The link between observation and execution of biological movement

– behavioural correlates and the underlying neural network

Dissertation

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Hamburg, den 2. Februar 2007

Hiermit versichere ich, dass ich die vorliegende Dissertation selbständig erarbeitet und keine anderen als die angegeben Hilfsmittel benutzt habe. Ich habe diese Dissertation weder in der gegenwärtigen noch einer anderen Fassung einer anderen Fakultät vorgelegt.

Hamburg, den 2. Februar 2007

Melanie Jonas

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RT Experiment 3 and parts of RT Experiment 1 and 4, as well as the fMRI study also are the subject of two research articles:

Jonas, M., Biermann-Ruben, K., Kessler, K., Lange, R., Bäumer, T., Siebner, H. R., Schnitzler, A., Münchau, A. (2007). Observation of a finger or an object movement primes imitative responses differentially. *Experimental Brain Research, 177(2),* 255-65.

Jonas, M., Siebner, H. R., Biermann-Ruben, K., Kessler, K., Bäumer, T., Büchel, C., Schnitzler, A., Münchau, A. (2007). Do simple intransitive finger movements activate fronto-parietal mirror neuron areas in humans? *Neuroimage, 36(Suppl 2),* T44-T53.

Contents

1. Introduction

1.1. Is there an explicit link between observation and execution of movements?

Imagine the following situation: your sister is going to marry next week, almost all her friends who are invited are members of a repeatedly awarded dance group – but you are unable to do even one step. What would you do to become socially acceptable just in time and without spending money you do not have? You could either visit your 90-year-old neighbour who was an excellent dancer at her time and ask her to explain the waltz to you from her rocking chair. Or you could lend out a dancing course on videotape. The most efficient plan would surely be to first visit your neighbour for tea-time, gratefully take the 5 Euros she always wanted to give to you during the last ten years and then get the videotape.

Both ways of learning to dance involve the execution of movement sequences (i.e. dance steps) but they differ in how those movements are instructed: your neighbour's words only circumscribe what you are supposed to do. However, the advantage of watching an expert dancer while trying to copy what she does is that your movements are instructed by observing the *same* movements in another person. It is evident not only by everyday life's experience that *imitation* is the most efficient way to learn new movement sequences: e.g. it has been shown already 15 years ago by Gray *et al.* (1991) that watching videos of ballet sequences leads to a better learning performance than looking at pictorial instructions or even still pictures of the single components that make up the movement sequence. A benefit of imitation is already demonstrable in a very simple task, i.e. when a person is asked to lift one of two fingers in response to either a videotaped finger movement or to another non-biological visual stimulus (symbolic or spatial instruction). People are always faster at imitating the moving finger (Bertenthal *et al.*, 2006; Brass *et al.*, 2001a; Brass *et al.*, 2000; Jonas *et al.*, 2007; Kessler *et al.*, 2006).

In everyday language, imitation simply means to *copy* a body movement observed in another individual, while matching (or trying to match) one's own movements to that of the model. However, imitation is not a unitary phenomenon but a generic term under which different types of phenomena have been subsumed (c.f. Rizzolatti *et al.*, 2002; Rizzolatti *et al.*, 2001). These range from *response facilitation*, defined as a selective enhancement of motor responses that are already present in the imitator's repertoire (Byrne, 1994), to what has been called "*true imitation*" by ethologists (see Byrne & Tomasello, 1995; c.f. Rizzolatti et al., 2001): a novel motor pattern or sequence (e.g. a dance step) has to be decomposed into a chain of elements which are part of the motor repertoire, and where *learning by imitation* has been supposed to take place through a recombination of these elementary movements (Buccino *et al.*, 2004b). There is, moreover, a controversy whether imitation is an innate capacity. The seminal results of Meltzoff and Moore (1977), who reported that newborns can match their buccal (facial) and manual gestures to those of others could not be replicated completely, and may be limited to tong protrusions (Kaitz *et al.*, 1988). There is also no complete agreement whether non-human primates are able to imitate or not (see Visalberghi & Fragaszy, 2001). Assuming the latter, it has been suggested that the ability to learn from other group members by imitation is one of the most important steps in the evolution of mankind.

However, imitation, or even a relatively short-lived *imitative act*, is always a very special case of motor behaviour where perception and motor performance are intimately linked. This close link becomes evident in the ease with which humans imitate, and, furthermore, in everyday observations of imitation which is not initiated at will but rather induced automatically by the perception of motor behaviour in other people: besides that infants and small children very often spontaneously imitate others during development (c.f. Rizzolatti *et al.*, 1999), involuntary imitative actions with explicit emotional or vegetative components (e.g. smiling, yawning) are also common in adults. People's social behaviour

is full of unconscious imitation: for example, they tend to whisper or speak louder when others do, or scratch their head upon seeing someone else scratch (Dijksterhuis & Bargh, 2001).

1.2. Scope and outline of this dissertation

As set out above, due to the similarity between perception and performance of movements, imitation lends itself to a subject for investigating the functional and neural mechanisms relating observed and executed movements.

The present work focuses on observation and imitation of *biological* or precisely *animate* movement, in terms of feasible movements made by biological entities or agents (Brass & Heyes, 2005). Of note, the usage of the terms *biological movement* or *biological motion* often also includes artificially constructed stimuli moving in the same way as biological entities. These are for example "point-light" stimuli (Johansson, 1976), or inanimate objects moving on the same trajectories as human body parts, e.g. as employed as control stimuli by Brass et al. (2001a) or Kessler *et al.* (2006) – and also in the present studies. Furthermore, disregarding possibly existent non-human imitative behaviour, and more complex forms of imitation in humans (e.g. those involving learning mechanisms) all present studies are concerned with copying of very simple *intransitive human* body movements. Intransitive movements are not directed towards an object, as are *transitive* movements. As defined by Rizzolatti et al. (2001), the term *action*, which is frequently used in the dedicated literature, specifically refers to the latter type of object-directed behaviour (that produces reward for the acting individual; e.g. grasping an apple). According to this nomenclature, the present studies do not deal with motor action, although, in its widespread use as a generic term, action includes any type of intentional behaviour.

The present experiments are furthermore embedded in a “neuro-cognitive” framework connecting (i) the idea of common sensory and motor coding for movements, that has been put forward in a number of cognitive approaches to perception-action mechanisms in general and imitation in particular, with (ii) neurophysiological research and evidence on shared or common brain bases for movement perception and movement planning/execution.

Section 1.3. refers to this framework. In sections 1.4. and 1.5., a brief review will be given on previous findings from behavioural and neurophysiological experiments, respectively, which are relevant with respect to the present research questions. In chapter 2, a series of four *reaction time* (*RT*) experiments will be reported, including two single-stimulus (sections 2.2. and 2.5.) and two priming/cueing studies (sections 2.3. and 2.4.). Chapter 3 deals with the event-related *functional magnetic resonance imaging* (*fMRI*) study. Section 3.2.1. provides a short introduction into the fundamentals of the fMRI method. In a general discussion (chapter 4), the presented behavioural and imaging results will be connected. Concluding, the fundamental issues of “how” (section 4.2.1.), “where” (section 4.2.2.) and “why” (4.3.) observation and execution of biological movement might be linked to each other will be tackled.

1.3. Approaches to the link between observation and execution of biological movement

Humans can achieve a very high imitation accuracy depending on the complexity of the movement and on experience. Nonetheless, the question how an observer actually transforms the visual input of a motor act into a corresponding motor output which matches the peer model, also referred to as the „correspondence problem“ (c.f. Brass & Heyes, 2005; Heyes, 2001), is still not fully solved.

There are on principle two classes of cognitive theories on imitation that offer explanations for the correspondence problem (c.f. Brass & Heyes, 2005): (a) “specialist” theories suggest that imitation is mediated by a unique mechanism which is dedicated to the special purpose of imitation, whereas (b) “generalist” theories, on the other hand, assume that imitation is accomplished by general mechanisms of associative learning and motor control.

Behavioural findings (see section 1.4.) and, particularly, new insight from neurophysiology (see section 1.5.) provide strong support against the notion of a special purpose mechanism for imitation: (i) first, there is evidence for various behavioural effects (e.g. response facilitation or *interference* effects; see below) implying that movement observation activates motor representations. (ii) Second, there is the discovery of visuo-motor *mirror neurons* in the macaque monkey in connection with parallel findings of a set of cortical brain regions in humans - neural structures which all respond to both the execution and the observation of certain movements. These findings are in favour of generalist theories assuming that imitation is accomplished by an activation of motor codes through movement observation. Whereas a special imitation mechanism should work only on instances where imitation is actually intended, behavioural and neurophysiological results suggest that motor activation by movement observation occurs automatically.

One well-established generalist theory, within its framework related approaches have been developed, is the *ideomotor theory* (e.g. Greenwald, 1970; Prinz, 1987, 2002). The ideomotor theory states that movements are represented centrally in the form of “response images” of the sensory feedback they produce. Due to the similarity between visual stimulus and motor response, movement observation activates the corresponding motor representation, which can be used to imitate (Fig. 1.1).

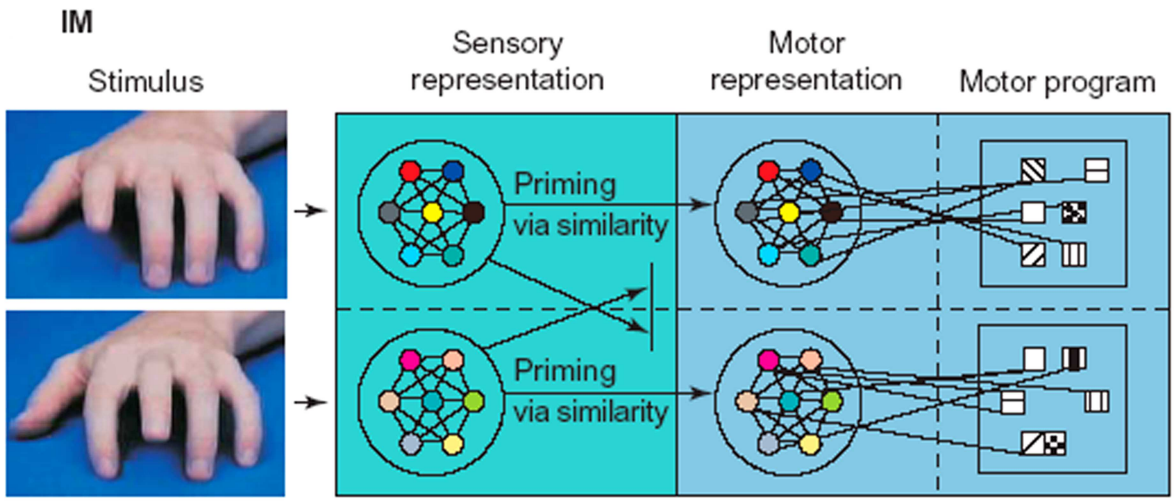

Fig. 1.1. Schematic illustration of the ideomotor principle. Ideomotor theory (IM) assumes that observation of a movement (left panel) activates (i.e. primes) its motor representation due to the similarity between the sensory and the motor code (right panel). Adapted from Brass and Heyes (2005) © 2005 Elsevier Science.

According to the concept of *ideomotor compatibility* (Greenwald, 1970), the ease with which a stimulus is transformed into an action depends on their similarity. The more a stimulus is similar to an action, the more action execution is facilitated (i.e. accelerated). Because in imitation the visual similarity between stimulus and response is very high, action observation activates the visual response image that in turn effectively controls the execution performance. Actually, the idea elaborated by Greenwald in his concept of a ideo-motor mechanism had been already formulated by William James (1890) almost hundred years earlier in his descprition of a so-called "ideomotor action: "... every representation of a movement awakens in some degree the actual movement which is its object …" (James, 1890, p. 526). The ideomotor compatibility dimension overlaps with the concept of *stimulus-response compatibility (SRC)*. In experimental psychology, this term originally refers to the finding that in choice reaction tasks (where participants have at least two response alternatives), a compatible mapping/assignment of the spatial position of stimulus and response leads to faster responses than an incompatible mapping (e.g. Fitts &

Deininger, 1954). According to Kornblum (1994), SRC effects arise to the extent that the stimulus and response sets in a certain task share some features.

The *common coding approach* (e.g. Prinz, 1990) is probably the most prominent theory of perception and performance of movements in general within the ideomotor framework. This approach explicitly proposes a common representational domain for perceived events and planned movements (here: "actions"). Event codes and action codes are considered to constitute the functional basis of percepts and action plans, respectively. Both codes share the same representational domain and are therefore commensurate. According to the central "action effect principle", cognitive representations of *action effects* (e.g. kinaesthetic feedback of a movement) play a critical role in the planning and control of these actions. Thus, motor plans of movements become automatically activated by visual events that correspond to their effects, e.g. in imitation. If action and perception share the same features, stimuli can on the one hand (i) *induce* actions. On the other hand (ii), assuming that the same code cannot be functional in action and perception at the same time, they can *interfere* with (i.e. impair or delay) each other. A prominent finding from an induction or SRC task is the *Simon effect* (Simon *et al.*, 1970): a standard Simon task requires the subject to press one of two keys, assigned to the left and right hand, in response to the identity of a stimulus (e.g. the pitch of a tone). The stimulus position (e.g. the tone coming from a loudspeaker on the left- vs. the right-hand side) is an irrelevant dimension. However, performance is clearly better when the stimulus and the response occur on the same side in extrapersonal space. According to the common coding approach, this is due to shared spatial properties of stimulus and response.

The observation of human movement has been shown to both induce movements in the perceiver (see section 1.1.), and to interfere with prepared movements, even when the movement constitutes a task-irrelevant dimension and response selection requirements are low (see section 1.4.).

The notion of shared representations for observed and executed movements is in contrast to classical (and historical) sensorimotor approaches that assume distinct sensory and motor representations on multiple hierarchical levels (e.g. Descartes, 1664; Massaro, 1990; Welford, 1968; Wundt, 1903). According to the above cognitive approaches (e.g. the common coding approach), however, no "translation" from one domain to the other is necessary because perception and performance use the same "language". Fig. 1.2. illustrates the contrary concepts of separate and common coding.

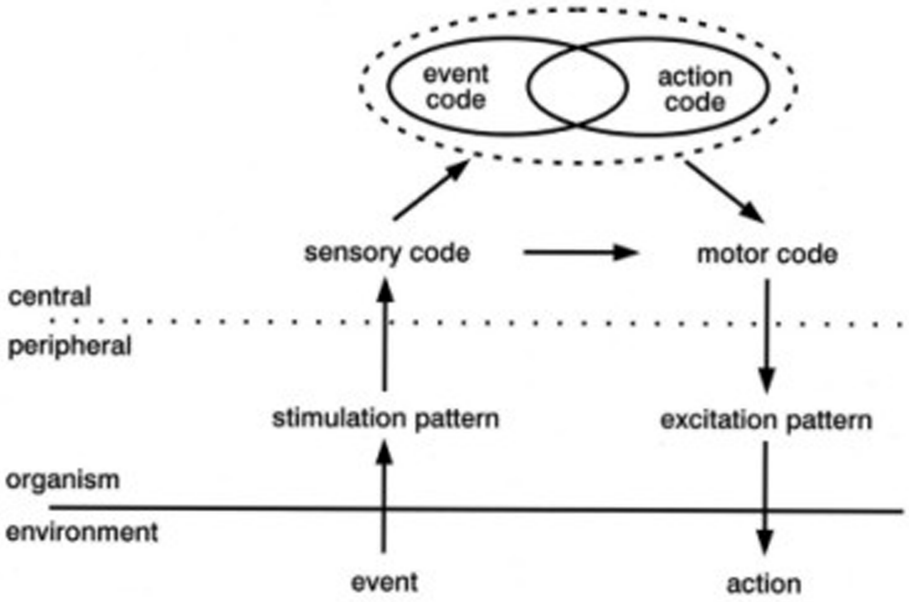

Fig. 1.2. Schematic illustration of separate versus common coding. Lower part (solid lines): separate sensory and motor coding and the translation between them. Upper part (dashed lines): common event and action codes and induction between them. Adapted from (Prinz, 1997) © 1997 Psychology Press, Taylor & Francis.

The common coding approach leads to the prediction that movement perception and performance also share a common structural, i.e. neural mechanism. So-called "neuro-cognitive" approaches link the idea of common coding to the accumulating

neurophysiological evidence on common brain bases for observation and execution of biological movement:

Based on studies on motor imagery that demonstrated behavioural benefits of mental practice on motor learning and subsequent performance (c.f. Feltz & Landers, 1983) and shared neural structures and physiological correlates of motor imagery and preparation (e.g. Decety, 1996; Fadiga *et al.*, 1999; Gerardin, 2000), Jeannerod (1994, 2001) assumed a close functional equivalence between motor imagery and preparation. He proposed that the motor system is part of a simulation network that is activated during motor planning as well as during observation of other's movements. A "neural simulation" (or: "internal imitation") mechanism is assumed to serve motor planning and learning, including the reproduction of movements like in imitation, and understanding of movements.

A more recent, but already very influential account, has been proposed by Rizzolatti and colleagues (Rizzolatti & Craighero, 2004; Rizzolatti et al., 2001). The authors associate neurophysiological findings with the cognitive *direct mapping approach* (Butterworth, 1990; Gray et al., 1991) that also assumes a direct perception-action-transfer and an activation of the motor system by the perception of an action. Rizzolatti and colleagues proposed a *direct matching* or *action observation-execution matching (AOEM)* to constitute the primary mechanism in understanding and imitation of actions in humans and primates (as far as concerned). Here, *action understanding* is defined as the capacity to achieve the internal description of an action, which comprises the recognition of its meaning, and to use it to organise future behaviour. Imitation furthermore involves an external manifestation of the internally represented movement.

As one possible explanation of action understanding (and imitation), the "visual hypothesis" states that action understanding is based on the visual analysis of an action's elements, mediated by exstrastriate visual areas, the inferior temporal lobule and the

superior temporal sulcus (STS), with no motor involvement required. In contrast, according to the “direct matching hypothesis”, the visual representation of an observed action is directly mapped onto the motor representation of the same action (i.e. activated). This means, the motor system of the observer “resonates”.

Rizzolatti et al. connected the assumption of an *AOEM mechanism* with neurophysiological findings in macaque monkeys and humans (see section 1.5.). They refer to visuo-motor *mirror neurons* in the macaque monkey, which discharge both when the animal executes an action and when it observes the same action in another individual, and to motor-related “mirror areas” in the human cortex with conjecturally homologous capacities (see 1.5.). The essential role of mirror neurons or mirror areas in action understanding and imitation is supposed to be the necessary transformation of visual into motor code: in resonating, they instantaneously code a seen movement in terms of its motor representation. Thus, they directly transform visual information into motor knowledge.

1.4. Effects of observation on execution of biological movement

There is a large body of evidence on *automatic* behavioural effects conveyed by observation of biological or animate movement (for reviews see Blakemore & Frith, 2005; Brass & Heyes, 2005). Automatic effects support the notion of a common sensory and motor coding, and a direct visuo-motor matching mechanism, respectively: if perception and performance of movements share the same representational code (Hommel *et al.*, 2001; Prinz, 1997), then the observation of a human body movement should automatically *facilitate*, or prime, its execution in the observer ("visuo-motor priming"; c.f. Vogt *et al.*, 2003), or *interfere* with ongoing motor planning, respectively. According to the direct

matching hypotheses, these effects would be mediated by resonance in motor areas of the brain.

Indeed, studies on stimulus-response compatibility (SRC) demonstrated that biological movement stimuli exert immediate facilitation as well as compatibility/congruency effects on the execution of concurring or overlapping motor responses: in general, RTs of imitative responses to human finger movements are faster as compared to responses to symbolic or spatial cues (Bertenthal et al., 2006; Brass et al., 2001a; Brass et al., 2000). Furthermore, animate movement information, even when irrelevant with respect to the task, strongly affects concurrent execution of finger, hand and arm movements, i.e. facilitating congruent movements or interfering with incongruent movements (Bertenthal et al., 2006; Brass et al., 2001a; Brass et al., 2000; Kilner *et al.*, 2003; Stürmer, 1997; Stürmer *et al.*, 2000).

Brass et al. (2000) and Bertenthal et al. (2006) instructed their participants to lift a finger in response to one of two simultaneously presented stimulus dimensions which were either congruent or incongruent: a videotaped finger lift or a symbolic or spatial cue (the latter was used only by Brass et al.) which indicated the finger to-be-moved. Responses to finger movements were faster as responses to symbolic or spatial cues. Furthermore, even when task-irrelevant, observed congruent finger movements significantly facilitated responses to other cues, while incongruent finger movements produced interference effects.

As has been shown by Stürmer and colleagues (Stürmer, 1997; Stürmer et al., 2000), congruency between observed manual gestures and concurrently executed manual gestures affected RTs, although participants were instructed by symbolic cues (colour change). Observed gestures led to RT advantages for concurrent execution of congruent as compared to incongruent manual gestures for SOAs ranging between 0 and 400 ms or 500

and 1000 ms, respectively, depending on the duration of the S1-movements (1 vs. 2 seconds).

Stürmer and colleagues reported congruency effects also for task-irrelevant *still* pictures of hand postures. Similarly, presenting a static hand posture that was congruent to the final state of an on-going movement led to faster RTs in other studies. In a simple response SRC study by Vogt et al. (2003), subjects had to perform already prepared grasping movements in response to a go-signal. Movements were initiated faster if a priming stimulus prior to the go-signal showed a final hand position that was congruent with the final position of the subject's response hand, as compared to trials where the prime showed an incongruent hand position (although the target object was not shown). In Craighero *et al.*'s (2002) study, participants were required to prepare to grasp a bar that was tilted either clockwise or anticlockwise with respect to the observer's vertical midline. RTs were faster when the go-cue was a picture presenting the hand in a position congruent to the actually required final position of the subject's hand. However, as Stürmer et al. (2000) pointed out, it is reasonable to assume that different mechanisms mediate priming effects of observed movements and "snapshots" of different movement stages (e.g. hand postures). Whereas the former mechanisms have full access to dynamic as well as static stimulus characteristics, the latter can only work on the basis of static attributes (e.g. the shape of the body part, spatial relations of different body parts).

Importantly, Brass et al. (2001a) found congruency effects with respect to the type of an observed and the type of a pre-instructed executed finger movement (lifting or tapping respectively) even in a simple response task with minimal response selection requirements. Simple response tasks are more informative than choice reaction tasks with respect to automatic response activation because in the latter participants are seeking information about required response in the stimulus. Brass et al. found no compatibility

effects when responses were triggered by moving squares. In addition, participants responded significantly faster to finger movements than to square movements.

The higher degree of automaticity regarding effects of observed biological movement might lead to the assumption that these effects are qualitatively different from those induced by other visual, symbolic or spatial, cues instructing motor responses, even when "artificial" stimuli provide the same kinematical information: while observation of a movement clearly interferes with the execution of an incongruent movement when the observed movement is performed by a human model, it could be shown that the observation of a robotic model performing the same movement induces either less interference/congruency effects (Press *et al.*, 2005) or none at all (Castiello *et al.*, 2002; Kilner et al., 2003). Kilner et al. (2003) demonstrated that an observed human arm movement which was kinematically incongruent with a simultaneously executed arm movement led to significantly stronger interference as compared to an observed incongruent robotic arm movement.

In addition to the above immediate effects of compatibility of concurrent stimuli and responses, effects of animate movement observation have also been observed in priming experiments, where the preparing stimulus (S1 or "prime") and the participant's response occur sequentially. Observation of an object-directed grasping movement improved the kinematics of a subsequent grasping movement that was congruent with respect to the size of the to-be-grasped object (Castiello et al., 2002). This held true even when the prime object's size predicted the size of the target object in only 20% of the trials (Edwards *et al.*, 2003). Importantly, no priming effects occurred if the observed movement was executed by a robotic arm or by a blindfolded human (Castiello et al., 2002), in the latter case cancelling out differences in kinematics for grasping of small or large objects. This

indicated that priming was only effective provided the observed model was human and the kinematical characteristics of observed and executed movements were also concordant.

The above reported findings are concordant with the notion that the perception of a movement automatically activates the corresponding internal motor representation that, in turn, has an effect on motor performance. Regarding instances, however, where at the moment of movement observation, the preparation of a motor response is ongoing or already completed, an influence might also come from the opposite direction, i.e. from motor preparation to perception. Accordingly, there are on principle two alternative explanations for the results obtained in the studies by Brass et al. (2001a); Craighero *et al.* (2002, 1996) and Vogt et al. (2003): (a) visuo-motor priming, as described above, where the observation of a movement, or a still picture of a movement, automatically activates the motor representation; (b) "motor-visual priming": here, the motor preparation of a pre-instructed response biases visual processing. More specifically, motor preparation is assumed to evoke the corresponding visual representation of the prepared movement which, in turn, competes with the visual representation of the observed stimulus. Due to the priming effects of the internal representation on the visual processing of the stimuli, this would lead to a facilitation of responses to matching stimuli. In contrast to a visuo-motor priming mechanism, a motor-visual priming mechanism would be constrained to situations where the observer has already prepared a response, thus having advance knowledge about the visual event (expected signal) at his disposal. Vogt et al. (2003) tested these alternative hypotheses, in contrasting pre-instructed simple responses (object-oriented grasping movements) primed by stimuli that presented a final hand posture either from the first- or the third-person perspective (with SOAs of o to 600 ms from the onset of the priming picture to the go signal). In conditions where, after instruction but before presentation of the prime, subjects fixated on a dot, a congruency effect was restricted to the third-person

perspective. This implied a visuo-motor priming mechanism. When, however, subjects fixated on a hand picture showing the starting position, the congruency effects was restricted to the first-person perspective, implying motor-visual priming. According to the authors' interpretation, the visuo-motor mechanism constitutes the experience-dependent pragmatic default mechanism, because in daily life, situations requiring rapid responses to unexpected encounters with body parts normally involve other people's bodies (e.g. when one has to make way for a playing child which is about to run into her), but not one's own body. Though, this default mechanism can be presumably overridden in situations where perceived body parts can be anticipated from the observer's own motor planning, which is the case when they are perceived in first-person perspective. Motor preparation thus drives a selective enhancement of visual processing of body parts which are associated with the prepared action, i.e. belonging to the actor himself who is preparing the movements.

