor assimilation was found for response selection. In the presence of dynamic motion information, perception of both, a human model and an object, interfered with response selection. This resulted in longer reaction times when the observed movement orientation was incongruent to the response orientation that was required by the imperative colour cue. For the static display condition, a similar prolonged reaction time was only found for the presentation of the human model, but not for the object. During response execution, effects of perceptuomotor crosstalk were observed in terms of movement variability, which was specifically tied to the presence of static and dynamic animacy cues, and movement orientation, which was found to be insensitive to animacy cues.

The origin of the perceptuomotor crosstalk effects during movement execution was more thoroughly investigated in Experiment 2, which replicated and extended the findings of Experiment 1. Perceptuomotor assimilation was found in terms of a systematic counterclockwise shift of response orientation in incongruent trials, which was independent of stimulus type and presentation mode, but was found to be contingent upon response orientation and directional mapping. More precisely, this counterclockwise shift of movement orientation only showed up for horizontal responses and a directional mapping of 90°, i.e., for simultaneous rightward response and upward stimulus motion and for leftward response and downward stimulus motion. Furthermore, Experiment 2 revealed a perceptuomotor contrast effect during the execution of horizontal movements in congruent trials. It was shown that overlapping movement orientations in action observation and execution led to an increased movement variability as compared to baseline movements. While contrast was limited to horizontal response movements, it was insensitive to whether perceived and executed movements were of same or opposite directions, i.e., it occurred for directional mappings of 0° and 180°.

Experiment 3 demonstrated that the modulation of the contrast effect by response orientation, which was observed in Experiments 1 and 2, was not tied to a particular reference frame. Furthermore, its result also support the notion of abstract coding of movement orientation as contrast was also found when the dynamic human stimulus was presented upside-down.

With respect to the generalizability of perceptuomotor contrast during movement execution, Experiment 4 showed that contrast turned into assimilation as the response movement became more complex, i.e., consisted of a circular instead of a linear motion. Nevertheless, crosstalk was still found to be specific for the observation of dynamic motion of the human model. This suggests that contrast and assimilation were based on the same functional mechanisms.

12.2 Animate Agency: On Topography and Kinematics

The results of all four experiments show that perceptuomotor contrast during movement execution emerged only in the presence of both a biological topography of the stimulus and biological kinematics of its motion; neither a biological velocity profile nor surface features alone were able to elicit this effect. Instead, it appears that both constitute necessary, but not sufficient preconditions for the activation of the action-observation-execution-matching system. Thus, on the one hand, the presence of biological form/surface features of the body seems to be required for the dynamic motion information to affect movement execution. On the other hand, if no dynamic motion information is present, no perceptuomotor contrast is observed during movement execution. Apparently, the presence of bodily features allowed the dynamic motion information to gain privileged access to the action-observation-execution-matching system as the observation of object motion did not exert a similar influence.

This is in line with the findings by Stanley et al. (2007) who suggested that in their experiment, the reported agency of the object motion was more important than the actual type of movement kinematics, i.e., biological vs. non-biological. Thus, biological kinematics were ruled out by Stanley et al. (2007) as being the cause of the observed sensitivity to animate actions. Instead, Stanley et al. (2007) favoured the perceived agency of the movement stimuli as being crucial for perceptuomotor crosstalk to occur.

The present results on perceptuomotor contrast during movement execution agree with this interpretation. The presence of the human body served as a perfect cue to communicate animate agency to the participants of each experiment. Based on this *agency cue*, the observed movements were processed differently as compared to the object movements, presumably within the action-observation-execution-matching system, and were thus able to interfere with movement execution.

Conceptually, such an agency account would be consistent with work by Wheatley, Milleville, and Martin (2007). They used fMRI to measure brain activation in response to moving shapes. The context of these shapes was varied in a way that they afforded the observation of the moving stimulus as an animate agent or as an inanimate object. They found no differential activation with respect to animacy in what they designated as the mirror system, i.e., the inferior parietal cortex and the ventral premotor/inferior frontal cortex. An increase in activation was found, however, in what Wheatley et al. (2007) referred to as the social network. Among other cortical and subcortical areas, this social network comprises regions in the temporal cortex, the superior temporal sulcus and the lateral fusiform gyrus, all of which were described in chapter 4 as a part of the occipito-temporal network that is responsible for the visual analysis of observed actions within the action-observation-execution-matching system. Based on their findings, Wheatley et al. (2007) argued that perceived animacy of a stimulus acts as a systemwide alert signal that gears up the action-observation-execution-matching system to process socially relevant information. This alert signal is generated during the visual analysis of observed actions within the social network in the occipito-temporal region including the superior temporal sulcus, which has been implicated in the perceptual and conceptual processing of biological motion. The alert signal then triggers a covert simulation of the observed movement within the action-observation-execution-matching system. This simulation of an observed action then interferes with the ongoing control of movement and leads to the present effects of perceptuomotor crosstalk that were specifically tied to the observation of animate agents.

The reported insensitivity of the fronto-parietal (mirror) part of the action-observation-execution-matching system, which did not show a modulation of activation by the presence of animacy in the study by Wheatley et al. (2007), casts doubts on its biological sensitivity and thus its viability as the origin of social cognition. Nevertheless its importance in terms of covertly re-enacting observed actions within a covert sensorimotor simulation process is still valid. Wheatley et al. (2007) suggested that the fronto-parietal part of the action-observation-execution-matching system might better be conceived to afford a domain-independent simulation process, which might be co-opted to interpreting actions of animate agents by domain-specific systems such as the social network regions, the superior temporal sulcus and the lateral fusiform gyrus, which were shown to be especially sensitive to the presence of animacy (e.g. Grossman et al., 2000; Grossman & Blake, 2001; Spiridon et al., 2006).