1.5. Common brain bases of observation and execution of biological movement

An even more convincing proof of a direct matching mechanism than behavioural effects are demonstrations of motor activations in the brain during the mere observation of biological movements, where the observer does not have to perform any action at all: numerous functional brain imaging studies using different imaging techniques (e.g. Decety *et al.*, 1997; Grafton *et al.*, 1996; Grèzes *et al.*, 1998; Iacoboni *et al.*, 2001; Iacoboni *et al.*, 1999; Nishitani & Hari, 2000; Rizzolatti *et al.*, 1996b) as well as electrophysiological experiments (e.g. Aziz-Zadeh *et al.*, 2002; e.g. Baldissera, 2001; Cochin *et al.*, 1999; Fadiga *et al.*, 1995; Gangitano *et al.*, 2001; Hari *et al.*, 1998; Patuzzo *et al.*, 2003; Strafella & Paus, 2000) have demonstrated that passive observation of a biological movement activates a set of frontal, parietal and temporal cortical brain regions that is also involved in the execution, including the imitation, of body movements (for reviews see Decety &

Grèzes, 1999; Grèzes & Decety, 2001; Rizzolatti & Craighero, 2004). During both observation and imitation, visual input seems to access the representation of the respective biological movement through a fast direct pathway from areas predominantly engaged in perception to areas involved in motor programming and execution. In line with earlier findings on imitation of reaching movements and stationary lip forms (Nishitani & Hari, 2000, 2002), Nishitani and coworkers (2004, 2000, 2002) showed by means of *magnetoencephalography* (*MEG*) the time-course of activations accompanying imitation of still lip forms. Activations progressed in 30 to 80 milliseconds steps from the occipital cortex to the STS, on to the inferior parietal cortex, and to the inferior frontal or premotor cortex, finally reaching primary motor areas 75 to 90 ms later. The same sequence of activations was found during mere observation.

Fig. 1.3 illustrates areas that have consistently been found to be active during observation and imitation of biological movements: the inferior frontal gyrus (IFG, pars opercularis and pars triangularis), the dorsal and ventral premotor cortex (PMd and PMv), the inferior parietal cortex (IPL), the superior parietal lobule (SPL) and the posterior superior temporal sulcus (pSTS).

Among these are regions with predominantly motor properties, i.e. the pars opercularis of the inferior frontal gyrus (BA 44 as a part of Broca's area, as regarding the left hemisphere), the ventral premotor cortex (as the lower part of the precentral gyrus) and rostral inferior parietal areas. These are supposed to constitute the human homologue of the *mirror neuron system* in the monkey brain:

As was discovered by means of single-unit recordings, there are visuo-motor neurons located in the ventral premotor area F5 and in the area 7b, or area PF of Von Economo (Von Economo, 1929) in the rostral part of the inferior parietal lobule of the macaque brain which discharge both when the monkey performs a certain hand or mouth action and, importantly, when the monkey simply observes another individual executing

the same movement and, thus, have been named *mirror neurons* (see Fig. 1.4; Fogassi *et al.*, 1998; Gallese *et al.*, 1996; Gallese *et al.*, 2002; for a review see Rizzolatti & Craighero, 2004; Rizzolatti *et al.*, 1996a).

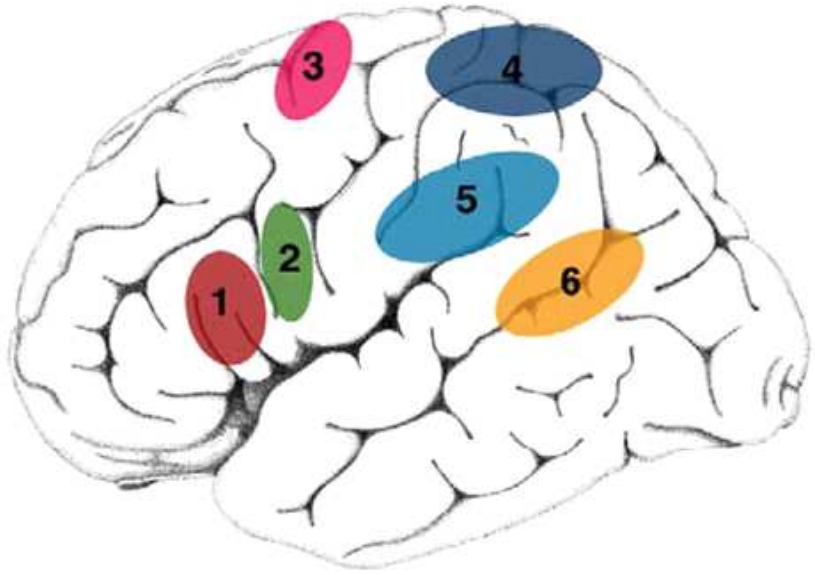

Fig. 1.3. Common activations during observation and execution of biological movements. A schematic lateral view of the human cortex. Areas that have consistently been found to respond during observation and imitation of biological movements are marked with coloured ellipses: (1) the pars opercularis and triangularis of the inferior frontal gyrus (IFG), (2) the ventral premotor cortex (PMv), (3) the dorsal premotor cortex (PMd), (4) the superior parietal lobule (SPL), (5) the inferior parietal cortex (IPL), (6) the posterior superior temporal sulcus (pSTS). Adapted from Brass and Heyes (2005) © 2005 Elsevier Science.

The above described functional property of mirror neurons is called "(type II) resonance behaviour" that, in contrast to "type I resonance behaviour", does not involve an overt motor response, and is proposed to underlie action understanding (see section 1.3.; Rizzolatti et al., 1999). Of note, area F5 receives no direct input from visual occipital areas. Its main cortical input comes from inferior parietal lobule, in particular anterior intraparietal area AIP and inferior parietal area 7b (Gallese et al., 1996). Importantly, virtually all mirror neurons show (more strict or rather broad) congruence between the action they code motorically and the action capable of triggering them visually. Moreover, F5 mirror neurons can be activated even without access to the visual features of actions:

some of these neurons were even found to respond to the specific sound of an action only (Kohler *et al.*, 2002). Umiltà *et al.* (2001) demonstrated, that more than 50% of recorded F5 mirror neurons in monkey fired also when only the beginning of an action was observed, but the rest was hidden behind a screen (beforehand, the monkey was shown that the object had been located behind the screen). However, mirror neurons in F5 neither respond to the presentation of an object alone (even when it is of interest to the monkey, e.g. food), nor do most of them respond to the sight of a pantomimed action (Gallese et al., 1996; Rizzolatti et al., 1996a). Again, these demonstrated properties of F5 mirror neurons argue against the "visual hypothesis" of action understanding (1.3.).

Moreover, a large number of visual neurons in the superior temporal sulcus (STS) of the monkey respond to the observation of a variety of body movements, including goal-directed hand actions, but also intransitive movements like walking, turning the head, moving the hand or bending the torso (see Jellema *et al.*, 2002; Jellema *et al.*, 2000; Perrett *et al.*, 1989). Paralleling the properties of mirror neurons, distinct cell populations in the anterior part of the STS selectively respond to limb movement in certain directions (Jellema et al., 2000). Further, the responses of these cells are modulated by the actor's attention (as indicated by head and body posture of the agent). Therefore, it has been hypothesised that STS neurons play an important role in determining the intention or purpose of a perceived action by integrating high-level visual information about the particular perceived action with information about the direction of the attention of the agent. Although not endowed with motor properties, thus not capable of exhibiting motor resonance behaviour like genuine mirror areas, the STS is considered to be strongly related to the mirror neuron system (Rizzolatti & Craighero, 2004). Of note, the inferior parietal lobule, which sends important output to the ventral premotor cortex including area F5 receives input from the STS. Because of their functional properties and connectivity, areas

F5 and PF and the STS have been proposed to constitute a circuit for coding actions in the monkey (Rizzolatti & Craighero, 2004).

Regarding homologies between the monkey and the human brain, the firing of STS neurons in the macaque may correspond to activation of the human STS region during observation of body movement (Grafton et al., 1996; Iacoboni et al., 2001; Pelphrey *et al.*, 2003; Puce *et al.*, 1998). Neurophysiological findings stress the selectivity of this area for the dynamics of biological versus non-biological stimuli (Allison *et al.*, 2000; Bonda *et al.*, 1996; Frith, 1995; Grossman *et al.*, 2000). Though, STS activity does not seem to depend on low-level visual features, as this area also responds to animated point-light figures (Bonda et al., 1996; Grossman et al., 2000) and to non-biological moving objects whose interactions induce the percept of animacy (Blakemore *et al.*, 2003; Blakemore & Decety, 2001; Castelli *et al.*, 2000; Schultz *et al.*, 2005; Schultz *et al.*, 2004).

Although strictly speaking, only single-unit recordings could provide final evidence for the existence of mirror neurons in the human brain, homologies between the monkey mirror system and human brain areas commonly activated by movement observation and execution have been proposed on the basis of functional and anatomical data (Rizzolatti & Craighero, 2004): the pars opercularis of the inferior frontal gyrus (BA 44), is assumed to constitute the homologue of area F5 in the macaque's ventral premotor cortex. BA 44, in the left hemisphere more widely known as a part of Broca's area and associated with speech representation, is proposed to contain also motor representations of distal hand and mouth movements (Binkofski *et al.*, 1999; Buccino *et al.*, 2001; Iacoboni et al., 1999). The human ventral premotor cortex (i.e. the lower part of the precentral gyrus) is assumed to be the homologue of monkey area F4, which is also part of the ventral premotor cortex in the monkey. In contrast to BA 44, human PMv is hypothesised to be predominantly activated by neck and proximal arm movements (Buccino et al., 2001).

Recently, the notion of a human mirror neuron system received some more direct support by intracranial electroencephalographic (EEG) recordings in a patient during surgery (Tremblay *et al.*, 2004): absolute power in the alpha rhythm band recorded over the primary hand motor area and the language motor (Broca's) area was significantly lower as compared to a control site during execution and observation of finger movements.

Rizzolatti et al. (2002) originally proposed that human mirror areas, like mirror neurons in area F5 of the monkey brain, code for *actions* proper, thus resonate only in response to transitive movements. However, some electrophysiological and neuroimaging findings on the observation and imitation of intransitive movements in humans challenged this view. These findings led Rizzolatti and Craighero (2004) to suggest that human mirror neurons also code for the (intransitive) *movements* that form an action rather than only for an action in the strict sense.

Probably as a result of evolution, some functional properties of the putative mirror regions in the human brain, are obviously lacking or at least poorly developed in monkeys (c.f. Buccino et al., 2004b): monkey F5 mirror neurons, on the one hand, "resonate" only when the animal perceives an interaction between a biological effector and an object (see Fig. 1.4), neither to the sight of intransitive movements or objects alone, nor if an agent is mimicking an action, or tools are used for an action (di Pellegrino *et al.*, 1992; Gallese et al., 1996; Rizzolatti et al., 1996a). The fact that F5 mirror neurons in macaques respond to the inferred goal of an action that is not even presented visually (Umiltà et al., 2001) would also lead to the assumption that the frontal mirror node in the monkey is tuned for goal-directed action.

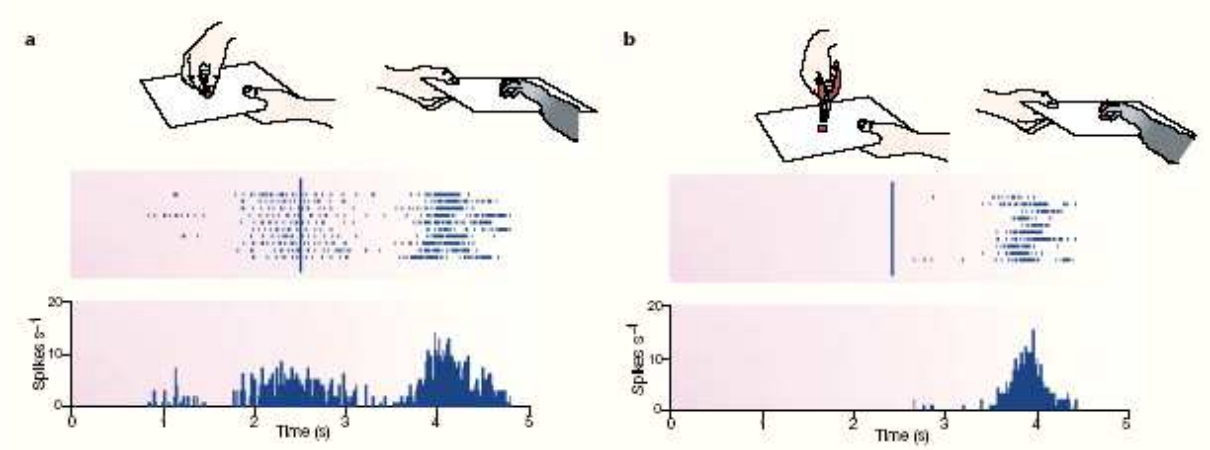

Fig. 1.4. Visual and motor responses of a mirror neuron in area F5. a. Uppermost part: a piece of food placed on a tray is presented to the monkey. The experimenter grasps the food, then moves the tray with the food towards the monkey. Lower panels: strong activation is present in F5 during observation of the experimenter's grasping movements, and while the same action is performed by the monkey. The neural discharge is absent when the food is presented and moved towards the monkey. **b.** Uppermost part: the experimenter grasps the food with pliers. Lower panels: the neural response is absent when the observed action is performed with a tool. Rasters and histograms (lower panels) show activity before and after the experimenter touched the food (vertical bar). Adapted from Rizzolatti et al. (2001) © 2001 MacMillan Magazines Ltd.

Using single-pulse *transcranial magnetic stimulation* (*TMS*), Gangitano et al. (2001) revealed that the corticospinal excitability of the human primary motor cortex, as reflected by *motor evoked potential* (*MEP*) amplitude, depends on the phase/time-course (i.e. the amount of finger aperture) of an observed grasping action: MEPs increased with increasing finger aperture and decrease during closure. Moreover, increases in motor cortical excitability have been demonstrated also for intransitive actions (Fadiga et al., 1995; Maeda *et al.*, 2002). These findings would suggest that, in contrast to monkey mirror neurons, the human mirror system codes also for intransitive movements that can form an action and not only for actions proper.

However, findings from neuroimaging studies diverge concerning the extent to which frontal and/or parietal mirror regions respond to the passive observation of not object-directed movements (c.f. Jackson *et al.*, 2006; see Rizzolatti & Craighero, 2004). Jackson et al. (2006) demonstrated engagement of primary and extrastriate visual areas, but not the premotor cortex, during the observation of intransitive hand and foot movements.

Similarly, Leslie et al. (Leslie *et al.*, 2004) did not find activation of left BA 44 during observation of intransitive finger or face movements. fMRI studies employing intransitive finger movement stimuli reported inferior frontal, but did not find inferior parietal lobule activation during an observation task (Iacoboni et al., 2001; Iacoboni et al., 1999; Koski *et al.*, 2003).

In contrast, Buccino et al. (2001) found the inferior frontal gyrus (BA 44), but not the inferior parietal lobule, to be activated somatotopically during the observation of action pantomimes performed with hand, mouth and foot. However, it is worth to point out that the distinction between intransitive and transitive movements does not rely on whether a related object is real or virtual (c.f. Bertenthal et al., 2006). Most pantomimes involve transitive actions even though no real object is present, e.g. those presented by Buccino et al. (2001). It is therefore highly questionable that the pantomimes were really processed as intransitive movements. Findings of Decety *et al.* (1997) cast further doubt on this: using *positron emission tomography* (*PET*) during an observation task, they did not find inferior frontal activation for meaningless intransitive hand movements, but for pantomimes of object-directed actions. In this respect it is interesting that most of the mirror neurons in area F5 of the monkey brain dot not respond to the sight of pantomimed actions (Gallese et al., 1996; Rizzolatti et al., 1996a), indicating functional differences between the frontal mirror areas in the monkey and the human.

Whereas neurophysiological findings are thus not entirely conclusive concerning the capacity of intransitive movements to elicit mirror neuron activity, it is a well replicated finding that humans are faster at *imitating* an intransitive finger movement than at performing the same movement in response to a non-biological cue (see section 1.4. Bertenthal et al., 2006; Brass et al., 2001a; Brass et al., 2000; Jonas et al., 2007; Kessler et al., 2006). This behavioural benefit has been proposed to be due to a direct matching

mechanism mediated by putative human mirror areas (Iacoboni et al., 1999; Rizzolatti & Craighero, 2004; Rizzolatti et al., 2001).

As was demonstrated (e.g. Schubotz & von Cramon, 2002), non-biological response cues are also capable of inducing motor activation when subjects recognize predictable dynamic patterns. However, observation of biological movement is obviously even more effective: as revealed by functional brain imaging and TMS, observation and imitation of human movements cause stronger activation of human mirror areas as compared to spatial cues (Heiser *et al.*, 2003; Iacoboni et al., 2001; Iacoboni et al., 1999; Koski et al., 2003). Using fMRI, Iacoboni et al. (2001, 1999) showed that activation in the operculum of the left IFG, the right anterior/superior parietal cortex, the right parietal operculum as well as the right STS was stronger in imitation of an intransitive finger movement than in control conditions where the execution of the same finger movement was instructed by a static spatial cue. The main findings were replicated by Koski et al. (2003).

Moreover, observing a human movement causes stronger frontal motor/mirror activation than observing a movement executed by a robotic or a "virtual" model: using PET, Tai *et al.* (2004) showed activation of the premotor cortex to be present during observation of human grasping, but not if the movement was performed by a robotic model, thus providing evidence that the putative human frontal mirror area is tuned for matching "natural" biological movements exclusively. In a way, this parallels the results of macaque studies where mirror neurons were found to be silent when tools were used for an action (di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996b). Also, no motor resonance has been found when human subjects watched point-light figures which move "biologically" (Grossman et al., 2000; Vaina *et al.*, 2001).

Costantini *et al.* (2005) reported stronger activation of the posterior parietal cortex (BA 40 and 7) during the observation of biomechanically impossible as compared to the

observation of feasible fingers movements. In an fMRI study by Perani *et al.* (2001), only the observation of real object-related hand actions activated the right inferior parietal cortex. Observation of two- or three-dimensional graphically reconstructed “virtual” hand actions only activated occipital areas engaged in higher visual processing.

Further results indicate that only actions associated with internal “personal knowledge” (see Merleau-Ponty, 1962) excite motor-related areas in the observer. Actions for which personal knowledge is lacking, i.e. performed by non-human biological agents, appear to be recognised essentially on a visual basis without motor involvement: as Buccino et al. (Buccino *et al.*, 2004a) found out, inferior frontal and parietal regions resonate in response to movements which are part of the human motor repertoire, even when performed by non-conspecifics (i.e. biting executed by a monkey or a dog), but do not resonate in response to movements that are not part of the human response repertoire (i.e. barking).

On the basis of these findings, inferior frontal and inferior parietal activations during observation and/or imitation of human movements have been supposed to reflect a direct mapping of observed actions onto their internal motor representations via resonance behaviour of human mirror neurons (Iacoboni et al., 1999; Rizzolatti et al., 2001; see section 1.3.).

Further fMRI evidence corroborated the assumption that the frontal mirror node (or BA44, respectively) is rather the part of the human mirror neuron system where the goals of movements are represented: Koski et al. (2002) found stronger activation of BA 44 during imitation of a finger movement with a visible goal object as compared to a comparable movement that was, however, not directed towards an object. Furthermore, Johnson-Frey *et al.* (2003) demonstrated that observation of the realised goal of a

prehensile action is already sufficient to activate inferior frontal gyri, even in the absence of a dynamic movement (the participants observed static pictures).

In contrast to the functionality of the inferior frontal area, the inferior parietal area is assumed to code the precise motor specification of the movement (e.g. the amplitude of the finger lift) (Iacoboni, 2005a, 2005b; Iacoboni & Dapretto, 2006; Iacoboni et al., 2001; Iacoboni et al., 1999).

Contrary to neural responses of the inferior frontal and parietal cortex, activation of the superior parietal lobule or anterior intraparietal sulcus, which is typically not present when subjects are instructed to observe movements without the aim to imitate them (e.g. Buccino et al., 2001), might not reflect genuine resonance phenomena (c.f. Rizzolatti & Craighero, 2004). Activity in this regions, as well as in the parietal operculum and the STS, possibly present somatosensory and higher-order visual copies of the intended movement, respectively: the superior temporal region has been proposed to serve as an „interface“ linking observed actions and reafferent motor-related copies of actions performed by the imitator (Iacoboni, 2005a, 2005b; Iacoboni & Dapretto, 2006; Iacoboni et al., 2001; Iacoboni et al., 1999).

A similar interpretation of the superior/anterior parietal activation is that the request to imitate produces, through backward projections, sensory, i.e. kinesthetic copies of the intended actions. Activation of the parietal operculum during imitation might represent a reafferent somatosensory copy of the intended movement which serves a monitoring purpose as the kinesthetic description provided by the anterior parietal region and the visual description provided by the STS (c.f. Rizzolatti & Craighero, 2004).

2. Reaction time experiments

In the following chapter, four reaction time experiments will be reported. These include two studies employing a cueing/priming paradigm and two experiments with single visual stimuli. The first section (2.1.) addresses the general objectives and hypotheses, with reference to section 1.4. Then, each behavioural experiment will be reported separately (sections 2.3. to 2.5.), concluding with a general discussion in section 2.6.

2.1. Main objectives

Behavioural evidence (see section 1.4.) strongly suggests the existence of specific automatic effects of animate movement observation on immediate as well as on delayed movement execution. However, depending on the characteristics of the employed stimuli, genuine effects of human movement may be confounded with effects of other unspecific, i.e. not genuine "biological" stimulus characteristics. For example, Berthental et al. (2006) demonstrated that finger movement stimuli that were spatially compatible with participants' responses to symbolic cues induced significantly larger congruency effects as compared to spatially incompatible finger movements.

What still remains unclear is the specific contribution of *human* movement as opposed to movement *per se*, irrespective of *what* is moving. So far, immediate and delayed behavioural effects due to observation of biological movement have not been analysed separately from congruency or correspondence effects that might also affect non-biological stimulus categories. Most previous experiments either failed to introduce appropriate control stimuli or involved control conditions that were not precisely controlled: some of the reviewed studies investigated priming by animate movements (or stationary stimuli implying movements) without any non-biological control condition (e.g. Stürmer, 1997; Stürmer et al., 2000; Vogt et al., 2003). Others used stationary

symbolic/spatial cues for comparisons (Brass et al., 2000; see also Iacoboni et al., 2001; Iacoboni et al., 1999; Koski et al., 2003), which were, moreover, markedly less salient than the finger movement stimuli (i.e. a black cross was used that appeared on one finger). In some experiments, kinematics of inanimate movements were matched with body movements (Brass et al., 2001a; Castiello et al., 2002; Edwards et al., 2003; Kilner et al., 2003), but animate stimuli and objects or robotic cues, respectively, differed on a number of important stimulus dimensions (shape of body part/object shape, size, colour, luminance). Thus, the results of these studies may also reflect unspecific effects of attention and leave open which of the presented stimulus dimensions (or which combination) can primarily be taken responsible for the reported behavioural effects. A recent study by Press et al. (2005) investigated automatic effects of observed human and robotic stimuli, i.e. still pictures of final movement positions, that were matched with respect to size, colour and brightness. When participants performed a prespecified movement (e.g. opening their hand) on the presentation of a human or robotic hand in the terminal posture of a compatible movement (opened hand) or an incompatible movement (closed hand) both the human and the robotic stimuli elicited compatibility effects. But, importantly, even when the human and robotic stimuli were closely matched the human hand had a stronger effect on performance, suggesting that effector shape was sufficient here to allow the AOEM system to distinguish human from robotic movement.

The present behavioural studies aimed at further contributing to the question which factors are responsible for the effects of observed biological movement, focusing on temporarily delayed effects and their dynamics. Although there is evidence on priming effects of observed transitive, i.e. object-directed actions, on subsequent motor responses of participants (Castiello et al., 2002; Edwards et al., 2003), delayed effects of priming by intransitive, i.e. not object-directed movements, have not been investigated yet.

Furthermore, behavioural studies (Stürmer, 1997; Stürmer et al., 2000; Vogt et al., 2003) provided some evidence on the temporal dynamics of effects on instances where the observation of a human movement (or a still picture of this) and the participant's response overlap: RT advantages for concurrent execution of congruent as compared to incongruent manual gestures were observed for SOAs ranging between 0 and 400 ms or 500 and 1000 ms, respectively, depending on the duration of the S1-movements (1 vs. 2 sec). If still pictures were presented, effects were observed at SOAs of 0 and 400 ms (with 1 sec prime duration; Stürmer et al., 2000) and 600 ms, respectively (with presentation of the prime ending 500 ms after movement initiation; Vogt et al., 2003). In fact, Stürmer and colleagues also observed inverted congruency effects (incongruent gestures being faster than congruent ones) for SOAs of 800 ms (1 sec-prime) or 1500 and 2000 ms (2 sec-prime), respectively. However, control experiments confirmed that this inversion was not an inhibitory after-effect but due to the turning of the stimulus movement's direction before instruction - at this time becoming effectively incongruent with the direction of the response movement. The authors reported congruency effects also for task-irrelevant static pictures of hand postures.

Thus, as so far evidence on the temporal dynamics effects is available only for instances where the observation of the priming stimulus and the participant's response overlap, the time-course of effects over different SOAs between a prime (S1) and a target stimulus (S2) was explored.

Before this background the basic S1-S2 paradigm was designed. The main objectives were to develop a behavioural paradigm that would permit to (i) pre-activate or prime the execution/imitation of a movement by observation of a corresponding human body movement, (ii) depict the behavioural effects resulting from movement priming, while (iii) separating genuine effects of observed body movement from those that might be due to

unspecific characteristics of an animate movement stimulus, i.e. observed movement per se, irrespective of *what* is moving (a biological entity or not) or the mere presence of a (static) biological shape or entity. Furthermore, (iv) the temporal dynamics of these effects should be elucidated. Finally, one ore more behavioural paradigms were sought to be established that would be suited for investigating the neuronal correlates of effects conveyed by animate movement observation with the use of functional brain imaging techniques (e.g. fMRI).

2.1.1. The basic S1-S2 paradigm

The basic paradigm for testing in healthy adults (Fig. 2.1A) was basically a supraliminal visual priming paradigm employing two successive picture sequences (videos) as stimuli and a two-alternative choice reaction task. Two main conditions presented either animate finger movements or *inanimate* dynamic-spatial instruction cues, i.e. moving dot stimuli that were closely matched with respect to kinematical properties and other characteristics of the stimulus array (see section 2.2.1. for details). As S1/priming stimulus, either (i) a single intransitive movement of the index or little finger of a left hand was shown or (ii) a dot moving on top of one of these two fingers was presented while the hand remained static. After a predefined interval S1 was followed by a target stimulus (S2) drawn from the same stimulus pool that was either congruent (if S1 and S2 indicated the same finger) or incongruent with respect to the finger position in S1. Subjects were instructed to respond to S2 immediately by lifting the indicated finger of their right hand. Two finger positions were used only as stimuli and response alternatives for the following reasons: (i) to ensure low response selection requirements, i.e. reduce the risk that demanding response selection processes might interfere with effects of interest to a minimum; (ii) to avoid an unequal predictability of congruent versus incongruent fingers. If more than two fingers were used

there would be multiple incongruent alternatives but only one congruent, resulting in a higher conditional probability for the congruent compared to any incongruent finger.

As subjects were instructed to respond with their right hand the visual stimuli were presented in a mirrored orientation. This orientation was chosen because there is evidence that humans, especially young children (c.f. Bekkering *et al.*, 2000), have a tendency towards *specular* imitation, where the model is imitated in a mirrored fashion, as compared to *anatomic* imitation, where model and imitator perform anatomically corresponding movements. Moreover, stronger activation of inferior frontal and parietal areas during specular as compared to anatomically correct imitation has been interpreted as reflecting a stronger engagement of AOEM mechanisms during this mode of imitative behaviour (Koski et al., 2003).

The set-up always included movement stimuli occurring either lateralised to the left (index finger) or to the right (little finger) with respect to fixation (the middle of the hand). In Fig. 2.1A, the specific spatial component inherent to the employed stimuli is illustrated: the index and little finger constitute distinct parts of the same (organic) object occupying clearly different spatial locations.

Actually, the simple spatial reference frame inherent to the presently used stimuli with two alternative fingers bears similarities to standard paradigms used in experiments on spatial (location) cueing. In their widely cited studies on this topic, Posner and Cohen (1984) presented simple boxes left and right of a fixation box (Fig. 2.1B). In their basic paradigm, a cue was shown in one peripheral box (i.e. the outline of the box was brightened for 150 ms) followed by a target stimulus (a bright filled square inside one of the boxes) at stimulus onset asynchronies (SOAs) varying between 0 and 500 ms. Participants were instructed to press a single key as soon as they could detect the target

(that was present in 80% of all trials and was located in the central box in 60% of the trials or either in the cued or the uncued peripheral position in 10% of the trials each).

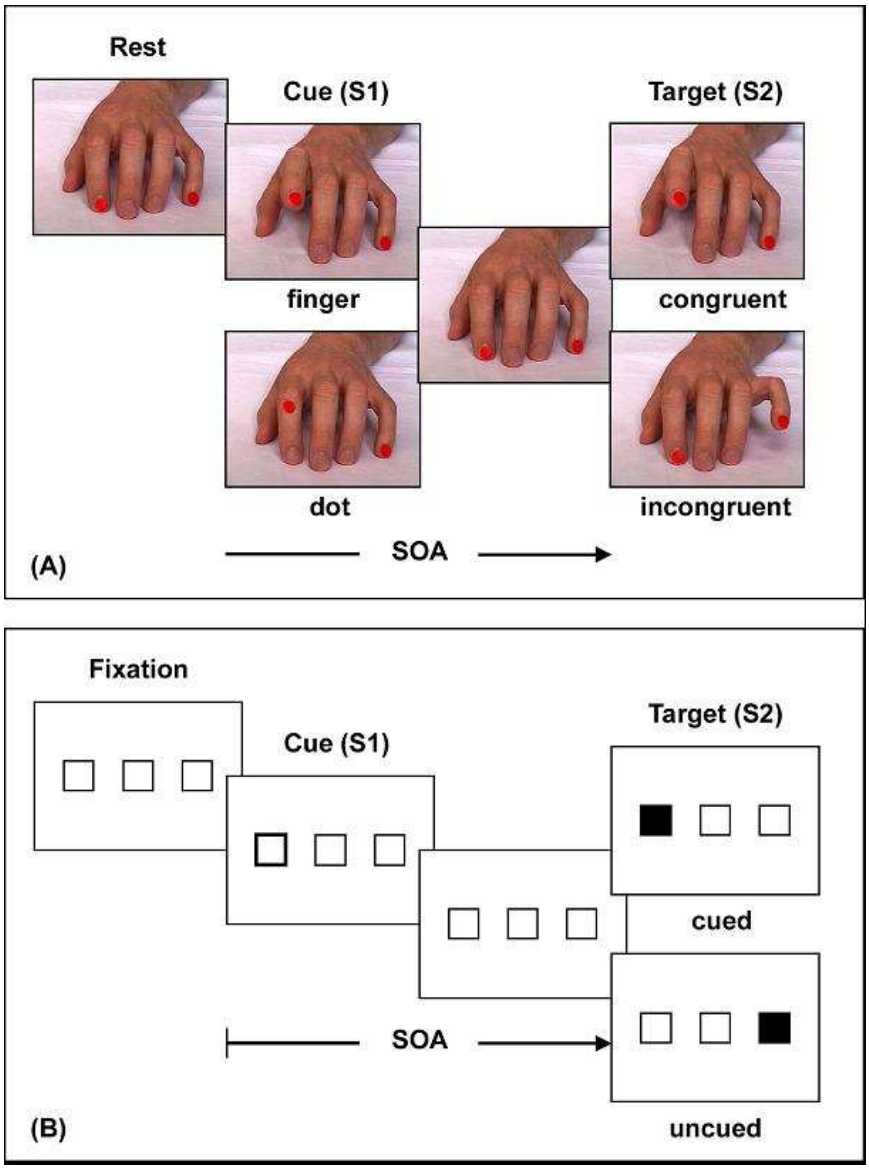

Fig. 2.1. A: Basic S1-S2 reaction time task used in the present studies. In the exemplary trial displayed, the index finger position is primed/cued by S1. The target (S2) is a finger movement. Upper rightmost panel: the target movement is presented in the congruent/cued position of the index finger. Lower rightmost panel: the target is presented in the incongruent/uncued position of the little finger. **B: Basic spatial cueing paradigm as employed by Posner and Cohen (1984).** In the pictured trial, the cue is presented in the left of two peripheral boxes. Upper rightmost panel: the target (S2) is presented in the cued position. Lower rightmost panel: the target is presented in the uncued position. Adapted, with permission, from Jonas et al. (2007) © 2007 Springer.

Consequently, in addition to visuo-motor priming processes specific to biological or animate movement, spatial cueing processes were expected to influence the sort of prime-target effects which would be revealed by the S1-S2 experiment to a considerable extent. Therefore, some major findings out of this area of research had to be taken into consideration: using the location cueing paradigm described above, Posner and Cohen (1984) reported a biphasic pattern in RTs depending on the interval between cue and target. At SOAs up to 150 ms *positive priming* (*PP*) was observed, i.e. responses to targets in the cued box were faster than responses to targets in the uncued box. With SOAs longer than 300 ms, however, PP turned into the opposite effect, i.e. responses to cued targets were slower than to uncued targets. As this was thought to reflect a tendency to avoid recently attended locations this effect was called *inhibition of return* (*IOR*)[1]. Results of Wright and Richard (2000), who systematically studied the facilitative and inhibitory effects of location cue validity on RTs in a target-detection task, indicated that facilitation (PP) is a reflexive consequence of cueing while inhibition appeared to depend on cue informativeness: whereas in their experiments, facilitation at short SOAs (66 and 100 ms) was not influenced by cue validity, IOR at longer SOAs (400 ms) was found only if the cue was not predictive with respect to the target location (i.e. if the ratio of valid and invalid is 50:50). If cue validity was very high (80% valid trials), even at longer SOAs facilitation was observed. According to that, IOR was thought to be only present when previously attended locations are irrelevant, i.e. when the preceding cue is not predictive with respect to the location of the subsequent target (Wright & Richard, 2000). This is the case in an *exogenous cueing* procedure where cued/congruent and uncued/incongruent trials occur with equal probabilities. Corresponding to the attentional account of IOR[1], in an *endogenous cueing* procedure, where cued and uncued trials are presented with different

[1] This "attentional" view of IOR presumes that slowed re-orienting of attention to a previously cued location leads to also slowed perceptual processing of the target presented in this location. Alternatively, other mechanisms are discussed which may be responsible for this phenomenon: IOR might reflect a reluctance to respond to targets in cued locations ("motor" view; see Taylor & Klein, 1998).

probabilities, rendering them informative as with respect to the target location, IOR should not be observed when a target appears in an expected location. Because of expectancy, the participant's attention should be oriented to that location, thus, no reorienting is necessary. However, Lupianez *et al.* (2004) could show facilitation at SOAs of 100 and 500 ms and IOR at SOAs of 1000 ms in a target detection task with non-informative as well as with informative cues (80% cued trials) independent of whether the target appeared in an expected or unexpected location. These results suggest that IOR may actually be independent of endogenous orienting and that exogenous and endogenous processes can also work in parallel.

IOR was initially assumed to be associated only with a location-based representation, that is, attention was inhibited from returning to a particular location. However, Tipper *et al.* (1991) conducted studies where, after cueing an object, the object moved to a new location before target presentation. In this case the inhibition moved with the object. Further experiments have shown that inhibition could in fact be associated simultaneously with both location- and object-based representations (Tipper *et al.*, 1994), and also with the representation of objects parts (Tipper *et al.*, 1999). Finally, if inhibition was associated with animate objects that bear a high social significance, i.e., faces, IOR has been shown to be very robust and may even affect representations in long-term memory (Kessler & Tipper, 2004; Tipper *et al.*, 2003).

Given that IOR can occur with moved objects and object parts (although, so far, only inanimate objects have been employed as stimuli) in a spatial setting similar to the one employed here, it was possible that some kind of "hand-based" IOR would be observed at longer SOAs (over 300 ms). That is, one would expect RTs to be generally slower rather than faster when stimuli are congruent compared to incongruent S1/S2 conditions. Note, that this IOR effect should be independent from whether S1 was a finger movement or a moving dot.

2.1.2. Main hypotheses

Taken together, one would predict that under the experimental conditions of the basic S1-S2 paradigm at least two different processes would be initiated: (i) direct matching of an observed S1-finger movement to its internal motor program, which would exclusively modulate priming effects of finger movements and (ii) a shift of spatial attention towards the location of the S1-finger or dot movement. Depending on the S1-S2 interval and the cueing procedure employed (exogenous vs. endogenous) this can lead to either PP or even IOR.

PP would lead to faster responses in congruent as compared to incongruent trials in both priming conditions, IOR would have the reverse effect. It was hypothesised that, whereas attentional orienting would be observed with inanimate and animate movement stimuli (regardless of whether strategic processes induced by informative cues or automatic processes due to exogenous cueing), direct matching processes would only be induced by biological finger movement stimuli. Therefore, S1-effects should be modulated specifically in the finger movement conditions. Apart from that, direct matching should generally facilitate responses in the conditions with an animate finger as compared to an inanimate dot target (S2).

Behavioural experiments

The following reaction time studies will be reported in the indicated order and sections:

2.2.: *RT Experiment 1*: First single-stimulus RT experiment

2.3.: *RT Experiment 2*: First priming/cueing (S1-S2) RT experiment

2.4.: *RT Experiment 3*: Second priming/cueing (S1-S2) RT experiment

2.5.: *RT Experiment 4*: Second single-stimulus RT experiment

2.2. RT Experiment 1: First single-stimulus RT experiment

2.2.1. Objectives

It has already been shown in previous behavioural studies on SRC that RTs of choice responses instructed by presentation of a biological finger movement are shorter than those instructed by symbolic or static spatial cues (Bertenthal et al., 2006; Brass et al., 2000). Also, predefined simple responses triggered by observation of a finger movement are faster than responses to moving objects (Brass et al., 2001a). However, as mentioned in the previous section, the reviewed behavioural studies that investigated priming or SRC effects of biological movements either did not use a non-biological control condition at all or evaluated responses to biological movements against responses to visual cues which did not control for all stimulus features that might possibly be responsible for the observed behavioural effects. Therefore, finger movement and object movement stimuli were matched as closely as possible with respect to their kinematical properties and, furthermore, with respect to the visual array of objects/entities: during the object movement, the finger was visible but remained in a resting position which at the same time served as the start and the end position of the finger movement in the biological stimulus. Vice versa, the object was visible in a static state during the finger movement. A good noticeable colour (i.e. red) was chosen for the moving dot, thus enhancing its perceptual salience.

First, the stimulus material was sought to be validated in a control experiment that required immediate responses to single stimuli, prior to conducting a S1-S2 experiment where priming and cueing-effects of S1 would interact with effects of S2. Therefore, single finger movement stimuli were compared with moving dot stimuli in a two-alternative choice reaction task.

2.2.2. Method

Participants

All participants in this and the subsequently reported experiments as well were free of neurological disorders, had normal or corrected-to-normal vision and were assessed as being right-handed according to a modified version of the *Annett Handedness Questionnaire* (*AHQ*) (revised; see Annett, 1970, 1985). Only subjects scoring "R pure", "R weak L", or at least "R mod L" were included, thus to obtain comparably distributed reaction times for all participants. Further, a consistent stimulus-response relation should be established, as stimuli should always represent a mirrored image of the participant's dominant hand (see *Stimuli* section). Subjects gave their informed consent prior to each of the experiments to which purpose they were naive and were paid for their participation. All studies were in accordance with the Declaration of Helsinki (1964).

RT experiment 1 was carried out at the University Medical Center Hamburg-Eppendorf (*UKE*). Eight subjects (five female and three male, 27 to 43 years, mean 33.1 years) were tested.

Stimuli

Stimuli consisted of animated picture sequences of a resting hand, implemented finger movements and dot movements, respectively (see Fig. 2.2 for an illustration).

Stimulus construction: first, a repeated 2 Hz finger tapping was videotaped. The tapping was performed by a right-handed male model with the index and little finger of his right hand. During the shooting red coloured paper dots were fixed on the nails of the two fingers. Afterwards finger movement stimuli were constructed by exporting 15 picture frames each from selected video sequences of approximately 500 ms duration and flipping

them in the vertical plane (from right to left) by standard image editing software (Photoshop, Adobe Systems Inc., San José, CA, USA). Each biological movement sequence was composed in a way that avoided detectable visual discontinuities within a rest – movement – rest-sequence. To design the kinematics and amplitude of an object movement in one of the two positions (index and little finger) very close to its corresponding finger movement, the videotaped dot was extracted as a layer from each picture frame of the finger movement sequence. A single layer was then pasted into a default picture showing all fingers in the resting position, as well as with the dot concerned in the to be constructed movement having been removed from the fingernail. Only slight corrections were made to the location of the dots in the horizontal plane, thus to ensure that the dot was moving on top of the finger rather than running next to it which would have appeared rather unnatural. Presenting the resulting 15 pictures in successive order gives the impression of the dot moving up and down on top of one finger.

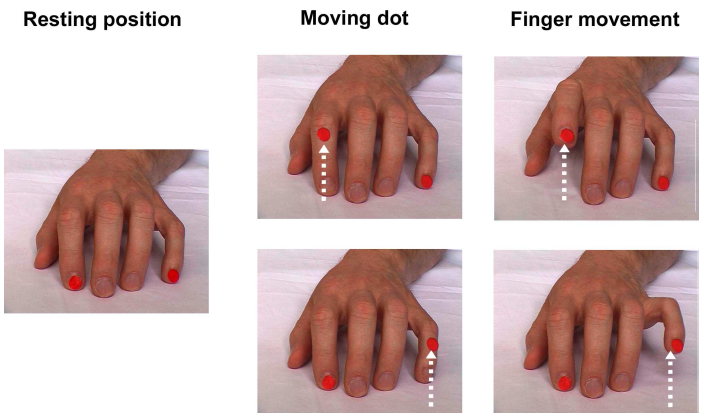

Fig. 2.2. Visual stimuli presented in RT Experiment 1. Resting position (left column): a picture of a static left hand with red dots on the tip of the little and index finger was shown at the beginning and the end of each movement sequence. Movements were always presented at the position of the index finger (top row) or little finger (bottom row): a moving dot (middle column) or a finger movement (right column). Each sequence consisted of 15 picture frames showing an upward and downward movement. Here, only the frames at maximum finger/dot lift are shown. The dotted arrows symbolise the upward movement.

This method conveys similarities to the point light technique developed by Johansson (1976) and a digital version of it applied by Brass et al. (2001a). In contrast to Brass and colleagues, the body part from which the object movement was constructed was not removed, but the moving object was superimposed on a still picture of the hand. This was done in order to match the visual array presented in the two movement conditions as close as possible.

Resting hand: subjects observed the left hand which was recorded from a slightly lifted frontal view (Fig. 2.2). The whole hand was visible including the wrist, with a white background. Red dots of approximately 0.9° diameter were mounted on the fingernails of the index and little finger. Fingertips were placed on a plain horizontal surface. This resting hand was shown at the beginning and the end of each movement sequence.

Movement sequences: movements could either be a single finger tap of the index or little finger (up-and-down movement including mounted dots) or a corresponding dot movement alone. One movement sequence lasted approximately 500 ms comprising 15 picture frames of about 33 ms each (corresponding to two refresh rates of the computer monitor).

A single trial started with the presentation of the resting hand lasting 1500 ms on average (range 1000 – 2000 ms, 200-ms steps). Then, the movement stimulus was presented, followed by the static hand lasting 500 ms. Average trial duration was therefore 2 sec. During a fixed inter-trial-interval of 2 sec the screen turned black.

In the ‘finger movement’ condition, the stimulus was a movement of either the index or little finger. In the ‘moving dot’ condition, a dot moving on top of one of these two fingers was presented.

Task

Subjects were instructed to observe all stimuli attentively while fixating the middle of the hand. They were instructed to either lift the same finger that was moving or the finger on top of which a dot was moving. Responses should be made as fast as possible.

Design

Within group factors were ‘type of movement’ (finger, dot) and ‘finger position’ (index, little). Each combination of factors movement type and finger position was presented 20 times, resulting in a total of 80 trials. Participants performed one block within which the order of trials was pseudo-randomised. Two bins of 40 trials each were separated by a break of at least 10 sec. Testing was preceded by 10 practice trials that were excluded from analysis. The whole experiment took approximately 10 minutes.

Data acquisition and processing

Stimulus presentation and acquisition of response data in this and the following studies in Hamburg and in Düsseldorf were controlled by personal computers using the same software (Presentation, Neurobehavioural Systems, Inc., Albany, CA, USA; except for RT Experiment 4, see section 2.5.). In the RT experiments, rectangular pictures were presented centrally against a black background on a 17 inch TFT computer monitor (Hamburg) or back-projected on a projection screen (Düsseldorf). Subjects were seated in front of the screen as to maintain a visual angle of approximately 19.3° diagonally.

During the experiments participants’ right hand rested in a custom made light barrier device. The device consisted of two light barriers mounted on a panel. The endings of two optical fibres were positioned laterally to the tip of the index and little finger with the fingers resting on a board in a slightly flexed position (Fig. 2.1A; Fig. 2.2). The light

barrier was opened as soon as participants lifted either the index or little finger from the base plate on which the light barriers were mounted. A positive response was registered each time the subject lifted one finger, enabling us to assess the corresponding response time. Responses were logged on-line together with presented stimuli and stored for subsequent processing.

For each trial, time of stimulus onset and motor response were extracted from the result file created by Presentation. The subjects' responses were quantified as reaction times and errors. RT in a single trial was calculated from the onset time of a visually presented movement in S2 (first frame) to the subject's response. Latencies exceeding plus/minus 2.5 standard deviations of the mean RT were excluded from further analysis. If an RT was shorter than 100 ms, thus implying that the response was initiated before the onset of S2, it also was excluded. Furthermore, erroneous trials were excluded from the RT analysis. A trial was considered invalid in case (a) the wrong finger was lifted, (b) multiple reactions were made, (c) subjects responded prior to movement onset in S2 or (d) no response occurred. Mean RTs of valid responses and error rates were calculated for each subject and condition.

Statistical evaluation

Mean RTs and error rates were calculated in each subject for each stimulus type. Data were analysed using standard statistics software (SPSS 11.0 and 13.0, respectively, SPSS Inc., Chicago, USA). A repeated-measurements ANOVA was calculated, including within-subject factors 'type of movement' (finger, dot) and 'finger position' (index, little). Mean RT or error rate, respectively, was the dependent variable. Degrees of freedom for *F*-tests were corrected for potential non-spherical distribution of the error term (*non-sphericity*) in the data according to the Greenhouse-Geisser method.

2.2.3. Hypotheses

Due to direct matching of observed and executed finger movements, an RT advantage was expected for responses to a finger movement as compared to responses to a moving dot, irrespective of the finger position.

2.2.4. Results

RTs

Mean reaction times and error percentages in all conditions are presented in Table 2.1.

Table 2.1. RT Experiment 1: Reaction time and error data

	finger movement				moving dot			
	RT		error rate		RT		error rate	
	mean	SD	mean	SD	mean	SD	mean	SD
index	395	25.07	0.6	1.77	409	20.02	0.6	1.77
little	407	34.75	11.9	4.58	416	29.81	2.5	2.67

RT (ms) = reaction time in milliseconds, error rate (%) = percentage of errors total; SD = standard deviation; index = index finger; little = little finger

Responses revealed a main effect of type of movement ($F(1,7) = 10.9$, $p < .05$; see Fig. 2.3). Responses to animate movements were on average 12 ms faster than responses to moving dots (401 ms, SD = 22.35 vs. 413 ms, SD = 24.03).

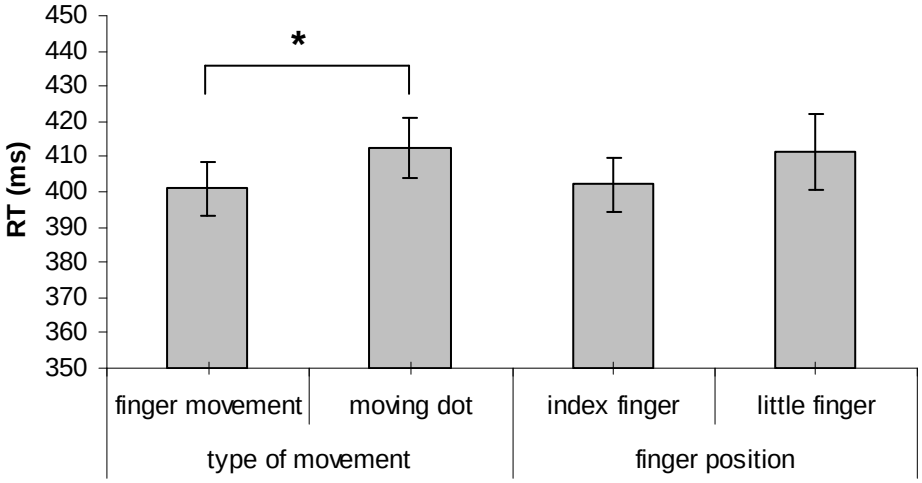

Fig. 2.3. RT Experiment 1: Main effects for 'type of movement' (finger, dot) and 'finger position' (index, little). Mean RT ± standard error of mean is displayed. Significant differences are marked (* $p < .05$).

Error rates

Mean percentage of errors was 3.9% (range 2.5-5.0%). A single false response was the least common error (0.5% of all trials), whereas responding more than once in a trial was observed most frequently (3.0%).

The ANOVA revealed significant main effects of type of movement ($F(1,7) = 13.2$, $p < .01$) and finger position ($F(1,7) = 49.0$, $p < .001$). Participants made more errors when responding to a finger movement (6.3%) as compared to a moving dot (1.6%). Little finger trials showed more errors (7.2%) than index finger trials (0.6%). There was furthermore a two-way interaction between type of movement and finger position ($F(1,7) = 18.1$, $p < .01$). Post-hoc tests revealed that a significant higher error rate for the finger compared with the dot movement condition was confined to responses with the little finger (mean difference: 9.4%, $t(7) = 4.3$, $p < .01$). In turn, significantly more errors in little than in index finger trials were observed only when subjects responded to finger movements (mean difference: 11.3%, $t(7) = -6.2$, $p < .001$).

2.2.5. Discussion

Using a two-alternative choice reaction paradigm with responses to single stimuli serving as both the instructive and the go-cue, the expected advantage for responses to a finger movement as compared to a moving dot was confirmed for the employed stimulus material.

Effects on error rates were complimentary to RTs, however only when comparing responses to finger movement and moving dot stimuli for which participants (correctly) used the little finger. Regarding the finger movement condition, multiple responses with the little finger were much more frequent than responses with the wrong finger (9.4% vs. 1.3%), whereas a less marked difference in the reverse direction was found for little-finger-responses to dot movements (1.9% vs. 0.6%). There was moreover a higher rate of multiple responses in finger movement compared with moving dot trials where participants responded with the little finger (9.4% vs. 1.9%), as well as more multiple responses to observed finger movements with the little finger as compared to responses with the index finger (9.4% vs. 0.6%). This supports, to my concerns, the interpretation that the majority of errors results from an executive “over-drive” due to automatic response tendencies towards the observed finger movement which were enhanced by the instruction to react as fast as possible. Probably because normal participants are less skilled in performing tapping movements with their little finger than with their index finger, there was a higher frequency of involuntary superfluous movements in the little finger trials.