12.3 On Assimilation and Contrast

12.3.1 Between-Studies

The present results support a specific sensitivity of the action-observation-execution-matching system to biological stimuli in terms of an increase in movement variability during the observation of animate actions. Thus, while this finding is in agreement with previous studies in terms of supporting the existence of specific perceptuomotor crosstalk for animate stimuli as compared to inanimate stimuli, they differ with respect to the nature of this crosstalk.

Previous studies, which used a similar paradigm, found perceptuomotor assimilation instead of perceptuomotor contrast (Kilner et al., 2003, 2007;

Stanley et al., 2007). More specifically, Kilner et al. (2003) argued that perceptuomotor crosstalk, i.e., larger orthogonal variance in incongruent than in congruent trials, originated from interference between response and stimulus orientation in incongruent trials. In contrast, Stanley et al. (2007) suggested that perceptuomotor crosstalk was due to facilitation of movement performance in the congruent condition instead of interference in the incongruent condition. In this respect, the present results in terms of movement variability seem to agree with the latter localization of the effect. In the present study, the observation of incongruent stimulus motion did not affect orthogonal variance during movement execution. Having agreed on the localization of the effect with Stanley et al. (2007), it still remains unclear why Stanley et al. (2007) found perceptuomotor assimilation, whereas the present experiment revealed perceptuomotor contrast.

In terms of the Theory of Event Coding (Hommel et al., 2001), assimilation and contrast correspond to the difference between coactivation and integration of feature codes within an event code (see chapter 5.2). Mere coactivation is unable to account for the observed contrast effect instead of assimilation. Instead, contrast arises in TEC from an integrative process that binds together the feature codes of an event. With reference to work by Treisman (1988) on the integration of features for perception, it is assumed that features can only be integrated within one event at a time. Thus, binding together feature codes makes them unavailable for other event codes, so that binding for perception interferes with binding for action. In the present study, this interference results in increased movement variability in congruent trials.

At this stage, it is unclear what might have triggered integration instead of coactivation in the present study, which would account for the observation of perceptuomotor contrast. However, it might be just this difference in binding that could explain the contrast effect in this experiment as compared to the assimilation effect in the studies by Kilner et al. (2003) and Stanley et al. (2007). A possible cause, but this is only speculative, could be the formulation of the control problem that the sensorimotor system has to solve. Participants of the present study were always instructed to carefully attend to the temporal synchronization of their response with the observed stimulus. Temporal synchronization was explicitly and repeatedly instructed as the sole demand of the task, whereas movement orientation should be ignored. A way to achieve temporal synchrony is to specify a detailed goal state of the system at each point in time, i.e., a spatial position of the end effector with respect to the model motion. The latter serves as a reference trajectory for all musculoskeletal degrees of freedom, and the controller has to generate muscle activations so as to force the plant to synchronize with this trajectory.

This, of course, would require integration of a feature code, which specifies movement orientation, but by both processes, the perception/prediction of model motion as well as the specification of response movements.

Finally, the differential findings of assimilation and contrast might, at least partly, be due to different dependent variables, which were used to assess perceptuomotor crosstalk. More specifically, the finding of contrast in terms of movement variability in congruent trials and at the same time assimilation in terms of movement orientation in incongruent trials implies that orthogonal variance that is not assessed with respect to the actual movement, but instead fixed to an extrinsic Cartesian frame of reference (cf. Bouquet et al., 2007; Kilner et al., 2003, 2007) might be somewhat problematic because it confounds orientation (in the present study insensitive to animacy) and variance (in the present study sensitive to animacy) in a single variable. This might distort the observed effects. If this, however, is sufficient to account for the observed between-study differences of assimilation versus contrast is doubtable.

12.3.2 Within-Study

The question of under which circumstances perceptuomotor assimilation or perceptuomotor contrast is observed is not limited to comparing the contrast effect to other studies. Even within the present study, there were effects of perceptuomotor assimilation that exhibited sensitivity to the presence of a human model: the reaction time effect observed for static displays that depicted postures of the human body (Exp. 1) and the assimilation effect of observed linear movements on the displacement of a circular motion (Exp. 4).

The differential effects of assimilation at response selection and contrast during movement execution of linear movements can be reconciled within the Theory of Event Coding in terms of activation and integration. Movement orientation is a defining feature of the response movement. Uncertainty about the upcoming response orientation leads to movement orientation receiving higher intentional weights, which in turn primes its perception. Upon stimulus onset, the imitable posture of the human stimulus exerts a greater influence on response selection because it depicts the respective goal state of one of the two response alternatives. It can be conceived as an instantiation of ideomotor compatibility as reported previously (e.g. Brass et al., 2001, 2000), where the observation of a potential goal state automatically activates its associated movement and interferes with the arbitrary stimulus-response mapping implemented by the imperative colour cue. As the movement is initiated, the feature code of orientation is bound with other feature codes to form an event code. During movement execution in congruent trials, this event code has to be unbound so that the feature code of orientation can be used by perception to track the observed movement trajectory. In incongruent trials, the event code can maintain its integrity throughout the whole movement as there is no overlap between movement orientations in the incongruent trials.

The finding of perceptuomotor contrast in Experiments 2 and 3, and of perceptuomotor assimilation in Experiment 4 is, of course, puzzling. On the basis of the present data, it is not possible to draw firm conclusions on the issue of why perceptuomotor contrast was observed during linear, but assimilation during circular response movements.

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