These results provide further evidence that the execution of an elementary finger movement is facilitated if the movement is visually instructed by itself, i.e. by observation of the very same finger movement, as compared to the observation of a moving but inanimate object. Extending the findings from previous behavioural studies (Brass et al., 2001a; Brass et al., 2000), this advantage is present although in the control movement condition the object is moving along the same trace as the corresponding finger and,

furthermore, the finger is visible in a resting position during the object movement. Thus, the observation of a "natural" finger movement, comprising both biological kinematics and a biological entity at the same time, is more advantageous than the observation of a salient stimulus that presents both "biological" kinematics and a biological entity, but where the movement is carried out by an inanimate object instead of a human body part. Concluding, each of these characteristics of a body movement might by itself lead to behavioural advantages if compared with even "less biological" stimuli (i.e. presenting movement with different kinematical properties or no movement at all). According to the concept of ideomotor compatibility (Greenwald, 1970), the more a stimulus is similar to an action, the more the execution of this action is facilitated. However, the behavioural effects of action observation found in the above cited as well as in the present study seem to rely on the combination of these characteristics in a biological movement rather than on any individual feature alone.

Using the present stimulus material in a S1-S2 paradigm furthermore aimed at investigating effects of pre-activation or priming by observation of a first biological movement on the execution of a subsequent second movement.

2.3. RT Experiment 2: First priming/cueing (S1-S2) experiment

2.3.1. Objectives

In the first control experiment, the immediate facilitative effect of a single intransitive finger movement stimulus on the performance of a corresponding finger movement had been confirmed for my stimulus material. Now, the purpose of RT Experiment 2 was to investigate delayed priming effects of a first observed intransitive finger movement

stimulus (S1) on the subject's execution of a movement in response to a subsequent second finger movement stimulus (S2) that is either congruent or incongruent to S1.

Paralleling the objectives of the control experiment, specific effects of observed intransitive finger movement were sought to be separated from unspecific effects of stimulus characteristics as motion per se or the mere presence of a (static) human body part. Again, responses to simple, intransitive finger movements were contrasted with responses to object movements which were matched with respect to their kinematical properties.

The paradigm compared (i) the imitation of a finger movement (S2) which is primed by a finger movement (S1) as well with (ii) the execution of a corresponding finger movement in response to a moving dot (S2) which is primed by an object movement (S1) of the same kind. As a baseline condition, trials were introduced where the stimulus in S1 was a colour change of the static dots on both fingers. This condition was introduced in order to evaluate a possible unspecific influence that the mere presence of S1 might exert on RTs by drawing attention to S2.

As was laid out in the introduction, due to the spatial nature of the present stimulus arrangement, RTs were expected to be influenced not only by (i) processes specific to observation-execution matching of biological finger movements but furthermore by (ii) location cueing/shifts of spatial attention, which would affect processing of both animate and inanimate movement stimuli.

Depending on the predictiveness of the prime stimulus with respect to the location of the target and the length of the temporal interval between prime and target, attentional control can be exerted more or less automatically or strategically, i.e. exogenously or endogenously. Lupianez and colleagues (2004) supposed that exogenous and endogenous cueing processes constitute two in parallel but partly independently working attentional

mechanisms which serve also different functions: on the one hand, processes related to bottom-up attentional capture which relative weight on performance is determined by the salience of distracting events, and on the other hand, mechanisms related to top-down spatial expectancy which relative contribution to performance is established by the strength of the strategic set. Whereas exogenous processes might be related to perceptual processing itself, endogenous processes might serve preparation for these perceptual processing. This view is also supported by neurophysiological studies suggesting that endo- and exogenous orienting are subserved by partially distinct neural substrates (Corbetta & Shulman, 2002).

The aim of the present study was to investigate automatic effects of observed biological movement on executed movements, and the interaction of these effects with more stimulus-unspecific effects of location cueing. An exogenous cueing procedure was chosen, thus two processes were investigated which presumably both rely on stimulus-driven, bottom-up mechanisms. Therefore, trials with either congruent or incongruent finger positions in S1 and S2 were presented with equal probability (50:50).

Furthermore, the SOAs of S1 and S2 were systematically varied to elucidate the temporal dynamics of priming effects of observed biological movement.

There is little evidence so far on the time-course of pre-activation or priming processes induced by animate movement. Some results suggest a rather short time window within which these processes are working. However, the actual boundaries are yet unknown. With respect to neurophysiology, neuromagnetic (MEG) recordings suggest a rapid cortical processing in observation and imitation of reaching movements and stationary lip forms (Nishitani et al., 2004; Nishitani & Hari, 2000, 2002). However, these findings do not provide information about the time span in which (pre-)activations in cortical “mirror” areas might affect subsequent processing of animate movement.

Previous behavioural studies on execution of hand postures and gestures (Stürmer, 1997; Stürmer et al., 2000; Vogt et al., 2003) could show PP effects at SOAs ranging between 0 and 1000 ms. However, important parameters as the use of static versus dynamic stimuli and stimulus duration differed between experiments. Vogt et al. (2003) proposed a lower limit of approximately 300 ms and an upper limit of 700 ms after prime onset (including mean RT values) for manifestation of (positive) visuo-motor priming effects on the behavioural level. Of note, Vogt and colleagues did not draw their conclusions from a comparison between responses that were primed by biological movement stimuli as contrasted with a control condition. They rather showed that the execution of an acoustically prompted object-directed grasping action was facilitated by the presentation of a congruent as compared to an incongruent static hand posture (500 ms) which was uninformative with respect to the actually required response. In contrast to the above findings, Edwards et al. (2003) found positive priming effects of an observed object-directed grasping movement on the kinematics of a subsequent action that was executed by the participants 3 sec after presentation of the prime (which had a duration of also approximately 3 sec). This held true for informative as well as for uninformative primes.

Due to important differences between the paradigms used in previous studies and the present S1-S2 paradigm, i.e. static pictures vs. movement stimuli, transitive vs. intransitive body movements, the validity of the reported time windows with regard to the present objectives is questionable.

With regard to the time-course of movement-related effects of location cueing, the stimuli used as primes and targets in previous studies on location cueing, to my knowledge, did not involve motion and, furthermore, presented mostly inanimate objects with the exception of a few studies (e.g. Kessler & Tipper, 2004; Tipper et al., 2003). Another factor hampering the comparability between the present S1-S2 paradigm and the literature on location cueing is that the task employed in the S1-S2 paradigm does not simply map

onto the tasks widely used in studies on location cueing. For instance, Lupianez *et al.* (1997) found out that the type of task employed with a standard exogenous location cueing procedure affects the time-course of facilitation and inhibition of responses seriously. The imitation task in the present S1-S2 paradigm might be best characterised as requiring a choice localisation response. Although the term location discrimination has occasionally been used to refer to comparable tasks in studies on location cueing, a discrimination task strictly speaking requires a perceptual feature analysis of the target object (c.f. Taylor & Donnelly, 2002). This is not met by differentiating merely between locations of a target. Thus, it is not clear to what degree pre-information about the time-course of IOR can be applied to the present study.

Finally, to raise chances of capturing any emerging priming effects of finger movement observation on imitation of a subsequent finger movement in the S1-S2 paradigm, the SOA was scanned in steps of approximately 350 ms from rather short SOAs (i.e. 533 ms) to intervals just below the ones used in previous S1-S2 experiments (i.e. 1900 ms). As the RT advantage for responses to animate over inanimate movement had already been confirmed in RT Experiment 1, S2 was always a finger movement.

2.3.2. Method

Participants

16 male subjects participated in the experiment (23 to 46 years, mean 31.1 years). Nine subjects were investigated at the University of Düsseldorf and seven at the University Medical Center Hamburg-Eppendorf.

Stimuli

Stimuli were animated picture sequences showing finger and dot movements, respectively, identical to those used in RT Experiment 1. Furthermore, control stimuli for S1 were constructed by replacing the red colour of both dots in the default picture (fingers resting on the underlying surface) by green colour. In this picture sequence, the on- and offsets of the colour change were matched to the beginning and end of the actual finger tap in the movement stimuli. The green colour was presented for 500 ms, then the colour of the dots turned back to red. Fig. 2.4 gives a schematic illustration of the stimuli used in this study.

Each trial started with the presentation of the resting hand for 1500 ms on average (range 1000 to 2000 ms, 200-ms steps). Then, the first movement stimulus (S1) was presented. With an SOA of 533, 850, 1200, 1550 and 1900 ms, the second movement stimulus (S2) was shown. During the interval between S1 and S2, the resting hand was shown. S2 was followed by the static hand lasting 500 ms. Therefore, the average trial duration was 3.7 sec. During a fixed inter-trial-interval of 2 sec the screen turned black.

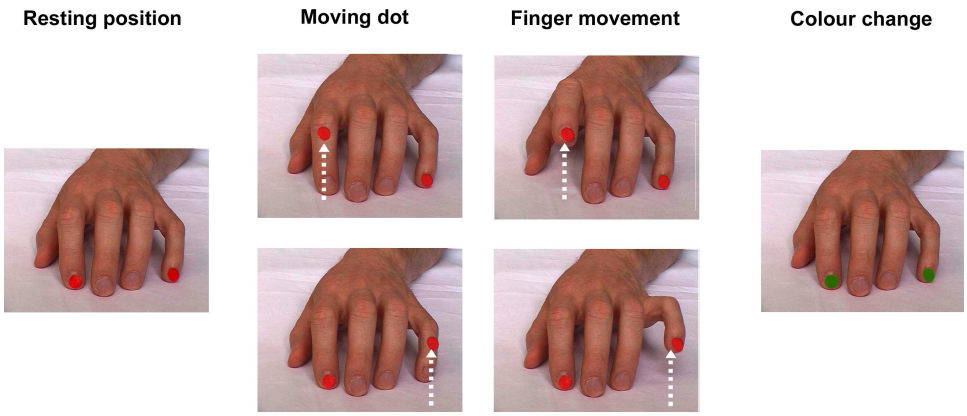

Fig. 2.4. Visual stimuli presented in RT Experiment 2. Resting position (first column): a picture of a static left hand with red dots on the tip of the little and index finger was shown at the beginning and the end of each movement sequence. Movements were always presented at the position of the index finger (top row) or little finger (bottom row): a moving dot (second column) or a finger movement (third column). In the control condition, a static hand was shown with both dots changing their colour from red to green and back (fourth column). Each picture sequence consisted of 15 frames. The dotted arrows symbolise the upward movement.

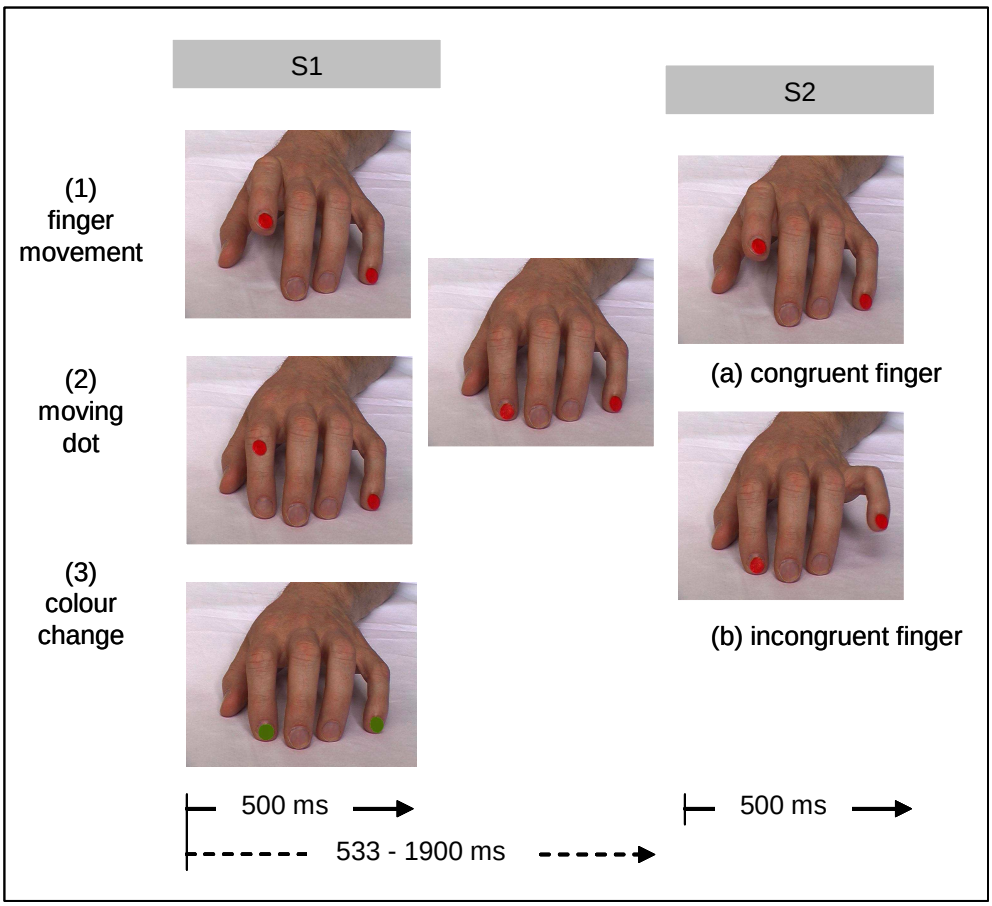

Fig. 2.5. Paradigm used in RT Experiment 2. In the exemplary trial displayed, the index finger position is cued/primed by S1. Left column: S1 is either a (1) finger movement, a (2) moving dot, or a (3) colour change of both dots. Right column: S2 is a finger movement. The finger/dot position presented in S2 is either (a) congruent or (b) incongruent to the position in S1. From left to right: S1 and S2 are presented for 500 ms each, with a stimulus onset asynchrony (SOA) of 533 to 1900 ms. In the inter-stimulus interval (middle column), a static hand in a resting position is presented.

In the movement priming conditions, S1 was a movement of either the index or little finger or a dot moving on top of one of these two fingers. S2 was always a finger movement. Trials with movement priming were either congruent or incongruent with respect to finger position. In the control condition, the resting hand was shown in S1, with the two red dots changing their colour. For an illustration of the paradigm see Fig. 2.5.

Task

Subjects were instructed to observe all stimuli attentively while focusing the middle of the hand. They were told to either lift the same finger that was moving or the finger on top of which a dot was moving in S2, as fast as possible.

Design

The experiment was divided into two blocks of trials. In one block a set of short S1-S2 intervals (short SOA set: 533, 850, 1200 ms) was applied, and in another block a set of long SOAs (long SOA set: 1200, 1550 and 1900 ms) was employed. An interval of 1200 ms was used in both sets to evaluate the influence of relative as opposed to absolute SOA length. Blocks of trials were administered in counterbalanced order across subjects to avoid order effects.

Within-group factors were ‘type of movement in S1’ (finger, dot), ‘congruency’ (congruent, incongruent) and ‘SOA level’ (short, middle, long, i.e. 533, 850, 1200 ms and 1200, 1550 and 1900 ms in the set of short and long SOAs, respectively). Congruent and incongruent trials were presented with equal probability (50:50). As only two finger positions (index, little) were used, S2 was not predictable from S1. Finger position was not introduced as a factor but balanced across all conditions. The control condition with finger-unspecific priming was presented with each SOA. All conditions were presented 20 times. Therefore, subjects performed 600 trials altogether, 300 trials in each block. The order of trials within a block was pseudo-randomised. To avoid fatigue, within-block bins of 60 trials each were separated by short breaks of at least ten sec. Between the two blocks there was a break of approximately two minutes. Participants started with 10 practice trials that were excluded from analysis. The duration of the whole experiment was approximately one hour.

Data acquisition and processing

Stimulus presentation and acquisition of response data was carried out in the same way as in preceding experiments. The participants' responses were registered by means of a light barrier device and quantified as RTs and errors.

Statistical evaluation

As the two sets of SOAs were administered in two separate blocks of trials, two set-wise 2 x 2 x 3 ANOVAs were calculated on mean RTs first, including factors type 'type of movement in S1' (finger, dot), 'congruency' (congruent, incongruent) and 'SOA level' (short, middle, long). To get more information about the time-course of effects, SOA-wise ANOVAs with factors 'type of movement in S1' (finger, dot) and 'congruency' (congruent, incongruent) were also conducted. RT analyses were complemented by analyses of mean error rates.

Effects of type of priming in S1, including the control condition, were analysed separately with ANOVAs on mean RTs, including factors 'type of priming in S1' (5 levels: congruent/incongruent finger movement, congruent/incongruent moving dot, colour change) and 'SOA level' (3), one for each set of SOAs.

Data obtained for the index and little finger was pooled and not distinguished in the ANOVA models. *F*-tests were corrected for non-sphericity of data. To specifically test the hypotheses, planned comparisons (paired *t*-tests) were performed, where *p*-levels were adjusted for multiple comparisons according to the Bonferroni method.

2.3.3. Hypotheses

Under the present experimental conditions, where equivalent finger and object movement stimuli are used in a spatial stimulus array and S1 is not predictive, one would predict that at least two different processes would be initiated: (i) a shift of spatial attention towards the location of the S1-finger or dot movement in both movement priming conditions leading to either PP or IOR depending on the SOA, and (ii) direct matching of an observed biological S1-finger movement to its internal motor program, which would exclusively modulate priming effects of finger movements. As a consequence, congruency effects were expected to be modulated by the type of movement presented in S1, reflecting an influence of AOEM in trials with a biological finger movement in S1.

According to the evidence provided by Posner and Cohen (1984) and Wright and Richard (2000), both using standard location cueing procedures with static non-biological stimuli, one would expect PP to be induced by exogenous cueing with SOAs up to approximately 150 ms, turning into IOR with SOAs above 300 ms. Regarding studies employing object-based frames of reference, IOR has been shown to persist for more than 4 sec (Paul & Tipper, 2003).Concluding from this tentatively, IOR rather than PP effects were expected to become apparent at all SOAs employed in the present paradigm, at least when effects independent of type of movement priming were concerned. According to the assumption that effects of (positive) visuo-motor priming by biological stimuli are rather short-lived (Vogt et al., 2003), AOEM-related response facilitation may even more rapidly turn into inhibition provided S1 is a biological finger movement and modulate congruency effects specifically in this priming condition. That is, enhanced activation of a response by an S1-finger movement which, however, has to be withheld according to the experimental task, may rapidly turn into even greater inhibition (provided S1 is not predictive). Apart from that, the type of movement in S2 was expected to exert a main effect on RT data, as a direct access of motor programs should be possible provided a biological finger movement

is presented in S2. This is strongly suggested by the above cited SRC-studies (Brass et al., 2001a; Brass et al., 2000). Moreover, this advantage of RTs had already been confirmed for the present stimulus material.

2.3.4. Results

Mean reaction times and error percentages in all conditions are presented in Table 2.2 (A: short SOA set, B: long SOA set).

RTs

For a clearer arrangement, effects involving the most interesting factors (type of movement, congruency) will be reported first in a separate paragraph, followed by effects of SOA duration exclusively and results of the additional analysis involving the control condition.

Effects involving factors type of movement and congruency

Although there was a general tendency for congruent S1-S2 sequences to be slower than incongruent sequences (mean differences = 20 ms and 16 ms in the short and long SOA set, respectively, Fig. 2.6), only in the set of short SOAs a main effect of congruency reached the level of significance ($F(1,15) = 4.7$, $p < .05$).

Congruency effects appeared to be modulated by SOA level in both sets (Fig. 2.6), with the most pronounced effects in the shortest SOA of a set each (533 and 1200 ms, respectively).

Table 2.2. RT Experiment 2: Reaction time and error data

A)		congruent				incongruent				no congruency			
		RT		error rate		RT		error rate		RT		error rate	
Short SOA set		mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
533 ms	finger	503	79.76	7.5	4.47	455	78.96	5.0	6.32	–	–	–	–
	dot	484	18.65	2.2	2.56	470	86.73	8.1	5.74	–	–	–	–
	colour	–	–	–	–	–	–	–	–	481	78.18	3.4	8.31
850 ms	finger	461	78.65	5.6	9.29	441	78.92	10.6	5.74	–	–	–	–
	dot	453	93.36	2.8	5.15	435	80.10	9.4	6.80	–	–	–	–
	colour	–	–	–	–	–	–	–	–	440	75.10		
1200 ms	finger	456	81.87	3.1	6.80	433	59.76	5.0	6.58	–	–	–	–
	dot	455	91.68	3.8	7.19	441	73.93	4.4	4.79	–	–	–	–
	colour	–	–	–	–	–	–	–	–	428	62.10	3.4	4.73

B)		congruent				incongruent				no congruency			
		RT		error rate		RT		error rate		RT		error rate	
Long SOA set		mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
1200 ms	finger	481	78.46	6.9	3.10	449	66.89	4.1	4.55	−	−	−	−
	dot	485	87.37	2.2	4.46	463	77.94	7.8	3.64	−	−	−	−
	colour	−	−	−	−	−	−	−	−	474	93.77	3.8	5.00
1550 ms	finger	452	72.22	2.2	2.56	441	78.68	8.1	4.03	−	−	−	−
	dot	453	83.68	2.5	3.65	451	71.23	7.5	3.65	−	−	−	−
	colour	−	−	−	−	−	−	−	−	452	86.23	3.4	4.37
1900 ms	finger	440	76.05	2.8	3.15	427	64.32	4.7	3.40	−	−	−	−
	dot	449	82.28	2.2	3.15	434	65.75	1.9	4.43	−	−	−	−
	colour	−	−	−	−	−	−	−	−	445	87.48	0.9	2.02

RT (ms) = reaction time in milliseconds, error rate (%) = percentage of errors total; SD = standard deviation; SOA = stimulus onset asynchrony, finger = finger movement condition, dot = moving dot condition, colour = colour change condition

Planned SOA-wise ANOVAs revealed that only at the shortest SOA level of each set responses in congruent trials were significantly slower than in incongruent trials (533 ms: main effect congruency $F(1,15) = 8.2$, $p < .05$, mean difference: 31 ms; 1200 ms: main effect congruency $F(1,15) = 7.4$, $p < .05$, mean difference: 27ms). However, only in the long SOA set there was a significant two-way interaction between congruency and SOA level ($F(2,30) = 6.1$, $p < .01$). Of note, when presented in the short SOA set, an SOA of 1200 ms duration yielded a numerically smaller congruency effect (approx. 19 ms) as compared to the same SOA presented in the long set (27 ms).

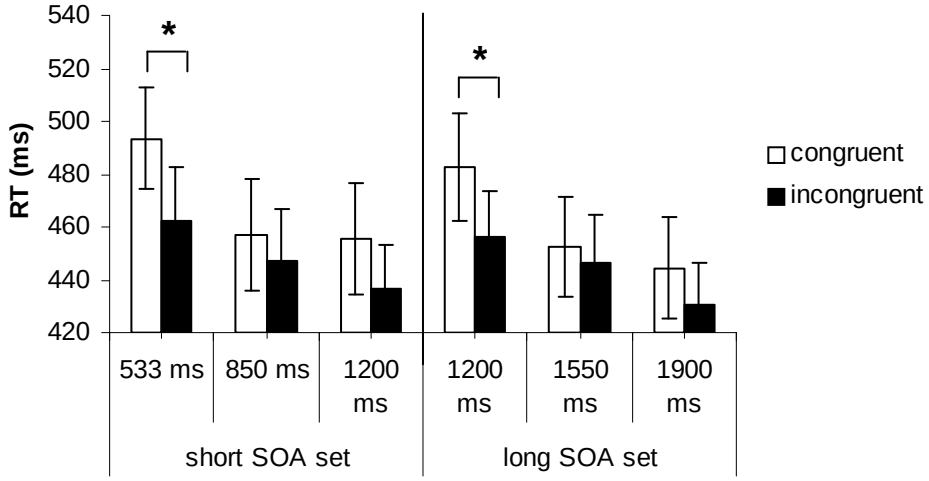

Fig. 2.6. RT Experiment 2: RT as a function of 'congruency' (congruent, incongruent) and 'SOA level' (short, middle, long) for both SOA sets (short, long). Significant differences are marked (* $p < .05$).

Most importantly, a two-way interaction between type of movement and congruency ($F(1,15) = 22.4$, $p < .001$) was found in the short SOA set only: first, regarding differences between congruent and incongruent trials (Fig. 2.7A), planned comparisons revealed significant IOR for finger (mean difference congruent-incongruent = 31 ms, $t(15) = 3.2$, $p < .01$) but not for dot primes (mean difference congruent-incongruent = 9 ms).

Second, with respect to differences between the S1-movement types (Fig. 2.7B), responses to incongruent finger movements were significantly faster (12 ms) than those to

incongruent dot movements ($t(15) = -3.9$, $p < .01$). Congruent finger movements were slower than congruent dot movements, although this difference (10 ms) did not reach the level of significance.

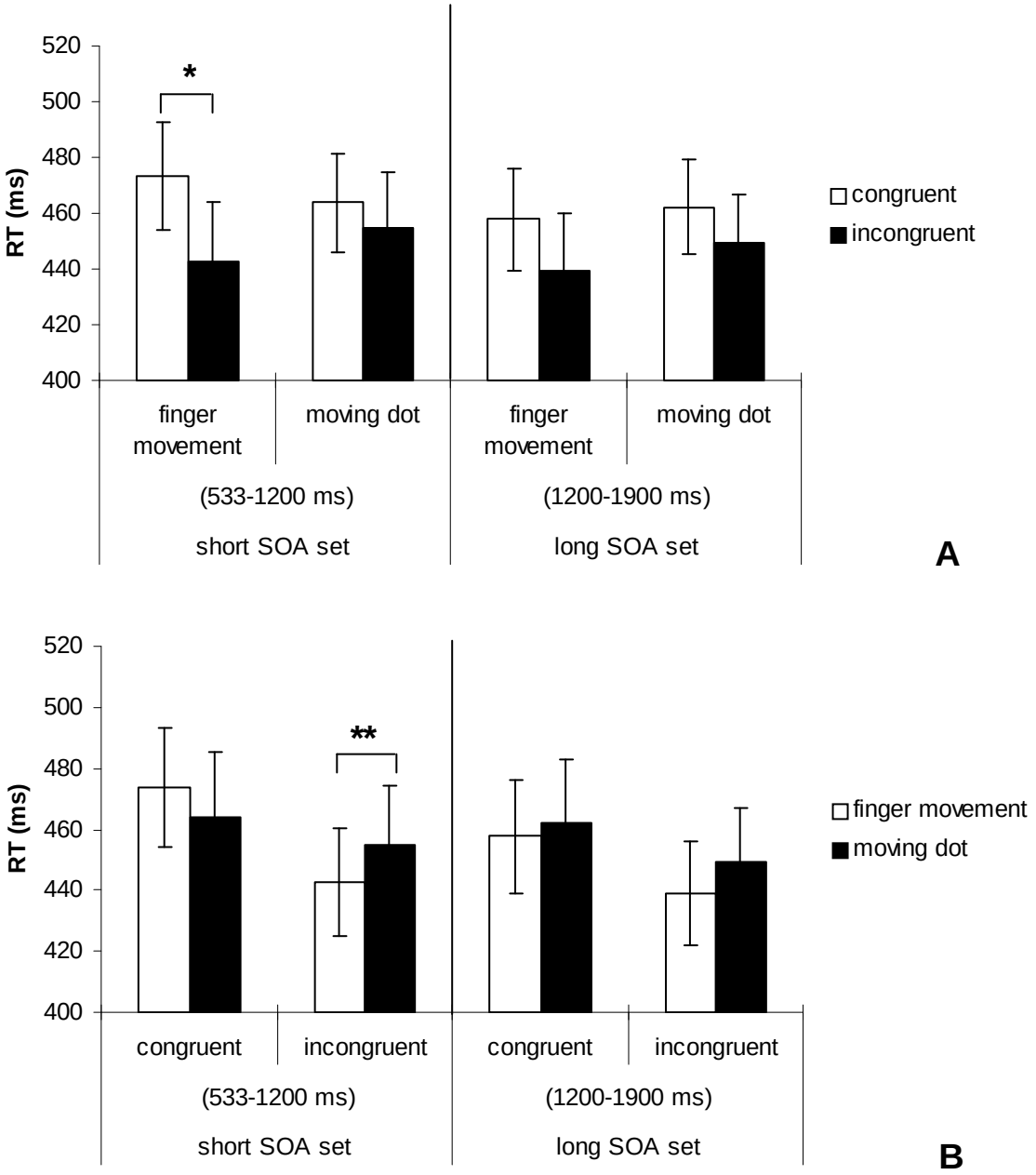

Fig. 2.7. RT Experiment 2: The interaction between 'S1-movement type' (finger, dot) and 'congruency of finger positions' (congruent, incongruent) in both SOA sets (short, long). Mean RT +/- standard error of mean is displayed. Significant differences between congruencies **(A)** and types of movement **(B)** are marked (* $p < .05$, ** $p < .01$). An interaction effect was significant only in the short SOA set.

Going into more detail concerning the time-course of the type of movement by congruency interaction (see Fig. 2.8), SOA-wise analyses showed different patterns:

at the 533 ms SOA, an interaction effect was significant ($F(1,15) = 15.2$, $p < .01$). The interaction was, first, due to responses to congruent finger movements being significantly slower (20 ms) than those to congruent dot movements ($t(15) = 3.0$, $p < .05$; Fig. 2.8A). Responses to incongruent finger movements also were faster than incongruent dot movements, although this difference (16 ms) did not reach the level of significance. Second, significant IOR was confined to trials with an S1-finger movement (mean difference congruent - incongruent = 49 ms, $t(15) = 3.6$, $p < .05$).

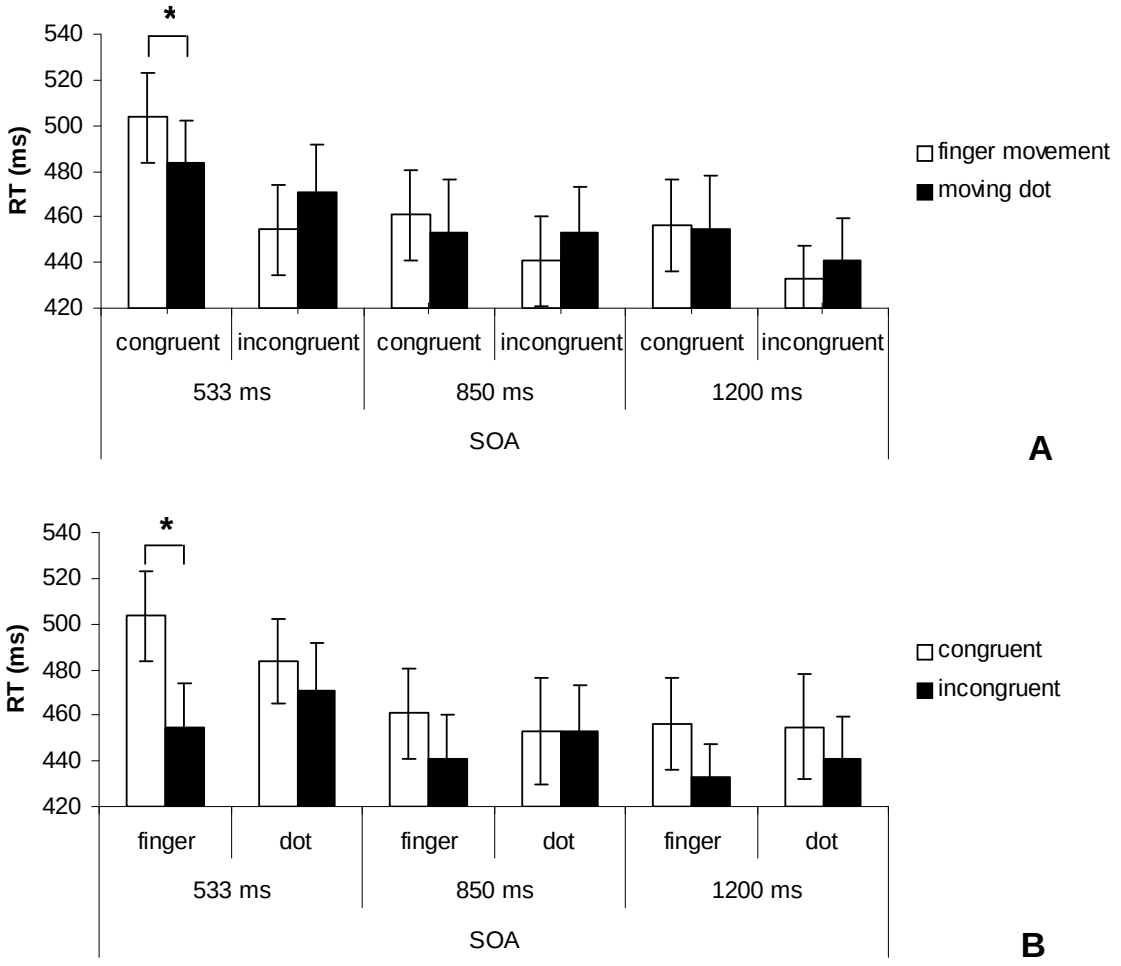

Fig. 2.8. RT Experiment 2, short SOA set: The interaction between 'S1-type of movement' (finger, dot) and 'congruency of finger positions' (congruent, incongruent) at the different SOA levels (short, middle, long). Mean RT ± standard error of mean is displayed. Significant differences between types of movement (A) and congruencies (B) are marked (* $p < .05$).

At both the 850 ms and the 1200 ms SOA there was no significant interaction. None of the planned paired comparisons regarding type of movement and congruency reached the (corrected) level of significance.

Effects exclusively involving factor SOA

In each SOA set, there was a significant main effect of SOA level (short SOA set: $F(2,30) = 33.1$, $p < .001$; long SOA set: $F(2,30) = 38.8$, $p < .001$). RTs decreased with increasing SOA (Fig. 2.9): RTs at short SOAs were significantly slower than at middle and long SOAs of the respective set (short SOA set: mean difference 533-850 ms SOA: 26 ms, $t(15) = 5.7$, $p < .001$; 533-1200 ms SOA: 32 ms, $t(15) = 6.8$, $p < .001$; long SOA set: 1200-1550 ms SOA: 20 ms, $t(15) = 6.8$, $p < .001$; 1200-1900 ms SOA = 32 ms, $t(15) = 6.7$, $p < .001$). Responses at middle SOA levels were also slower than at long SOA levels, although this difference was significant only in the long SOA set (short set: 6 ms; long set: 12 ms, $t(4)$, $p < .01$).

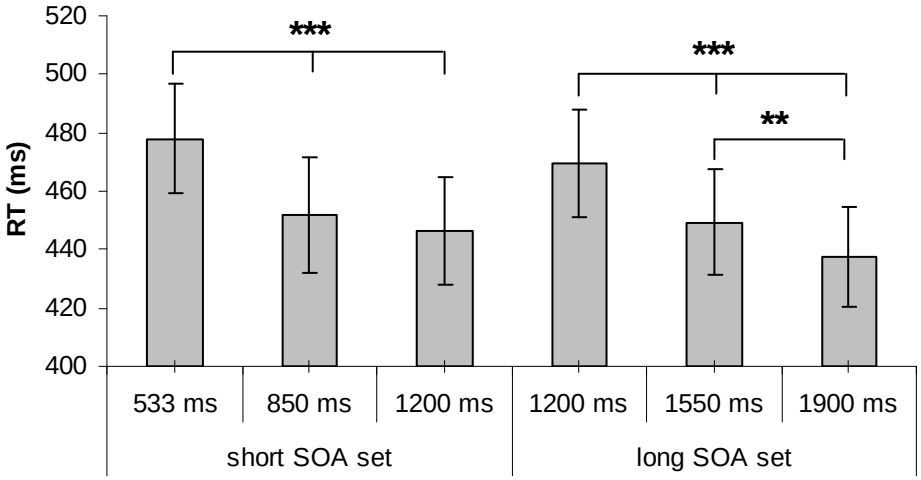

Fig. 2.9. RT Experiment 2: SOA levels (short, middle, long) in both SOA sets (short, long). Mean RT ± standard error of mean is depicted. The control condition (colour change) is not included. Significant differences are marked (** $p < .01$, *** $p < .001$).

Supplementary analysis including the control condition (colour change in S1)

Although a trend was present in the short SOA set, a main effect of factor type of priming (5 levels: congruent/incongruent finger movement, congruent/incongruent moving dot, colour change) failed to reach significance when a non-sphericity correction was applied ($F(4,60) = 3.1$, $p = .053$). The same held true for the interaction between SOA level and type of priming ($F(8,120) = 2.3$, $p = .053$). Numerically, mean RT in the colour change condition (450 ms) ranged between the congruent and incongruent finger movement priming conditions (incongruent: 443 ms, congruent: 474 ms) and was shorter than both moving dot conditions (incongruent: 455 ms, congruent: 464 ms).

Concerning the long SOA set, neither a main effect of factor type of priming nor an interaction between type of priming and SOA level was found. Mean RT in the colour change conditions was 457 ms, thus ranging between the congruent and incongruent trials in both movement priming conditions (finger incongruent: 439 ms, finger congruent: 458 ms; dot incongruent: 449 ms, dot congruent: 462 ms), numerically. For illustration see Fig. 2.10.

When SOAs were considered in SOA-wise ANOVAs, a significant main effect of type of priming was revealed at the 533 ms SOA ($F(4,60) = 4.5$, $p < .05$) and at the 1200 ms SOA in the long SOA set ($F(4,60) = 3.3$, $p < .05$). There were, however, no significant differences between conditions with and without movement priming.

Finally, as expected, a main effect of SOA length reached the level of significance in both SOA sets (short SOA set: $F(2,30) = 47.7$, $p < .001$; long SOA set: $F(2,30) = 47.3$, $p < .001$). RTs decreased from shorter to longer SOAs.

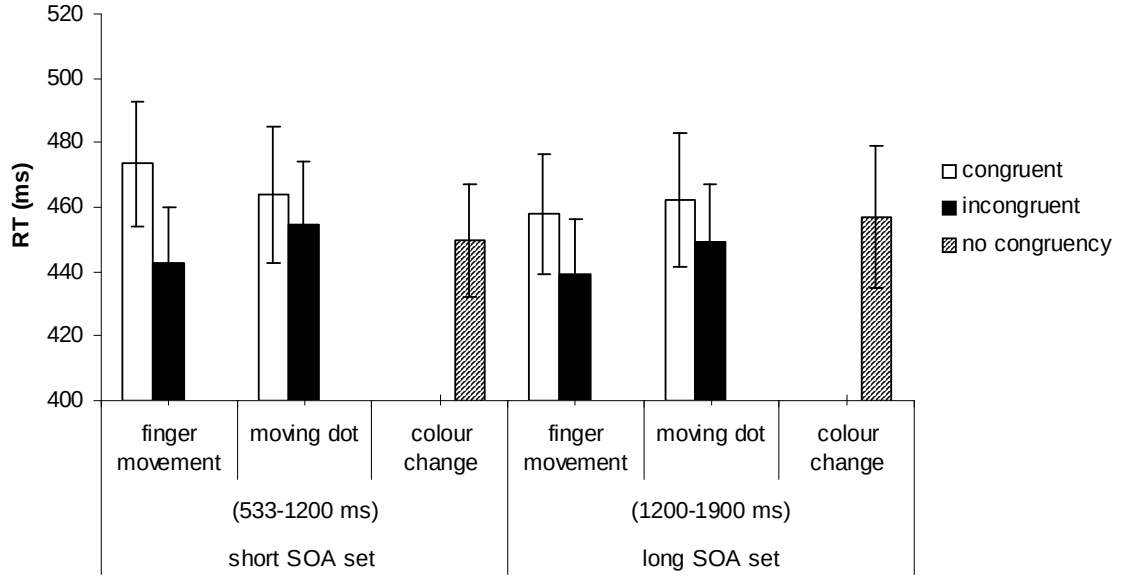

Fig. 2.10. RT Experiment 2: 'Type of priming in S1' (congruent/incongruent finger movement, congruent/incongruent moving dot, colour change) in both SOA sets (short, long). Mean RT ± standard error of mean is depicted. Significant differences between conditions with movement priming are not marked.

Error rates

Mean percentage of errors was 4.6% (range 2.2-12.2%). A single false response was the least common error (0.1% of all trials), whereas responding more than once in a trial was observed most frequently (3.5%).

Effects involving factors type of movement and congruency

ANOVAs revealed significant main effects of congruency in both the short and the long SOA set ($F(1,15) = 29.4$, $p < .001$; $F(1,15) = 29.3$, $p < .001$) that were directed contrary to RTs, with fewer errors in congruent than in incongruent trials (short SOA set: 4.2 vs. 7.1 %; long SOA set: 3.2% vs. 5.7%).

There was, moreover, a significant interaction between type of movement and congruency in the short ($F(1,15) = 6.0$, $p < .05$) but not in the long SOA set. In the short

SOA set, participants made significantly less errors in congruent as compared to incongruent moving dot trials (4.4%, $t(15) = -6.0$, $p < .001$). Error rates were, furthermore, higher in congruent finger movement as compared to congruent moving dot trials (2.5%), but this difference did not reach the corrected level of significance.

Tracing the time-course of the movement type by congruency interaction in the short SOA set, error rates, in contrast to RTs, tended to be lower in congruent as compared to incongruent trials (533 ms SOA: 4.8 vs. 6.6%; 850 ms SOA: 4.2 vs. 10.0%; 1200 ms SOA: 3.4 vs. 4.7%). However, SOA-wise ANOVAs revealed only a trend for a congruency effect at 533 ms ($F(1,15) = 3.2$, $p = .094$), a main effect of congruency at the 850 ms SOA ($F(1,15) = 24$, $p < .001$), but no effect at all at the 1200 ms SOA.

An interaction between movement type and congruency reached significance exclusively at the 533 ms SOA ($F(1,15) = 31.9$, $p < .001$). Subjects made less errors in congruent as compared to incongruent moving dot trials (5.9%, $t(15) = -4.5$, $p < .001$). In line with RTs, error rate was higher in congruent finger movement trials than in congruent moving dot trials (5.3%, $t(15) = 5.0$, $p < .001$).

2.3.5. Discussion

Effects involving factors type of movement and congruency

The present data suggest that the employed S1-S2 paradigm with a non-predictive S1 induced an IOR-like reverse effect of congruency. More specifically, responses were slower in congruent trials than in incongruent trials irrespective of the type of movement priming, i.e. both biological finger movements and moving dots in S1 induced IOR. The principal finding that with non-predictive cues and SOAs over 300 ms IOR-like effects were induced, is in concordance with well-replicated results from research on visual priming with standard search paradigms (Klein, 2000; Wright & Richard, 2000).

A main novel finding is that the observation of human finger movements can induce such an effect on choice responses. It seems that the spatial nature of the task induced IOR among spatially distinct parts (fingers) of an object (hand), or distinct inanimate objects (dots) similar to the findings of Tipper and colleagues who reported IOR in experimental set-ups using object-centred frames of reference and moved (biological) objects (Kessler & Tipper, 2004; Tipper et al., 1991; Tipper et al., 1999).

Although the observed IOR-like effect was numerically present across all S1-S2 intervals, it reached statistical significance only at the relatively shortest SOA levels of a given set (533 and 1200 ms, respectively). This interaction between relative SOA length and congruency could be due to the fact that at the shortest interval of a set there was no opportunity for subjects to optimise their responses according to expectancies regarding the occurrence of S2 in time, thus leaving some leeway for congruency effects to become apparent. At longer relative SOA levels response settings could be optimised, possibly obliterating the more subtle congruency effects (more information about effects of SOA level is provided below).

Importantly, although generalised spatial cueing clearly contributed to the observed congruency effects, a distinct influence of finger movement priming was also evident. Depending on the absolute SOA length, inhibition and facilitation differed significantly between the types of priming in terms of strengths and patterns.

At SOAs ranging between 533 and 1200 ms (short SOA set), a movement specific IOR effect was observed. This effect was actually due to the very shortest SOA of 533 ms: here, significant IOR was confined to finger movement cues. Response inhibition in congruent trials was stronger when responses were cued by a finger movement than by a moving dot in S1, i.e. responses in congruent trials were slower when cued by a finger

movement as compared to a moving dot. Thus, this behavioural effect was specific, i.e. confined to a real human body movement. It also seemed to be rather transient, i.e. confined to short intervals, suggesting that this effect might be due to direct matching of observed animate movements and corresponding responses.

The pattern of mean error rates turned out to be complimentary to RTs, on principle. Paralleling the interpretation of the error results of RT Experiment 1, this could reflect occasional failures to inhibit imminent response tendencies to S1. Whereas only in very few trials participants actually responded with the wrong finger (0.8%), multiple responses in a single trial were much more frequent (20.8%). A higher rate of multiple responses in incongruent than in congruent trials (1.1 vs. 0.6%) further supports the assumption that these errors result from conflicts between automatic response tendencies and responses initiated according to S2.

Effects involving factor SOA level

RTs were found to decrease from shorter to longer SOAs. This effect was relative in nature in that the differences between the short and long SOA sets were much weaker than the differences between the relatively short, intermediate and long SOAs within each set. These findings most probably represent a “temporal warning” or “foreperiod” effect (e.g. Niemi & Näätänen, 1981), that is well known to appear in RT experiments where subjects can build up expectations about the time span between a precue and the actual response (i.e. the foreperiod). Expectation about the timing of an event, on the other hand, can be used to optimise response behaviour (Coull & Nobre, 1998; Nobre, 2001). This optimisation can be attributed to motor preparation which can progress even when a movement is not yet completely specified (Wild-Wall *et al.*, 2003). Thus, response readiness increases with the probability of the go-signal. In line with that, activation of

brain areas involved in motor preparation was shown to be present only in long cue-target intervals in a priming paradigm (Coull *et al.*, 2000). As a consequence, the longer the SOA between S1 and S2 in the present experiment the better subjects can prepare a response to S2.

Supplementary analysis including the control condition (colour change in S1)

The type of priming in terms of either congruent or incongruent finger or dot movements or a colour change of both static dots did not make a significant difference in this S1-S2 paradigm. Apart from that, numerical RT differences can be tentatively interpreted as rather supporting the assumption of a hand-based IOR-like effect. Mean response times in the control condition where a colour change was used as a cue ranged between those in incongruent (faster) and those in congruent (slower) movement priming trials. Thus, the non-lateralised S1-colour cues presumably led to an unspecific arousal of attention to S2. This unspecific arousal, however, was not as effective as the finger(position)-specific shifts of attention, which were induced by the dynamic-spatial movement cues (i.e. S1-finger movement or S1-moving dot), in terms of determining responses.

At last, it is important to state that S1 and S2 were visually identical in congruent finger (S1) – finger (S2) movement trials but not in congruent dot (S1) - finger (S2) movement trials (compare Fig. 2.5). Therefore, the question remains open of whether the movement specific cueing effect above was actually attributable to direct matching or whether there might be an alternative explanation in terms of visual concordance between S1 and S2. Hence, a better perceptual match between S1 and S2 in the finger movement condition, rather than direct action matching, might be responsible for the modulation of congruency effects by the type of movement in S1.

2.4. RT Experiment 3: Second priming/cueing (S1-S2) experiment

2.4.1. Objectives

RT Experiment 3 was carried out to exclude perceptual overlap or concordance between prime and target stimulus as an alternative explanation for the modulation of congruency effects by S1-movement type that was obtained in RT Experiment 2. The design of RT Experiment 3 paralleled that of RT Experiment 2, except that both movement types (finger, dot) were presented in S1 as well as in S2 (in all combinations). Furthermore, only one set of SOAs was used, and no S1-control condition was included.

2.4.2. Method

Participants

16 subjects were investigated at the University Medial Center Hamburg-Eppendorf (19 to 35 years, mean 25.7 years), half of which were female and half were male.

Stimuli

Visual stimulation was identical to RT Experiment 2 (see Fig. 2.11), with the exception that a yellow fixation cross (of approximately 0.6° in diameter) was placed in the middle of the picture frame vertically and in equal Euclidian distance from both fingertips horizontally to discourage eye movements.

A single trial started with the presentation of the resting hand lasting 1500 ms on average (range 1000 to 2000 ms, steps of 200 ms). Then, the first movement stimulus (S1) was presented for 500 ms. With an SOA of 533 ms, 1200 ms, or 1900 ms, the second movement stimulus (S2) was presented. Finally, the static hand lasting 500 ms was shown.

The average trial duration was 3.7 sec. During a fixed inter-trial-interval of 1 sec the picture of the static hand turned from colour into greyscale.

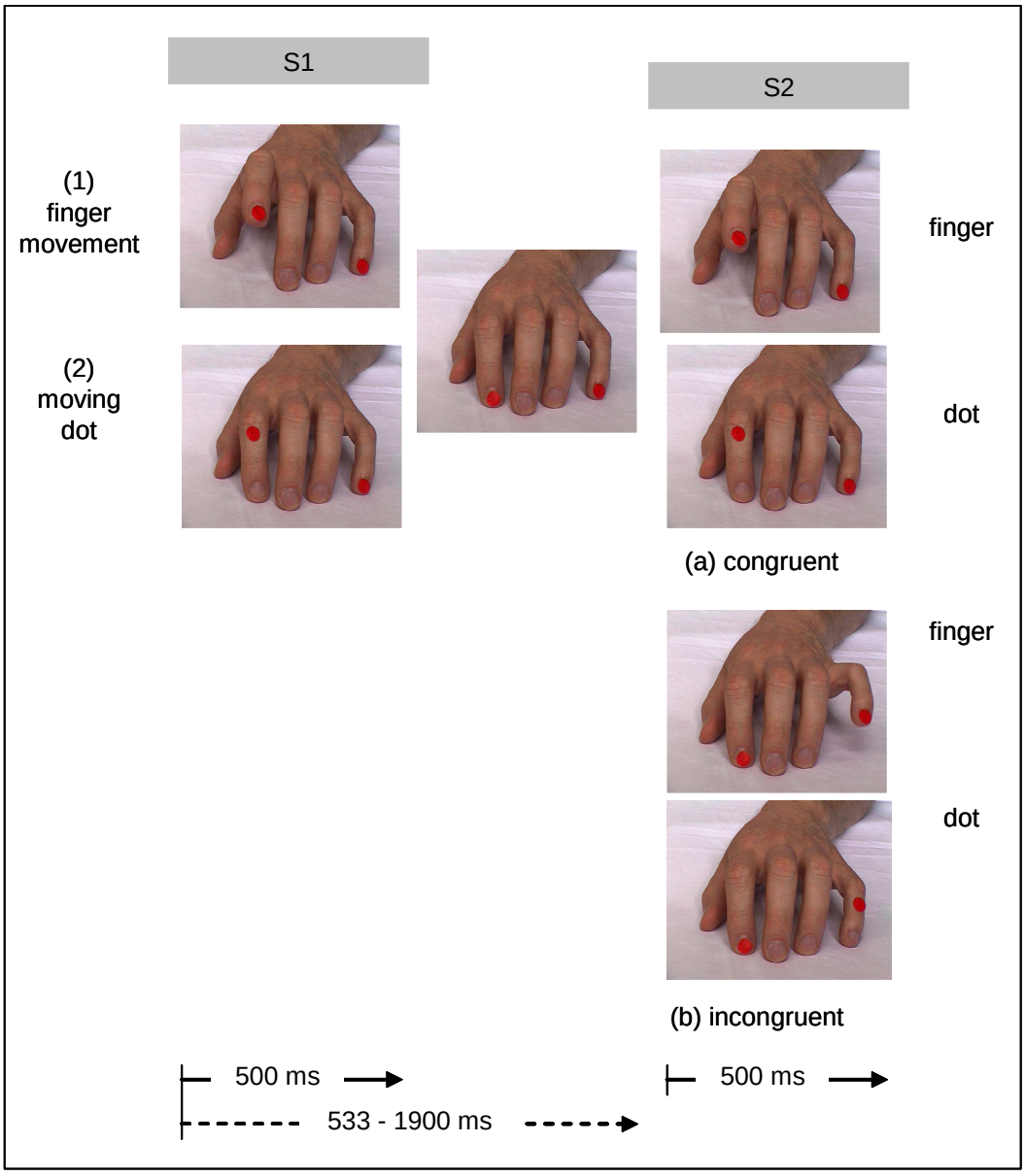

Fig. 2.11. Paradigm used in RT Experiment 3. In the exemplary trial displayed, the index finger position is cued/primed by S1. In the exemplary trial displayed, the index finger position is cued by S1. Left column: S1 is either a (1) finger movement or a (2) moving dot. Right column: S2 is either a finger movement or a moving dot. The finger/dot position presented in S2 is either (a) congruent or (b) incongruent to the position in S1. From left to right: S1 and S2 are presented for 500 ms each, with a stimulus onset asynchrony (SOA) of 533 to 1900 ms. In the inter-stimulus interval (middle column), a static hand in a resting position is presented.

S1 was a movement of either the index or little finger or a dot moving on top of one of these two fingers. S2 also presented a finger movement or a moving dot. Trials were either

congruent or incongruent with respect to finger position. For an illustration of the paradigm see Fig. 2.11.

Task

Subjects were instructed to observe all stimuli attentively while focusing the fixation cross. They were told to lift the same finger that was moving or the finger on top of which a dot was moving in S2, as fast as possible.

Design

The set-up was identical to RT Experiment 2 except that in S2 both biological finger movements and moving dots were presented. Three different SOAs were chosen, 533 ms, 1200 ms, and 1900 ms, covering the range of RT Experiment 2. At the same time, this allowed for repeating all conditions of interest frequently enough within a reasonable time period that would not lead to fatigue in the subjects. Moreover, to simplify the design no different SOA sets were presented that would provoke interaction effects of absolute und relative SOA duration as found in RT Experiment 2. Also, as the information from a non-lateralised control cue (colour change of both dots) had already been evaluated in the preceding experiments, it was not necessary to include one in RT Experiment 3. This, furthermore, reduced the total number of conditions in the experiment.

Within group factors were ‘S1-movement type’ (finger, dot), ‘S2-movement type’ (finger, dot), ‘congruency’ (congruent, incongruent) and ‘SOA level’ (short, middle, long, i.e. 533, 1200, 1900 ms). Congruent and incongruent trials were presented with equal probability (50:50). Finger position was balanced across all conditions.

All conditions were presented 20 times. Subjects performed 480 trials presented in one block in a pseudo-randomised order. The block was separated by short breaks (10 sec minimum) into 10 bins of 48 trials each to avoid fatigue. Testing started with 20 practice

trials that were excluded from analysis. The entire experiment lasted approximately 45 minutes.

Data acquisition and processing

Stimulus presentation and acquisition of response data was carried out as in the preceding experiments.

Statistical evaluation

First, a 2 x 2 x 2 repeated-measurements ANOVA was calculated on mean RT or error rates, respectively, for each SOA separately, including within-subject factors 'S1-type of movement' (finger, dot), 'S2-type of movement' (finger, dot), and 'congruency' (congruent, incongruent). Data obtained for the index and little finger was pooled. Planned comparisons (paired *t*-tests) and statistical corrections were performed as in the preceding studies.

2.4.3. Hypotheses

As in RT Experiment 3 an exogenous location cueing procedure was applied, a general effect of location cueing was expected. According to the results of the preceding S1-S2 study, congruent trials should lead to slower RTs than incongruent trials (IOR effect) at all SOAs. Furthermore, due to matching of observed and executed action a main effect of type of movement in S2 should be present, with responses to a finger movement in S2 being generally faster than to a moving dot in S2.

Regarding the attempt to disentangle priming (S1-) effects mediated by direct action matching and effects of visual concordance between S1 and S2, now, S1 and S2

were better matched visually in those conditions where they presented the same movement type (even more in congruent than in incongruent trials) as compared to conditions with different S1- and S2-movement types. This held true irrespective of whether S2 was a finger movement, as in RT Experiment 2, or a moving dot. Assuming that biological finger movement primes would exert a stronger influence on execution of S2 via direct matching mechanisms than moving dot primes, an SOA-dependent interaction between S1-movement type and congruency was expected, corresponding to that in RT Experiment 2: resulting from stronger facilitation or inhibition by S1-finger movements, respectively, subjects should respond faster in trials with an incongruent S1-finger movement as compared to an incongruent S1-moving dot. This relation should be reversed in congruent trials (S1-finger movement > S1-moving dot). Furthermore, significant IOR was expected in trials with an S1-finger movement which should be more pronounced than in trials with an S1-moving dot. This pattern should most probably show up at the shortest SOA of 533 ms, where movement-specific cueing effects had been found in RT Experiment 2.

If, however, visual concordance between S1 and S2 was responsible for modulation of congruency effects, a three-way interaction between S1-movement type, S2-movement type and congruency would be expected: facilitation and inhibition would be stronger in trials with more similar stimuli. Thus, for finger movements in S2 the pattern would be comparable to that described above. For moving dots in S2, however, participants would be expected to respond slower in trials with a congruent S1-moving dot as compared to a congruent S1-finger movement, and perhaps also to respond faster in trials with an incongruent moving dot prime as compared to an incongruent S1-finger movement. Moreover, effects of visual similarity would not be expected to be qualitatively different at the different SOAs, thus, this pattern of results should show up with all intervals. Of note, results might turn out to be less clear as formulated here, as interactions of priming by S1 and immediate effects of S2 might not simply add up.

Finally, the use of three different SOAs should lead to a temporal warning effect as in RT Experiment 2, with responses generally speeding up with SOAs getting longer.

2.4.4. Results

Mean reaction times and error percentages in all conditions are presented in Table 2.3.

RTs

Effects involving the factors type of movement and congruency

As was expected, SOA-wise ANOVAs revealed a main effect of type of movement in S2 at each single SOA, with responses to finger movements being faster than those to moving dots (see Fig. 2.12A; 533 ms: $F(1,15) = 90$, $p < .001$, mean difference: 29 ms; 1200 ms: $F(1,15) = 36$, $p < .001$, mean difference: 18 ms; 1900 ms: $F(1,15) = 78$, $p < .001$, mean difference: 24 ms).

Moreover, there was a congruency or IOR-effect, respectively, at all SOAs: subjects responded slower in congruent as compared to incongruent trials (533 ms: $F(1,15) = 11$, $p < .01$, mean difference: 19 ms; 1200 ms: $F(1,15) = 22.5$, $p < .001$, mean difference: 27 ms; 1900 ms: $F(1,15) = 13.8$, $p < .01$, mean difference: 21 ms; Fig. 2.12B).

A significant main effect of S1-movement type was revealed only at the shortest SOA ($F(1,15) = 11.9$, $p < .01$; Fig. 2.12C). Here, subjects responded significantly slower in trials which were primed by a finger movement as compared to those primed by a moving dot in S1 (9 ms).

SOA-wise ANOVAs and planned comparisons revealed different patterns regarding the interaction between S1-movement type and congruency (Fig. 2.13).

Table 2.3. RT Experiment 3: Reaction time and error data

			S2 finger				**S2 dot**			
			RT (ms)		error rate (%)		RT (ms)		error rate (%)	
SOA	**S1**	**congruency**	mean	SD	mean	SD	mean	SD	mean	SD
533 ms	finger	con	477	97.01	0.8	1.64	518	92.05	0.5	1.01
		incon	456	87.05	3.1	1.12	486	87.10	0.7	1.02
	dot	con	473	93.95	0.5	1.02	488	10.68	1.8	1.37
		incon	454	87.22	1.0	1.72	485	90.25	0.5	0.79
1200 ms	finger	con	462	97.41	0.7	1.37	488	93.26	0.6	0.79
		incon	433	91.00	1.0	1.31	445	88.45	2.0	1.02
	dot	con	459	90.83	2.3	2.00	477	100.02	0.5	0.77
		incon	443	90.17	0.7	1.02	458	96.06	2.1	1.35
1900 ms	finger	con	443	103.27	0.8	1.11	472	89.71	2.0	1.02
		incon	420	88.07	0.7	0.79	443	99.31	0.9	1.09
	dot	con	436	93.05	1.0	0.82	460	101.00	2.0	1.11
		incon	423	84.77	0.9	0.88	442	81.21	2.6	1.25

RT (ms) = reaction time in milliseconds, error rate (%) = percentage of errors total; sd = standard deviation; SOA = stimulus onset asynchrony, finger = finger movement condition, dot = moving dot condition; S1 = priming stimulus, S2 = target stimulus; con = congruent trials, incon = incongruent trials

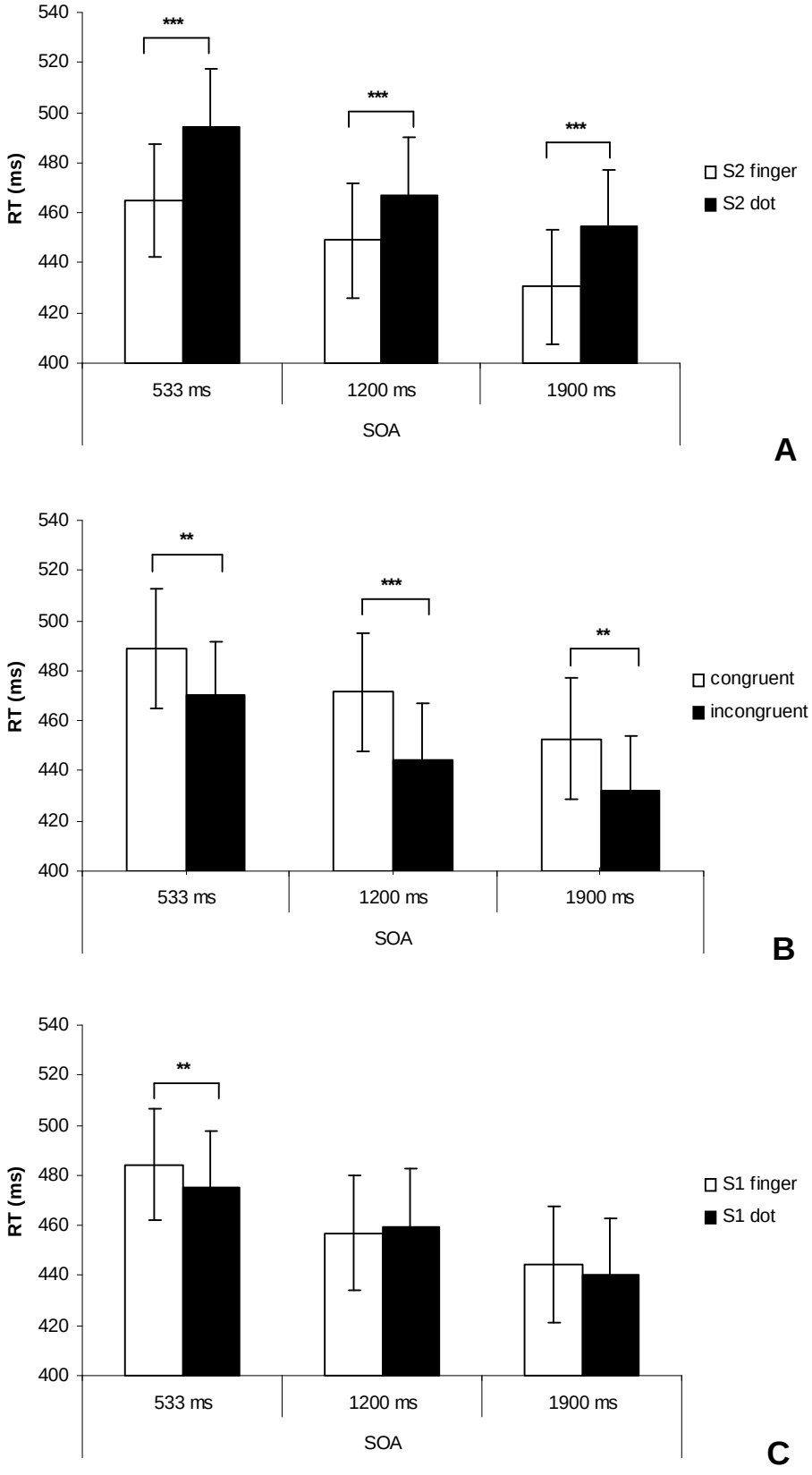

Fig. 2.12. RT Experiment 3: Main effects at the different SOA levels (short, middle, long). A: 'type of movement in S2' (finger, dot). B: 'congruency' (congruent, incongruent). C: 'type of movement in S1'. Mean RT ± standard error of mean is displayed. Significant differences are marked (** $p < .01$, *** $p < .001$). Modified, with perm., after Jonas et al. (2007) © 2007 Springer.

At the 533 ms SOA, there was a significant interaction effect involving type of movement in S1 and congruency ($F(1,15) = 11.6$, $p < .01$): responses in congruent trials were slower when S1 was a finger movement as compared to a moving dot (mean difference: 17 ms, $t(15) = 5$ ms, $p < .001$; Fig. 2.13A). Further, an IOR effect was significant in trials with a finger movement prime (mean difference congruent-incongruent = 27 ms, $t(15) = 5.3$, $p < .001$; Fig.2.12B) but not in those with a moving dot prime (mean difference congruent-incongruent = 11 ms).

At the 1200 ms SOA, type of movement in S1 and congruency also interacted significantly ($F(1,15) = 8.6$, $p < .05$): responses in incongruent trials were significantly faster when S1 was a finger movement as compared to a moving dot (12 ms, $t(15) = -3.6$, $p < .01$; Fig. 2.13A). Significant IOR effects were present in trials with both a finger and a dot movement prime ($t(15) = 5.2$, $p < .001$; $t(15) = 2.9$, $p < .05$; Fig. 2.13B), although the effect was numerically larger with a finger movement (36 ms) than with a dot movement (18 ms).

At the 1900 ms interval, there was no significant interaction between S1-movement type and congruency. Planned comparisons showed slower RTs in congruent trials with a finger movement as compared to a moving dot prime (9 ms, $t(15) = 3.5$, $p < .01$; Fig. 2.13A). An IOR effect was significant with both S1-movement types (finger: 26 ms, $t(15) = 4$, $p < .01$; dot: 16 ms, $t(15) = 2.5$, $p < .05$; Fig. 2.13B).

There was no three-way interaction between type of movement in S1, type of movement in S2 and congruency.

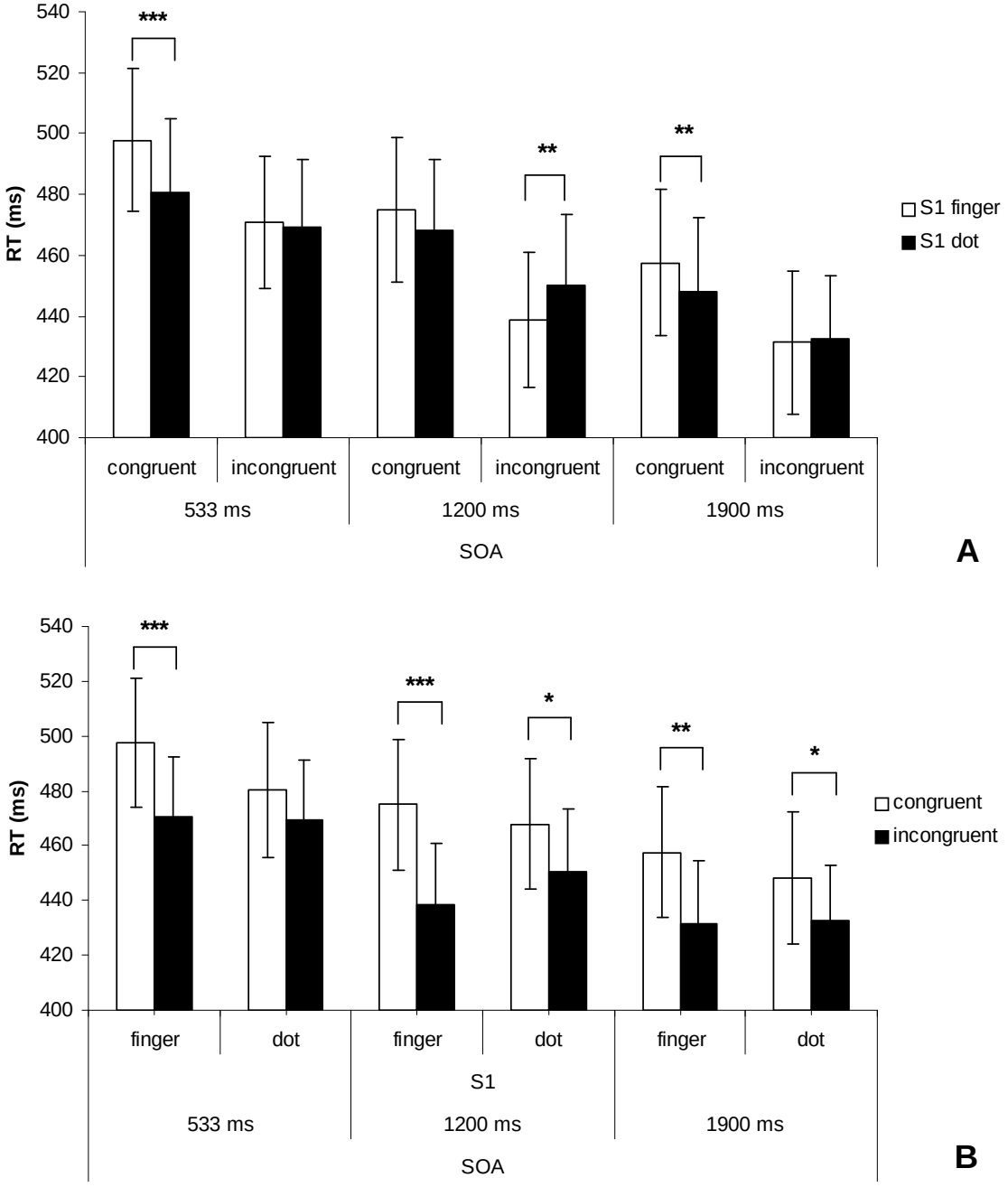

Fig. 2.13. RT Experiment 3: The interaction between 'S1-type of movement' (finger, dot) and 'congruency of finger positions' (congruent, incongruent) at all SOAs (short, middle, long). Mean RT ± standard error of mean is displayed. Significant differences between types of movement **(A)** and congruencies **(B)** are marked (* $p < .05$, ** $p < .01$). Modified, with permission, after Jonas et al. (2007) © 2007 Springer.

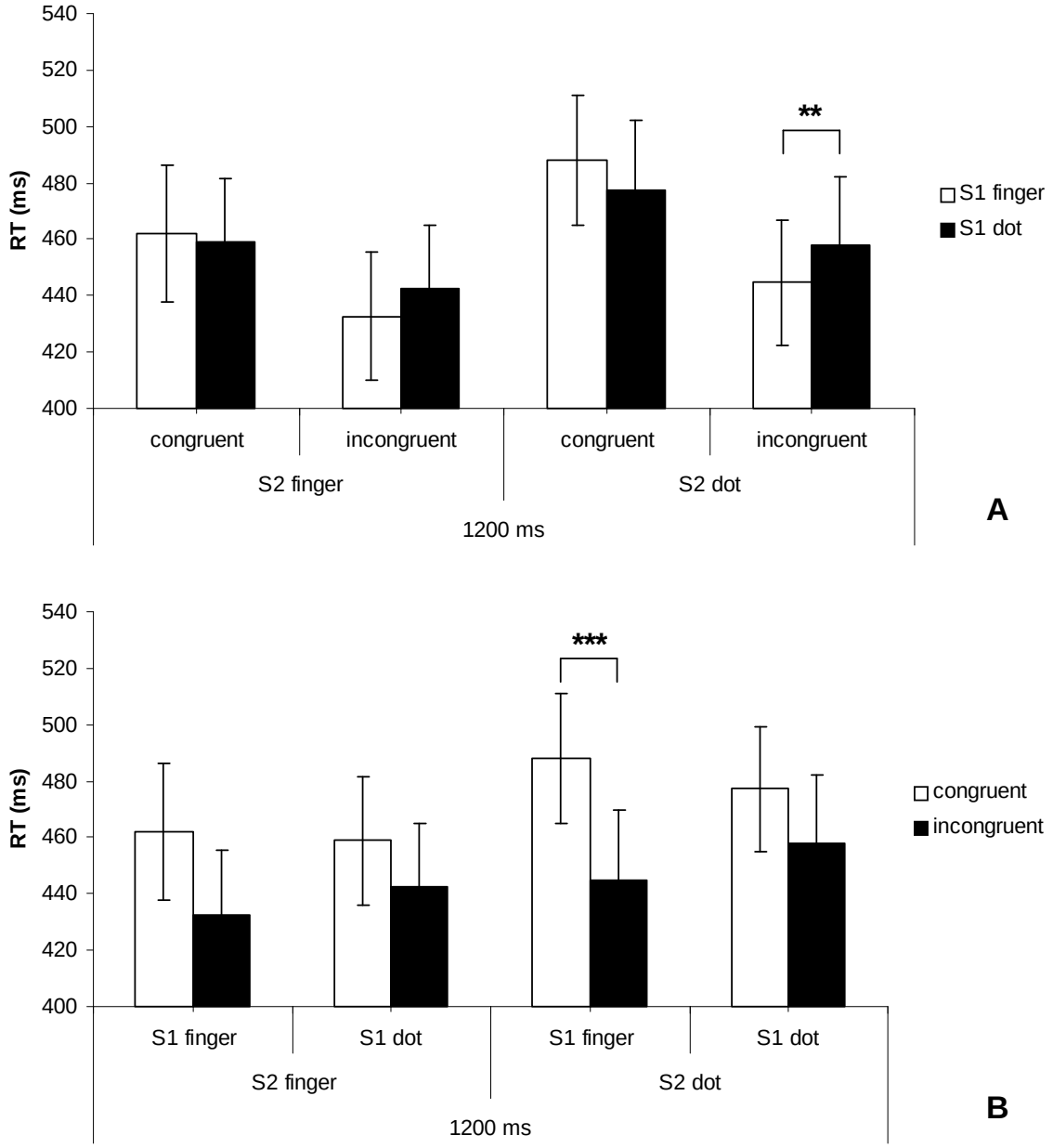

Fig. 2.14. RT Experiment 3, 1200 ms SOA: The interaction between type of movement in S1 (finger, dot) and congruency (congruent, incongruent) for both types of movement in S2 (finger, dot). Mean RT ± standard error of mean is displayed. Significant differences between S1-movement types **(A)** and congruencies **(B)** are marked (** $p < .01$, *** $p < .001$).

1200 ms SOA: analysis by types of movement in S2

Results of RT Experiment 2 and the present study diverged in that a significant interaction between type of movement and congruency was confined to the short 533 ms SOA in RT Experiment 2, but showed up also in the middle 1200 ms SOA in the present experiment.

As in RT Experiment 2 only finger movements had been presented as S2, we explored the relative contributions of the different types of S2-movement employed in the present experiment by means of two follow-up ANOVAs confined to the 1200 ms interval:

interestingly, an interaction between S1-movement type and congruency reached the level of significance ($F(1,15) = 9.8$, $p < .01$) only when S2 was a moving dot: in incongruent trials, S1-finger movements led to faster responses (13 ms) as compared to S1-moving dots ($t(15) = -3.4$, $p < .01$; Fig. 2.14A). Significant IOR was confined to trials where responses were primed by an S1-finger movement (mean difference congruent-incongruent: 43 ms, $t(15) = 6$, $p < .001$; Fig. 2.14B). There was no main effect of S1-movement type.

Effects exclusively involving factor SOA level

Planned comparisons revealed that subjects responded significantly slower (22 ms) at the short 533 ms SOA as compared to the intermediate 1200 ms SOA ($t(15) = 6.3$, $p < .001$) as well as compared to the long 1900 ms SOA (mean difference: 37 ms, $t(15) = 9.9$, $p < .001$). Moreover, RTs at the 1200 ms SOA were also slower (16 ms) than at the long SOA ($t(15) = 5.7$, $p < .001$).

Error rates

Mean percentage of errors was 1.6% (range 0.6 - 3.4%). Responding too early in a trial was the least common error type in both experiments (0.2% of all trials), while responding more than once in a trial was observed most frequently (3.2%).

In contrast to RTs, planned comparisons between the SOA levels did not yield differences in error rates.

A main effect of S2-movement type was found at the 533 ms SOA ($F(1,15) = 6$, $p < .05$) and at 1900 ms ($F(1,15) = 47.8$, $p < .001$), but not at 1200 ms. Whereas this effect was directed contrary to RTs at 533 ms, i.e. error percentage was higher with an S2-finger movement, it was similar to RTs at the 1900 ms SOA.

Main effects of congruency were significant at both the 533 ms and the 1200 ms SOA, but not at the 1900 ms SOA. These effects were directed contrary to RTs, with fewer errors in congruent trials.

An interaction between S1-movement type and congruency reached significance at all SOAs (533 ms: $F(1,15) = 68.1$, $p < .001$; 1200 ms: $F(1,15) = 11.4$, $p < .01$; 1900 ms: $F(1,15) = 7.1$, $p < .05$). At the 533 ms and the 1200 ms SOA, the error pattern was again complimentary to RTs: in congruent trials, subjects made fewer errors when S1 was a finger movement. Only with an S1-finger movement, there were fewer errors in congruent than incongruent trials.

At the 1900 ms SOA, however, the error pattern corresponded to RTs: fewer errors were made in incongruent trials with an S1-finger movement compared to a dot.

2.4.5. Discussion

Effects involving factors type of movement and congruency

As expected on the basis of RT Experiment 2 and previous studies on location cueing using object-centred frames of reference (Tipper et al., 1999) and moved (biological) objects (e.g. Kessler & Tipper, 2004), the present data also suggested that the employed S1-S2 paradigm induced IOR, or an IOR-like effect, among distinct fingers and dots, respectively.

Also in line with the previous S1-S2 experiment, effects of spatial cueing were modified by the type of movement priming employed: actually at all SOAs, RTs were

longest with congruent finger movement primes. Obviously, finger movement primes induced more pronounced effects on reaction times than moving objects which are closely matched to the biological movements.

Furthermore, the relationship between congruency and the type of movement priming in S1 was affected by SOA length: at the 533 ms SOA, the inhibition of responses in congruent trials was significantly stronger (i.e. responses were slower) with S1-finger movements as compared to S1-moving dots. At the 1200 ms SOA, however, facilitation of responses in incongruent trials was stronger (responses were faster) with S1-finger movements. Third, a significant IOR effect at the 533 ms SOA was confined to S1-finger movements. Thus, priming by a human finger as compared to an object movement led to stronger inhibition of congruent response tendencies, and to stronger facilitation of incongruent responses, respectively.

Results paralleled those of the preceding S1-S2 experiment at the 533 SOA (i.e. the shortest SOA of the set) and the 1900 SOA (the longest SOA, where no significant interaction between S1-movement type and congruency was found). However, apparently contradicting RT Experiment 2, S1-movement type and congruency interacted also significantly at the 1200 ms SOA (the middle SOA). Response inhibition or facilitation, respectively, was modulated by type of movement in S1: the facilitation of responses in incongruent trials was significantly stronger (i.e. responses were faster) with finger movements as compared to moving dots in S1. As revealed by separate analyses for the two different types of movement in S2, the movement-specific congruency effect at the 1200 ms SOA was actually due to the S2-moving dots, which, of note, had not been used in the preceding S1-S2 experiment.

Taken together, results are in correspondence with those obtained RT Experiment 2, in that (ii) a movement-unspecific IOR-like effect on RTs was observed at SOAs of 533 ms and

more, and (ii) depending on SOA, cueing effects induced by finger movements differed significantly from effects produced by moving objects. Therefore, as in RT Experiment 2, the finger movement-induced cueing effects here were specific, i.e. they differed from the effects produced by moving objects in their size and patterns of inhibition and facilitation.

Importantly, the modulation of congruency effects was not affected significantly by type of movement in S2, indicating that visual similarity between the prime and the target stimulus was not responsible for the effects observed here.

Well in line with the hypotheses, there was furthermore a main effect of type of movement in S2 at all SOAs, with participants' responding consistently faster when a finger movement was used as target stimulus as compared to a moving dot. This result confirms findings of previous RT experiments (Bertenthal et al., 2006; Brass et al., 2001a; Brass et al., 2000), a recent MEG study where my collaborators at Düsseldorf University employed the stimuli developed for the present behavioural experiments in a choice reaction task (Kessler et al., 2006), and the results of RT Experiment 1 with single movement stimuli. Moreover, these findings were now extended to an S1-S2 paradigm.

Effects on error rates were complimentary to RTs. This could be interpreted as occasional failures to inhibit imminent response tendencies to S1. Whereas only in very few trials participants actually responded with the wrong finger (0.2%), multiple responses in a single trial were much more frequent (3.2%). A higher rate of multiple responses in incongruent than in congruent trials (2.7% vs. 3.6 %) supports the interpretation that these errors result from conflicts between automatic response tendencies and responses initiated according to S2.

These findings suggest that, while the over-all congruency effects in the present study represent generalised object- and/or location-based effects of visual cueing, the movement-specific modulation of congruency effects is mediated by AOEM, i.e. direct matching of

observed biological finger movements and corresponding responses. Accordingly, the RT benefit for responses to S2-finger movements can be attributed to direct matching processes.

Finally, in line with RT Experiment 2, the use of three different SOAs obviously lead to expectancies regarding the timing of S2, as was reflected in an acceleration, i.e. an optimisation, of responses with SOAs getting longer.

2.5. RT Experiment 4: Second single-stimulus experiment

2.5.1. Objectives

Recurring to the RT advantages for immediate responses to a finger movement as compared to a moving dot obtained in RT Experiment 1 and 2 (in the latter: main effect of type of movement in S2), there were still alternative explanations to be excluded: in the stimulus array used in the preceding experiments, a dot was always attached to the moving finger. Furthermore, according to the task instruction, participants responded in the same way (i.e. according to the same spatial stimulus-response mapping rule) to finger movements as to moving dots in RT Experiment 1 and 3, where both types of movement were presented as target stimuli.

To re-iterate, both finger movements and moving dots represented targets with an identical (spatial) stimulus-response mapping. Thus, RT advantages in the moving finger condition might simply represent an effect of redundant targets or a ‘redundancy gain’, which describes the observation that in behavioural experiments participants’ responses are faster in the presence of multiple targets at the same time (here, finger plus moving dot). In the classical redundant-targets effect paradigm subjects respond to stimuli that are lateralised either to the left or to the right of fixation or presented bilaterally. However,

response facilitation has also been observed for responses to unilateral multiple targets (Pollmann & Zaidel, 1999).

Secondly, the finger movement was probably rendered noticeably more salient than the moving dot, as a dot was virtually moving together with the finger. Therefore, a higher perceptual salience of the finger movement as compared to the moving dot, resulting in a higher capacity of the finger movement to draw visuo-spatial attention, might have affected RTs. To exclude these alternative interpretations for the observed RT advantage, a second control experiment was carried out. Responses to single movement stimuli were compared in a choice reaction task. In addition to the finger movement and moving dot stimuli used so far, a third stimulus condition was introduced where only a finger moved while the red dots remained still at their resting position.

2.5.2. Method

Of note, this study was conducted after my colleagues in Düsseldorf had done an MEG study (Kessler et al., 2006) employing a simple choice reaction task and single finger- and dot movements as stimuli which paralleled my fMRT study on observation and imitation of finger movements (see chapter 3). In order to be able to draw conclusions also with respect to the MEG study, certain aspects of the stimulation in RT Experiment 4 were adapted to the paradigm used with MEG, and therefore differed from the previous behavioural experiments.

Participants

10 subjects participated in the experiment (half female and male, 26 to 45 years, mean age 34 years). All were investigated at the University of Düsseldorf.

Stimuli

As in RT Experiment 1, stimuli consisted of single finger and dot movements. Moreover, new control stimuli were constructed: these were identical to the finger movement stimuli used in the preceding studies regarding the starting and final position. During the finger movement, however, the red dot in the position of the moved finger (index, little finger) was not attached to the nail of the finger. Instead of being moved together with the finger, it remained in its initial place just above the surface on which the hand rested.

Thus, movement stimuli could be either (i) a single finger tap of the index or little finger where the mounted dot was being moved together with the finger, (ii) a finger movement alone with the dot remaining static in its resting position or (iii) a corresponding dot movement alone (see Fig. 2.15 for an illustration of the stimuli). One movement sequence lasted approximately 400 ms comprising 12 picture frames of about 33 ms each.

Moreover, paralleling RT Experiment 3, a white fixation cross was placed in the middle of the picture frame vertically and in equal Euclidian distance from both fingertips horizontally to discourage eye movements.

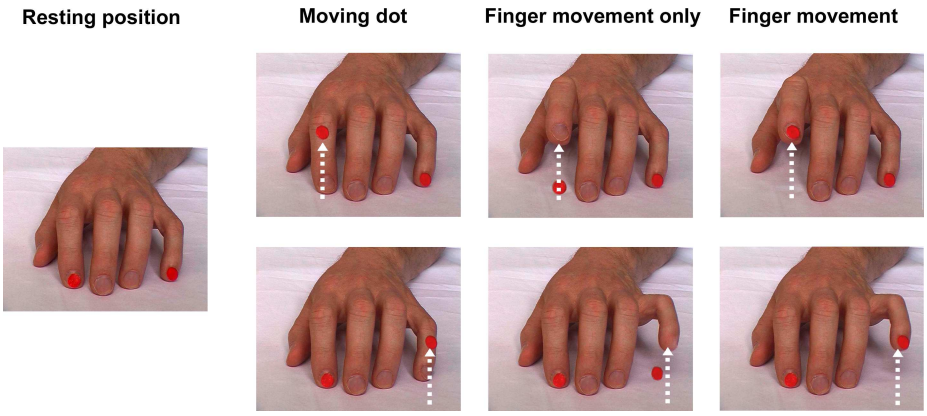

Fig. 2.15. Visual stimuli presented in RT Experiment 4. Resting position of the left hand which was shown at the beginning and the end of each movement sequence (first column). Movements were presented at the position of the index finger (top row) or little finger (bottom row): a moving dot (second column), a finger movement with the dot remaining static (third column) or a finger movement with the dot attached (fourth column). Each picture sequence consisted of 12 frames. The dotted arrows symbolise the upward movement.

Prior to each trial, the word “start” was superimposed on the picture of the resting hand for 1 sec. In the context of the above mentioned MEG experiment, subjects would be asked to make unavoidable eye-blinks during this period, as eye movements and blinks cause serious artefacts in the magnetic signals. As in the preceding experiments, each trial started with the resting hand being presented for 2000 ms on average (range 1500 – 2500 ms, 200-ms steps). Then, the movement stimulus was presented, followed by the static hand lasting 1500 ms. The average trial duration was therefore 4.9 sec (including the “start” period). During a fixed inter-trial-interval of 2 sec the screen turned black.

In the ‘finger movement’ condition, the stimulus was a movement of either the index or little finger, with a dot attached. In the ‘finger movement only’ condition, a movement of an index or little finger was presented without a dot attached. In the ‘moving dot’ condition a dot moving on top of one of these two fingers was presented.

Visual stimuli were backward-projected on a screen with a diagonal extension of 48.5 cm. Subjects were seated at a viewing-distance of 1 m in front of the screen. Thus, the stimuli comprised a visual angle of approximately 27.3° diagonally.

Task

Subjects were instructed to observe all stimuli attentively while focusing the fixation cross and lift the finger indicated as fast as possible.

Design

Within-group factors were ‘type of movement’ (finger movement, finger movement only, moving dot) and ‘finger position’ (index, little). Each combination of factors type of movement and finger position was presented 12 times, resulting in a total of 72 trials. Participants performed one block within which the order of trials was pseudo-randomised.

Two bins of 36 trials each were separated by a break of at least 10 sec. Testing was preceded by 12 practice trials that were excluded from analysis. The whole experiment took approximately 8 minutes.

Data acquisition and processing

Stimulus presentation and acquisition of response data were carried out as described above, except that different software was used for stimulus delivery (E-Prime, Psychology Software Tools Inc., Pittsburgh, USA).

Statistical evaluation

A repeated measurements ANOVA was calculated on mean RTs or error rates, respectively, including within-subject factors 'type of movement' (finger movement, finger movement only, moving dot) and 'finger position' (index finger, little finger). Planned comparisons (paired samples *t*-tests) and statistical corrections were performed as in the preceding studies.

2.5.3. Hypotheses

Confirming results of RT Experiment 1 and RT Experiment 3, an RT advantage for responses to a finger movement as compared to a moving dot was expected. If mediated by direct matching of observed and executed finger movements this RT difference should be present regardless of whether a dot was being moved together with the finger or not. However, if the RT advantage for responses to a finger movement over responses to a moving dot was due to redundant targets and/or higher perceptual salience speeding up responses, it should appear only when a dot was moved together with the finger.

2.5.4. Results

Mean reaction times and error percentages in all conditions are presented in Table 2.4.

Table 2.4. RT Experiment 4: Reaction time and error data

	index				little			
	RT (ms)		error rate (%)		RT (ms)		error rate (%)	
	mean	SD	mean	SD	mean	SD	mean	SD
finger & dot	349	47.81	0.0	0.00	364	52.14	0.8	2.64
moving dot	382	65.20	0.0	0.00	374	67.35	2.5	7.91
finger	363	66.17	1.7	3.51	352	37.29	3.3	5.83

RT (ms) = reaction time in milliseconds, error rate (%) = percentage of errors total; sd = standard deviation; finger & dot = combined finger & dot movement condition, finger = finger movement without dot, index = index finger, little = little finger

RTs

There was a significant main effect of type of movement ($F(2,18) = 6.3$, $p < .05$). Post hoc tests (paired *t*-tests) revealed significant faster responses to both (i) a finger movement where a dot was being moved together with, and also to (ii) a finger movement where the dot remained static as compared to responses to a moving dot (mean differences: 22 ms and 21 ms, respectively, $t(9) = -2.9/-2.4$, $p < .05$). Comparing responses to finger movements showed, however, that it actually did not make a difference whether a dot was being moved together with the finger or not (both mean RT: 357 ms). See Fig. 2.16 for illustration.

There was no significant main effect of finger position.

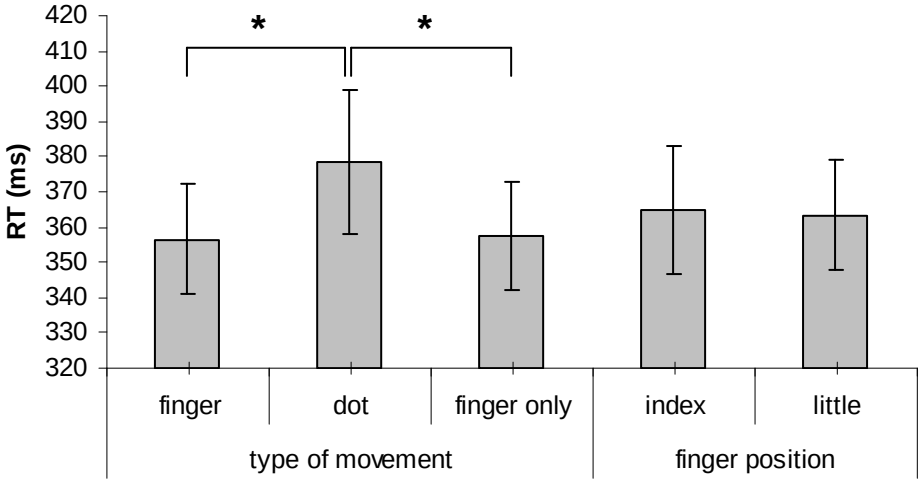

Fig. 2.16. RT Experiment 4: Main effects of 'type of movement' (finger, dot, finger only) and 'finger position' (index, little). Mean RT ± standard error of mean is displayed. Significant differences are marked (* $p < .05$).

Error rates

Mean error rate was 1.4% (range 0.0 – 4.2%). Multiple responses in one trial constituted the only type of error that occurred.

The ANOVA on error rates revealed no significant effects of the factors type of movement and finger position. Although mean error percentages were numerically different for the three types of movement (finger movement: 0.4%, finger movement only: 2.5%, moving dot: 1.3%), these differences did not reach the level of significance in planned comparisons.

2.5.5. Discussion

Results clearly showed that the RT advantage for responses to a finger movement over responses to a moving dot was also present when the dot was not moved together with the finger, i.e. when only a single target was present in the stimulus array. Error rates did not indicate any speed-accuracy-tradeoff. Thus, the observed RT-advantages for responses to

animate as compared to inanimate movement could not be attributed to an effect of redundant targets and/or attentional salience with respect to the present stimulus material.

2.6. General discussion: Reaction time experiments

The main objectives of the S1-S2 studies had been to measure automatic behavioural effects, i.e. pre-activation/priming effects, of observed human body movement on the execution/imitation of a similar movement in a healthy subject. More precisely, (i) specific effects which can be attributed to the biological nature of an observed human movement should be separated from unspecific effects that might be due to those stimulus characteristics which can also be present in other stimulus types, i.e. motion per se, irrespective of *what* is moving (a biological entity or not), or the mere presence of a (static) biological shape or entity. An additional objective was to explore (ii) the temporal dynamics of the above priming effects.

To this aim, an S1-S2 reaction time paradigm was designed, by means of which the execution of a simple intransitive finger movement was depicted that is (a) primed either by a finger movement itself or by a dot moving on top of a static finger (S1) and which is, furthermore, (b) instructed and prompted by a second movement stimulus (S2) drawn from the same stimulus pool as S1. In contrast to previous SRC or priming studies on effects of biological movement observation, the inanimate control stimulus (moving dot) was closely matched to the finger movement with respect to kinematics as well as to the presence of distinct objects in the visual array (i.e. shape of body part, dot).

Another relevant feature of both types of movement stimuli was the spatial arrangement of the two finger/dot positions used (i.e. movements were lateralised to the left and right of the array corresponding to responses with the left and rightmost finger of the subject's right hand) which rendered the paradigm to serve also as a kind of location

cueing procedure. Thus, effects of action observation were investigated here in interaction with effects of location cueing.

Before investigating priming effects, however, data obtained in a single-stimulus choice reaction paradigm showed that the employed finger movement stimuli were actually capable of inducing automatic effects: a finger tap was performed faster when executed immediately in response to a corresponding finger movement stimulus as compared to an observed object movement. In a second control experiment, this effect was present both when (i) a dot was attached to the finger during its movement, thus moved together with it, and when (ii) only the finger moved while the dot remained in a static position. Thus, the RT advantage was not attributable to the presence of redundant targets (a moving finger and a dot being moved) in the original finger movement condition or a mere higher perceptual and attentional salience of the finger movement, but actually to observation of the biological movement itself.

Further, employing finger movements and control stimuli in the S1-S2 paradigm resulted in priming effects which were specific for the biological movement: with an exogenous cueing procedure employed, (i) both biological finger movements and inanimate objects movements, respectively, induced an IOR(-like) congruency effect on RTs at SOAs of 533 ms and longer. Most importantly, (ii) depending on the SOA, congruency effects were significantly modulated by the type of movement presented as a prime stimulus in terms of their size and temporal patterns of inhibition and facilitation.

Thus, both biological finger movement stimuli as well as moving objects were obviously capable of inducing location cueing effects. Presumably by means of motion, fingers were processed as (spatially) distinct parts of the hand, as were the dots. This finding of a kind of “movement-based” IOR extends the original findings on location-

based cueing effects and evidence on IOR in experimental set-ups using object-centred frames of reference (Tipper et al., 1999) and biological objects (Kessler & Tipper, 2004; Tipper et al., 1991).

However, these IOR(-like) congruency effects which were evident for animate as well as inanimate movement stimuli, showed a movement-specific modulation of at SOAs ranging between 533 and 1200 ms. At these intervals, biological finger movements in S1 led to stronger inhibition of congruent response tendencies, or stronger facilitation of incongruent responses, respectively, as compared to moving dots.

As could be shown in RT Experiment 3, the above interaction between congruency and S1-type of movement was found regardless of whether the target stimulus represented a biological movement or an inanimate movement. Thus, these effects are indeed specific for biological movement in S1 and cannot be attributed simply to different degrees of visual similarity between the prime and the target stimulus.

Moreover, the finding of a general RT advantage for immediate responses to single finger movement stimuli was confirmed and extended in RT Experiment 3, as subjects responded faster in trials where S2 was a finger movement, irrespective of whether the preceding prime stimulus was a finger or a dot movement.

Taken altogether, the movement-specific modulations of the congruency effects observed in the present S1-S2 experiments can be interpreted as interactions between (i) effects of selective attention, i.e. object- and/or location-based effects of attentional orienting in space, induced by animate finger movement primes as well as by inanimate moving dots, and (ii) automatic priming effects of observed biological finger movements on corresponding responses.

These behavioural results are readily compatible with the assumption that both the RT benefit for responses to S2-finger movements and the movement-specific modulation

of congruency effects are mediated by a direct matching of the visual representation of a finger movement to its corresponding motor code. Thus, an automatic response tendency towards imitation of the corresponding finger (or: motor contagion) is elicited.

However, the direct matching mechanism elicited by observation of biological movement is involuntary and automatic, and thus does not operate only when overt imitation is actually intended. This is implied by behavioural evidence (see section 1.4.) and also by electrophysiological studies (see section 1.5.): similar to the period immediately preceding internally triggered movements (Chen *et al.*, 1998) net corticospinal excitability increases during passive action observation. Moreover, the amplitude of motor-evoked potentials (MEPs) increases specifically in those muscles that would be involved in the execution of the observed actions (e.g. Fadiga et al., 1995). In a number of functional brain imaging studies movement observation activated motor-related cortical areas (see section 1.5.), even in a somatotopic fashion (Buccino et al., 2001; Sakreida *et al.*, 2005; Wheaton *et al.*, 2004). Importantly, although non-biological response cues are also capable of inducing motor activation (e.g. Schubotz & von Cramon, 2002), even stronger activation has been found during the observation of human biological movement (Iacoboni et al., 1999; Tai et al., 2004).

While observation of a biological movement seems to immediately pre-activate the corresponding motor code and, thus, prepare the individual for its imitation, the expression of imitative behaviour is not appropriate in most situations. In the special case of the S1-S2 paradigm participants actually were explicitly instructed not to imitate S1 but to react only to S2. If, however, the response tendency is not immediately processed further but held in store and/or the go signal (S2) is not predictable in terms of the required response then inhibition follows. This activation followed by an inhibitory process seems to be highly specific as it is confined to (i) “real” finger movements and (ii) one effector (a single

finger). Such an interpretation would explain why no behavioural advantage was observed for congruent biological finger movements (as for example reported by Brass et al., 2000). Different time courses of inhibition and facilitation led to an inhibition of congruent finger movements at the 533 ms SOA but a facilitation of incongruent responses at the 1200 ms SOA. The facilitatory effect at the 1200 ms SOA probably reflected a "secondary" facilitation following initial inhibition of the congruent finger. One may speculate that the 533 ms SOA was too short to allow for this late facilitation effect to occur. Also, temporal expectancies regarding S2 might have led to a secondary facilitation at the 1200 ms SOA (see below).

To sum up: firstly, observation of human biological movement is obviously more effective than any other kind of visual instruction stimulus in activating motor representations and, moreover, preparing an individual to perform the observed movement. This holds true for copying of simple intransitive finger movements as used in the studies by Brass and Bertenthal and colleagues (Bertenthal et al., 2006; Brass et al., 2001a; Brass et al., 2000) and the present behavioural studies, but also for far more complex forms of imitation, as implicated by in the study on imitational learning by Gray et al. (1991): learning of a ballet sequence was significantly enhanced in quality by observation of a human model performing the to-be-learned movements as compared to observation of still pictures. Findings suggest that in healthy humans an initial imitative response tendency is elicited by observation of biological movement via direct matching mechanisms. This motor activation leads to a facilitation of immediate responses to a finger movement stimulus.

Secondly, the automatic activation of motor representations has also costs, as they may interfere with the observer's ongoing voluntary behaviour. Consequently, there have to be dedicated inhibitory mechanisms for the control of arising imitative response tendencies, which presumably were also effective in the case of the S1-S2 task. Above

cited studies suggest that motor activation by observation of biological movement is effector-specific or somatotopic, respectively (Buccino et al., 2001; Sakreida et al., 2005; Wheaton et al., 2004). Therefore, the present results are consistent with the interpretation that suppression of a finger-specific activation elicited by S1 led to slowed responses to congruent or speeded responses to incongruent movements in S2, respectively.

Third, as inferred from the above evidence and the present behavioural results, it seems to be an interplay of several specific characteristics of biological movement which makes up its special capacities: i.e. a movement being executed by a human model or at least a human body part, which is part of the normal human motor repertoire and which, furthermore, is biomechanically feasible. These features altogether, although each by themselves capable to some degree to generate motor activation, seem to make up the entity of a biological movement which is the most powerful in activating motor representations, as only here direct action matching processes can take place. In any case, as was demonstrated by contrasting intransitive finger movements with a “biologically” moving salient object (i.e. a red dot), the “movement” component per se is not sufficient to exert the same effects on motor behaviour as a real body movement.

A further question relates to the results concerning the temporal dynamics of the above proposed priming effects: when regarding the extent to which specific priming effects of biological movement depended on SOA length in S1-S2 experiments 1 and 2, results were partly divergent. Whereas a significant interaction between type of movement and congruency was confined to the 533 ms SOA in RT Experiment 2, it showed up in the 533 ms and also in the 1200 ms SOA in RT Experiment 3. In the two studies the 1200 ms SOA was presented in different relative positions in a set of SOAs - i.e. while in RT Experiment 3 the 1200 ms SOA was the middle interval, in RT Experiment 2 it represented the longest interval of the short SOA set and the shortest interval of the long SOA set. Thus, findings

point in the direction that the presence of direct matching effects was affected by the relative rather than by the absolute length of the prime-target interval.

Inferring from their study where (static) pictures of hand postures led to congruency effects in RTs of pre-instructed hand movements at SOAs between 0 and 600 ms, Vogt et al. (2003) presumed that the observed congruency effects were short-lived (with a tentative time window of 300 to 700 ms SOA) because they were influences by temporal expectancies in the subjects: with increasing likelihood of the go-signal to appear, i.e. with SOA getting longer, motor preparation might have changed its focus from the hand's target orientation to its concurrent state. Of note, movement preparation can operate even although the parameters of a movement are not yet completely specified (c.f. Wild-Wall et al., 2003). Consequently, congruency effects were reduced with increasing temporal proximity of the movement onset. In the present S1-S2 studies, responses were not pre-defined but, as was proposed, effector-specific (here: finger-specific) motor preparation was induced involuntarily by the mere observation of a finger movement in S1, then turning into inhibition of the prepared response. Thus, in conditions with the longest SOA of a given set, a mechanism similar to that proposed above might have operated: after a period of response inhibition motor preparation might have come into play again, but now focused on the hand's concurrent, resting, state rather than on the effector-specific motor response (particular finger movement) that was pre-activated by S1.

These processes are further more assumed to be specific for trials with a biological movement prime. Thus, the absence of a movement-specific modulation of congruency effects at the 1900 ms SOA (RT Experiment 3) and the 1200 ms SOA (RT Experiment 2) which were presented as the longest intervals of a set could be explained by such a mechanism.

This might explain why the movement-specific modulation of the congruency effect at the 1200 ms SOA was confined to RT Experiment 3, where this SOA was the

middle, rather than the longest, interval. It would, however, not explain why there also was no movement-specific congruency effect when the 1200 ms SOAs was the shortest interval of the long SOA set in RT Experiment 2. Presumably, a second factor affecting the interaction between SOA level and the movement-specific congruency effects was the choice of movement types present in S2. In RT Experiment 3, RTs were generally prolonged when S2 was a moving dot. Moreover, although there was no significant interaction between type of movement in S1, congruency and type of movement in S2, the additional analysis concerning the 1200 ms SOA revealed that the movement-specific congruency effect was actually attributable to the S2-moving dots which had not been employed in RT Experiment 2.

Taken altogether, the time-course of direct matching-related priming effects in the S1-S2 experiments seemed to be influenced by effects of temporal expectancy as well as stimulus characteristics of the go-/instruction stimulus. Future research will have to clarify in detail how the relative and absolute temporal relation between observation of a biological movement and movement execution modulates effects of direct matching, for example when contrasting pseudo-randomised presentation at different SOAs (as in the present experiments) with blocked testing (i.e. only one SOA length administered in one block of trials) where participant's temporal expectancies can not differentially affect RTs at different SOAs. Moreover, as visual S1-S2 paradigms do not permit simultaneous or overlapping presentation of two (supraliminal) movement stimuli, exploration of AOEM dynamics, including a comparison of simultaneous and serial processing of an instructive stimulus, will have to be continued with other paradigms.

It is worth mentioning that factors "biologicity" or "animacy" and attentional salience are to a certain degree still confounded in the present studies: except for RT Experiment 4, the moving dot was always contrasted with a finger that moved virtually simultaneously with a

dot, as a dot was attached to the fingernail. Thus, the moving finger (plus dot) was probably a more salient visual stimulus than the moving dot alone. Although the results of RT Experiment 4 indicate that the difference in stimulus salience was not crucial for response facilitation, further attempts have to be made to disentangle the behavioural effects of the "biological" from the mere visuo-attentional component in observation of human body movement.

Finally, recurring to the main objectives of the present series of studies on the link between observation and execution of biological movement, the hypotheses concerning the neural network underlying the observed behavioural effects have to be proven using functional brain imaging techniques. This will be the issue of the following chapter.

3. fMRI experiment

The following section deals with the event-related fMRI study. First, the main objectives and hypotheses of the study will be addressed (section 3.1). The section on methods (3.2.) starts with an introduction into the fundamentals of the employed fMRI method (3.2.1.), including the analysis of fMRI data. Then, the present fMRI experiment will be reported (sections 3.3. to 3.6.).

3.1. Objectives

As was laid out in the first chapter, there is converging evidence for the existence of a "mirror" or "mirror neuron" system in the human brain paralleling the mirror neuron system discovered in the macaque monkey with respect to anatomical and functional properties (see section 1.5.; Rizzolatti & Craighero, 2004). However, phylogenetic evolution may have led to certain changes in the human mirror system's functionality: some neuroimaging studies suggest that, in contrast to mirror neurons in area F5 of the monkey brain, the inferior frontal mirror area in humans also responds to *intransitive* movements (Iacoboni et al., 1999; Koski et al., 2003). Using fMRI, the authors showed that observation and specular imitation (i.e. imitation in a mirrored mode) of simple non-object directed finger movements activated the frontal opercular cortex in human subjects.

Moreover, Iacoboni et al. (2001, 1999) reported stronger activation of the left frontal operculum, the right anterior intraparietal sulcus, opercular parietal areas and the right pSTS during imitation as compared with the execution of the same movements in response to static spatial cues. Activation in the frontal operculum, the anterior parietal sulcus and the superior temporal area was also present during mere observation, however, to a lesser degree than during imitation. Authors took the stronger premotor and parietal activations during imitation compared to control motor tasks as "mirror activity" that was

due to a direct matching or AOEM mechanism (Rizzolatti & Craighero, 2004; Rizzolatti et al., 2001) linking observed and executed movement during imitation.

Accordingly, a stronger activation of the bilateral inferior frontal and right posterior parietal cortex during specular as compared to anatomic imitation of finger movements demonstrated in a companion fMRI study by Koski et al. (2003), was interpreted as reflecting a stronger engagement of AOEM mechanisms during the naturally preferred mode of imitative behaviour (see section 2.1.1.).

However, regarding fMRI results on imitation of finger movements, two features of the observed activation pattern are not readily compatible with the predicted activity for brain regions that might subserve a direct matching mechanism, i.e. the inferior frontal and parietal areas: first, the mere observation of intransitive movements activated the left frontal operculum and the right STS only, but failed to increase the activity in the left inferior parietal lobule (Iacoboni et al., 1999) which is regarded the second important "node" of the human mirror neuron system. Second, none of the above studies (Iacoboni et al., 2001; Iacoboni et al., 1999; Koski et al., 2003) reported increased activation of the frontal operculum for plain observation of finger movements compared to control stimuli, indicating that the observation of finger movements failed to elicit "mirror activity" in the absence of a motor response. Preferential activation in the premotor cortex has been demonstrated, however, for the observation of object-related human as compared to robotic action (Tai et al., 2004).

Furthermore, Williams *et al.* (2006), using virtually the same protocol as Iacoboni and colleagues (1999), were unable to replicate frontal (and temporal) increases in BOLD signal during imitation as compared to the execution control condition.

Moreover, the control stimuli employed in the studies by Iacoboni et al. (2001, 1999) and Koski et al. (2003) were non-moving cues (e.g. a black cross appearing either on the index or middle finger of a static hand, or on a grey rectangle). Thus, it was not

possible to dissociate specific effects of *human* movement from effects of movement *in general* in their results.

Finally, though authors suggested a mediation of the behavioural benefit for imitation by human mirror areas, none of the above fMRI studies reported any RT data. In a companion MEG study (Kessler et al., 2006), my colleagues in Düsseldorf used the same stimuli and task and part of the stimuli as in the present fMRI experiment. Participants imitated a combined finger-dot movement or responded to a moving dot. An analysis of long-range synchronisation during imitation revealed that finger movement imitation as compared to responses to the moving dot was associated with an increase in synchronisation at a frequency around 10 Hz in two distinct time windows (100-250 and 400-500 ms after the onset of cue presentation). Increased synchronisation was observed in a widespread network involving the left ventral premotor cortex, bilateral posterior parietal cortex, right basal ganglia, right occipito-temporal cortex, right temporal pole, and right primary sensorimotor cortex. Importantly, the RT advantages for imitation correlated with a relative increase in synchronisation of the left ventral premotor cortex with the right posterior parietal cortex and the right temporal pole 108-240 ms after stimulus onset. These findings are compatible with the interpretation that the observed behavioural advantage was due to a direct matching process which neuronal correlate were premotor and parietal mirror neuron areas, in interaction with the temporal cortex, the basal ganglia and other motor areas (cerebellum, sensorimotor cortex). However, stronger cortical synchronisation during finger movement imitation was not confined to connections between putative mirror neuron areas. Furthermore, connections in this network peaked in narrow time windows after stimulus onset. As there were, moreover, no qualitative differences between finger and dot movements in terms of the involved cortical areas, it cannot be excluded that other processes of visuo-motor transformation worked in parallel or even alternatively to AOEM during the observation-execution task. The tighter inter-regional coupling during the RT

period might indicate a functional interaction between the visuospatial network (i.e. the right PPC) and the AOEM system (i.e. left vPMC) which was crucial to produce the response facilitation for imitative cues. Finally, while MEG is capable of detecting also early and transient imitation-specific changes in connectivity between mirror neuron areas and other brain regions, it remained open whether the BOLD-fMRI method would be sensitive to these.

Following-up on previous fMRI studies by Iacoboni et al. (2001, 1999) and Koski et al. (2003), the present event-related fMRI study was designed to investigate the role of human mirror neuron areas in observation and imitation of simple intransitive finger movements. The experiment specifically focused at examining the proposed role of the core regions of the mirror system, i.e. the posterior inferior frontal gyrus (pIFG) and the anterior inferior parietal lobule (aIPL), in the mediation of the behavioural advantage for imitative responses as compared to non-imitative visual stimuli. To evaluate task-related neuronal activity that is specific to human body movement, observation and imitation of intransitive finger movements were contrasted with dynamic spatial control stimuli which were matched to the finger movements in terms of kinematical properties.

The fMRI study was disposed to investigate the neuronal correlates of immediate motor responses to imitative versus non-imitative stimuli rather than delayed priming effects and effects of temporal expectancy as the S1-S2 RT experiments. Thus, a simple RT task was chosen to measure effects of observed biological finger movements unaffected by inhibitory mechanisms and temporal allocation of attention. The behavioural paradigm paralleled RT experiments 1 and 4, employing single visuospatial stimuli in the context of a two-alternative choice reaction task.

The same “finger movement” and “moving dot” stimuli as used in the behavioural experiments (see chapter 2) were presented. Furthermore, paralleling the static control cues

used in previous fMRI studies (Iacoboni et al., 2001; Iacoboni et al., 1999; Koski et al., 2003), a non-moving spatial cue was presented.

The finger movement stimuli presented in previous fMRI studies (Iacoboni et al., 2001; Iacoboni et al., 1999; Koski et al., 2003) were perceptually more salient than the spatial control stimuli (i.e. a static black cross appearing on a finger) they were contrasted with. As salient stimuli automatically attract visuospatial and motor attention, this may have had a substantial influence on the magnitude and pattern of neuronal activity in the inferior frontal and parietal ROIs due to top-down processes. Although the imitative and control cues were matched as closely as possible (see chapter 2 for stimulus construction), the original finger movement stimulus, where a dot was attached to the fingernail and moved together with the finger, also was presumably more salient than the dot. However, by introducing the less salient "finger movement only" stimulus, where the dot remained static while the finger was moving, it could be shown in RT Experiment 4 (section 2.5.) that the RT advantage for imitative responses was present with both types of finger movement stimuli which differed in terms of their perceptual salience. The finger movement and the finger movement only condition neither differed with respect to absolute mean RTs nor effect sizes of the behavioural benefit. Despite that behavioural effects were not affected by stimulus salience, both types of finger movement stimuli were employed in the fMRI study to estimate the influence of imitation-specific as compared to unspecific effects of top-down modulation by attentional salience on regional BOLD responses.

In previous fMRI studies (Iacoboni et al., 2001; Iacoboni et al., 1999; Koski et al., 2003), only one type of cue was presented during a single block, and consecutive blocks were separated in time by a period of rest without any stimulus presentation (*block design*). The blocked stimulus presentation may have facilitated an "imitative set" during imitation of finger movements, and the use of different response strategies for the different cues. An

event-related study design with intermingled presentation of different stimulus conditions in single trials was employed in the present study to minimise activity related to cognitive sets and strategies, including task switching costs. See section 3.2.

Maintenance of attention during the course of the experiment, particularly during mere observation, was ensured by an oddball condition.

3.2. Methods

3.2.1. Fundamentals of functional magnetic resonance imaging

3.2.1.1. Physiological background

The phenomenon called *nuclear magnetic resonance* arises from the interaction of nuclei having a magnetic momentum with an applied magnetic field. *Magnetic resonance imaging* (*MRI*) as a tool for picturing the anatomy as well as the function of the brain, exploits the magnetic properties of organic tissue, most commonly the sensitivity of the hydrogen H^1 atoms in water molecules to magnetic forces. As a H^1 nucleus consists of only one proton (and only one electron), its nucleus (proton and neutron) has a nuclear momentum known as *spin*: the H^1 proton constantly *precesses* about its principal axis, i.e. it moves in a gyrating fashion like a child's spinning top. The spin of the electrically charged proton creates a magnetic dipole field which is orientated randomly as long as it is unaffected by strong magnetic forces. When, however, a subject is placed within the static magnetic field produced by the MRI machine (with a field intensity ranging between 1.5 to 3.0 Tesla for standard clinical or research purposes) the spins of the H^1 nuclei in her/his body will tend to align either parallel or anti-parallel with the direction of the magnetic field (B_0) defined as the *z*-direction. As slightly more spins will align parallel to the field, this results in a net magnetisation of the complete sample parallel to B_0.

Now, in order to *excite* a measurable signal, the spins are perturbed out of equilibrium by applying a *radiofrequency* (*HF*) pulse, i.e. a magnetic field (B_1) in the *x*,*y*-plane which is oscillating at the same frequency of precession as the spins, the so-called *Larmor frequency*. By absorbing the energy of the radio waves the spins undergo a transition from a low-energy state to a high-energy state (for more details see Schoell, 2005). Depending on the magnitude and duration of the HF pulse the spins are to a certain degree knocked out of alignment with B_0. The net magnetisation is flipped from the longitudinal (*z*-) axis to the transverse (*x*,*y*-) plane. The stronger the energy of the HF pulse the further the net magnetisation tips from the *z*-axis, up to a maximum *flip angle* of 90° where all spins are in phase.

As soon as the HF waves are turned off, the process of *relaxation* will start: the spins return to their equilibrium state by realigning themselves with B_0 again. The exponential process of relaxation is described by three time constants: T_1 is related to the longitudinal magnetisation, whereas T_2 and T_2* are both related to the transverse magnetisation. T_1 relaxation is the time required for the longitudinal magnetisation to return to thermal equilibrium due to the spins dissipating the energy back into their environment. Consequently, the intrinsic properties of the tissue (i.e. fat, muscles, white and grey matter, cerebrospinal fluid) determine T_1. T_2 relaxation is the time required for the transverse magnetisation to return to zero. It decays as spin-spin interactions between neighbouring nuclei inevitably make the spins in the probe dephase. The transverse magnetisation begins to precess about B_0 at the Larmor (resonant) frequency, producing an alternating voltage in the receiving coil which is detectable as electromagnetic radiation within the range of HF waves. The time-course of this alternating voltage is the MR signal. T_2 is also specific for different matters, i.e. it is shorter in solid bodies than in fluids.

However, due to magnetic field inhomogeneity and microscopic spin-spin interactions the transverse magnetisation in fact decays faster than T_2, namely with the

effective relaxation time T_2*, leading to a loss of MR-signal. In order to be able to estimate T_2, the spins are re-phased again by an additional HF pulse: at a time τ (*Tau*) after the 90° HF pulse the probe is excited by a 180° pulse that flips the transverse magnetisation about the *x*-axis. After another time τ the spins will be in phase again for a short time, and after a time of 2τ, the *time of echo* (*TE*), the refocused *spin echo* signal will reach its maximum. In a spin echo sequence the pulse sequence 90°-180° is repeated with a *time of repetition TR*. The relation of TE and TR in a pulse sequence determines the weighting of an image with respect to T_1 or T_2 relaxation: A tissue-distinct T_1 weighted contrast which is often used for anatomical scans, is achieved by using a short TR and a short TE. A T_2^* weighted contrast, which is used for standard functional imaging (measuring BOLD contrast, see below), is accomplished by using a long TR and a long TE.

Finally, to get full spatial information about the sample, *slice selection*, *phase*- and *frequency encoding* are used. Three orthogonal pulsed magnetic *field gradients* are added to the main homogenous static magnetic field. These gradients produce a small linear variation in the *z*-, *y*- and *x*-component of the main field, i.e. the precession frequency of the spins in the probe varies with their position in space. Consequently, there is a phase change that is proportional to the position coordinate parallel to the gradient direction. By means of Fourier transforms, the rows and columns of a 3-D matrix can be reconstructed from the measured MR signal, assigning a greyscale value to each *voxel (volume pixel)*.

First, to selectively excite only a specific slice of the probe, the main magnetic field is made inhomogenous by adding the field gradients at the time of excitation, and, furthermore, applying a HF pulse of a certain frequency bandwidth. Second, the main magnetic field is made inhomogenous during the signal readout. Thus, different frequencies in the MR signal can be separated by applying a Fourier transform. Third, by repeatedly adding the field gradients of different intensities for short periods (ms) between excitation and readout, differences in phase between the spins which are related to their

spatial position can be calculated by Fourier-transforming the signal with respect to field strength.

When a characterisation of (cognitive, sensory or motor) information processing in the human brain is addressed, the most widely used fMRI method makes use of the *blood oxygenation level dependent (BOLD)-contrast*. The BOLD-contrast exploits the fact that during increased focal neural activation the degree of blood oxygenation is actually higher than in a comparable "resting" condition: increased neural activation also causes an increase in the metabolic consumption of oxygen which, in turn, is compensated for by the vascular system through an augmentation of the *regional cerebral blood flow (rCBF)*. As this response of the vascular system is overshooting ("luxury perfusion"), it makes BOLD-imaging possible. Whereas oxyhemoglobin (hemoglobin that is oxygenated, i.e. bound to oxygen) is diamagnetic, thus repels the local magnetic field applied, desoxyhemoglobin (hemoglobin that is desoxygenated, i.e. not bound to oxygen) is paramagnetic, i.e. attracts the magnetic field and distorts its homogeinity. Thus, the BOLD-contrast reflects the distortions of the magnetic field (in the order of 0.5-3% at a magnetic field strength of 1.5 Tesla) caused by the different magnetic susceptibility of desoxy- versus oxyhemoglobin in the blood (Matthews, 2001). Of note, the magnetic susceptibility is not homogenous across the brain. At tissue boundaries (e.g. the sinus cavity at the frontal pole) and close to large blood vessels (i.e. in the medial temporal lobe) *susceptibility artifacts* can arise. In the time-course of the measured MR signal, the BOLD contrast is reflected in differences in the T_2* relaxation time.

An advantage of BOLD-fMRI over other functional brain imaging methods (e.g. *positron emission tomography, PET, or electro-/magnetoencephalography, EEG/MEG*) is the possibility to achieve a high spatial resolution, i.e. in the order of voxel sizes below

$1mm^3$ (Menon, 2001). For economic reasons, though, i.e. to shorten scanning time (the TR, for whole brain measures is usually 2-4 s), mostly lower resolution are used.

The method has, furthermore, some limitations: first, the BOLD-contrast is an indirect measure of neural activation. Its amplitude and extension are most closely correlated with local field potentials (with a delay of 4-5 s), as results of simultaneous fMRI and intra-cortical electrode measurements by Logothetis *et al.* (2001) showed. Thus, the BOLD-contrast predominantly reflects the energetically expensive regional synaptic input at local dendrites rather than multi-unit spiking activity of neurons which corresponds to the output of a region. Second, the temporal resolution of BOLD-fMRI is limited by the dynamics of the hemodynamic response (Fig. 3.1A): the neural activity sets in milliseconds after onset of stimulus presentation, increasing the *cerebral metabolic rate of oxygen ($CMRO_2$)* that reflects the metabolic demand of the local tissue (Ugurbil *et al.*, 1999). The BOLD-signal, in contrast, actually decreases during the first second (*initial dip*), because the oxygen consumption increases faster than the compensatory vascular response. Due to luxury perfusion, the BOLD-signal increases from approx. 2 sec after stimulus onset, peaks at 5 sec, again decreases below baseline (*poststimulus undershoot*) and is recovered at 12-18 sec (Matthews, 2001). The length of the whole individual BOLD response is approximately 30 sec.

3.2.1.2. Processing of fMRI data

Prior to the statistical analysis, imaging data have to undergo temporal and spatial pre-processing. In the present work, images were processed and analysed using *Statistical Parametric Mapping 2* (*SPM2*) (Wellcome Department of Cognitive Neurology, London, UK) implemented in Matlab 6.5 (Mathworks, Sherborn, MA). The following two sections describe the processing procedures provided by SPM2 and customised toolboxes which are

available and commonly employed in our laboratory, i.e. the Department of Systems Neuroscience at the University Medial Center Hamburg-Eppendorf (see also Gläscher, 2005; Wolbers, 2005).

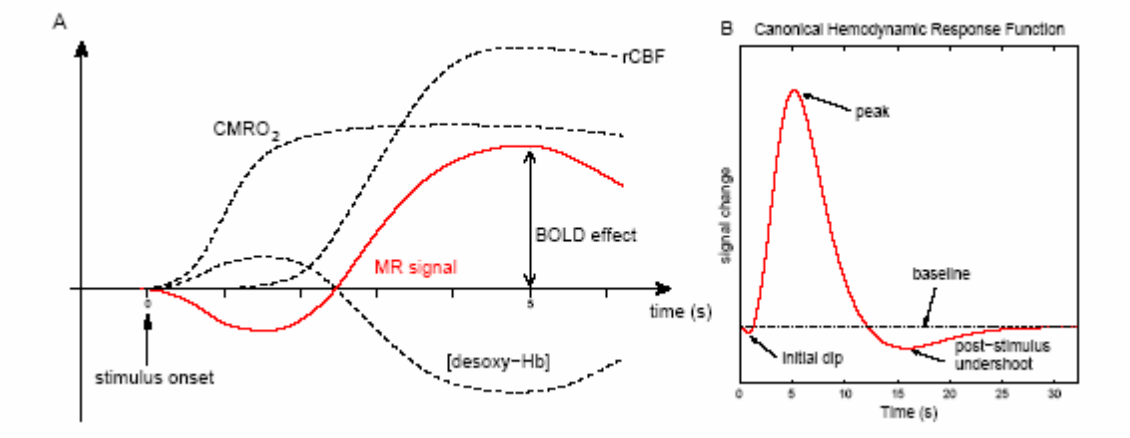

Fig. 3.1. A. Physiology of a stimulus-evoked hemodynamic response. The different metabolic influences ($CMRO_2$ = cerebral metabolic rate of oxygen, rCBF = regional cerebral blood flow, desoxy-Hb = desoxyhemoglobin) affecting the homogeneity of the applied magnetic field, i.e. the measured MR (= magnetic resonance) signal (red line) or BOLD (blood oxygen level dependent) effect (indicated by a double-headed vertical arrow). The schematic display comprises approx. 5 s after stimulus onset. **B. Mathematical model of the hemodynamic response.** A canonical hemodynamic response function as used to model the hemodynamic response in SPM. The display comprises an entire BOLD response. Subfigure A modified after Ugurbil et al. (1999) © 1999 IOS Press. Subfigure B adapted, with permission, from Gläscher (2005).

Slice time correction adjusts for the sequential acquisition of slices within a scan. While the measurement of an entire brain volume takes usually 2-4 sec (employing a standard T_2*-weighted *echo-planar imaging (EPI)* sequence), the BOLD response is triggered simultaneously in the whole brain, leading to a *phase offset* for all slices following the first one. By use of a Fourier transform the phase is corrected as if all slices had been acquired at the same time as the particular reference slice (the middle slice is often selected to minimise the inevitably resulting interpolation error).

Image realignment adjusts for a subject's head motion during an fMRI run or session, basically for *translations* (i.e. head position shifts in the direction of one of the three image-dimensions, i.e. the *x*-, *y*- or *z*-axis) and *rotations* (shifts around one of the

three axes) between different images of a series. Motion correction is necessary as a shifting of voxels in space induces movement artifacts, i.e. signal changes (1-8%) that can be even larger than the experimentally induced changes (maximally 5%). Whereas random movements that are independent of the experimental manipulation decrease the *signal-to-noise ratio (SNR)*, stimulus-correlated movement often leads to spurious activations at the edges of the brain. Images are re-aligned by application of so-called "rigid-body transformations" (affine transformations allowing for any linear transformation of a three-dimensional image). The realignment is an iterative procedure within which transformation parameters corresponding to the (translational and rotational) head movements are estimated with the aim of minimising the sum of squared differences between two images.

During *spatial normalisation*, the individual brain of a subject is matched to a standardised brain template. This is done in order to permit comparisons across different subjects and experiments and to admit the use of standard brain atlases (Friston *et al.*, 1995a). The employed template is defined either by the Talairach (Talairach & Tournoux, 1988) or the Montreal Neurological Institute (*MNI*) space (Evans *et al.*, 1993). Both affine and nonlinear deformation parameters are computed. By affine transformations, first, an initial gross anatomical matching of the whole individual head to the template is carried out and, second, the brain is matched to the template by minimising the sum of squared differences between them. During nonlinear transformation, the precise fitting of regional differences is accomplished.

Spatial smoothing is applied to the image data for several reasons: (i) to enhance the SNR, (ii) to improve the error-term-distribution, which is a requirement for applying parametrical statistical tests subsequently. (iii) smoothing corrects for remaining anatomical differences between subjects, though, at the expense of decreasing the spatial resolution. During smoothing, images are spatially filtered by means of a 3-D-Gaussian

filter of a specific width (the Gaussian kernel normally has 2-3 times *full-width-at-half-maximum (FWHM)* of the voxel size (Friston *et al.*, 2000).

3.2.1.3. Statistical analysis of fMRI data

Functional imaging data are analysed in a two-step procedure, in which the effects of the experimental manipulations are estimated independently for each voxel (*mass univariate approach*).

At the *1st level* of analysis, the effects of the experimental manipulation on brain activation are estimated for each subject independently. Here, a multiple linear regression within the framework of the *general linear model (GLM)* is used to explain the measured time series at each single voxel. In this regression function, the data Y are modelled by the weighted sum of a set of predictor variables or *regressors* (P) and a residual error term e which represents the differences between the data and the predicted response, i.e. noise: $Y = X\beta + e$.

The regressors that represent the experimental conditions and the onsets of stimuli during the course of the experiment are specified in a design matrix X (see Fig. 3.2 for an example). This design matrix can contain also additional explanatory variables, as for example the transformation parameters resulting from the previous realignment procedure of images, or covariates like participants' behavioural test scores, reaction times or age.

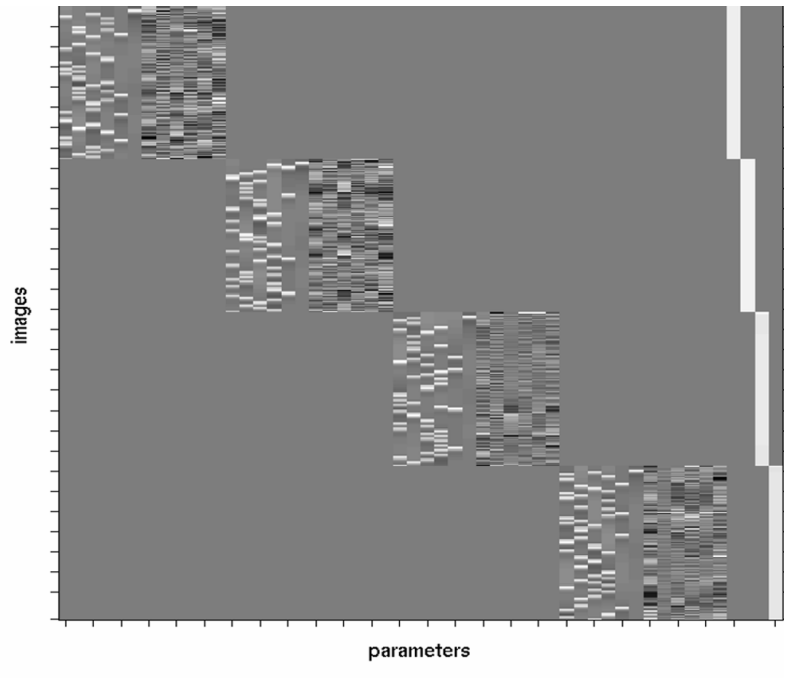

Fig. 3.2. Graphic display of a single-subject design matrix. The exemplary first-level design matrix contains four sessions. Acquired images (scans) are displayed on the ordinate, predictor variables (parameters/regressors) are depicted on the abscissa. Four blocks of columns: four sessions with 12 regressors each (five regressors representing the experimental conditions, one regressor modelling errorneous events, six regressors containing the realignment parameters). Rightmost columns: session-specific constant terms.

The stimulus onsets usually are modelled as trains of delta functions convolved with a standard canonical *hemodynamic response function (HRF)* (see Fig. 3.1B; Friston *et al.*, 1998a). An HRF is a mathematical model of the hemodynamic response (constructed of two Gamma functions) that describes an individual stimulus-evoked BOLD response in the brain. As fMRI time-series have a particular autocorrelative structure, not simply their mean may be used for predicting the data. Instead, a hypothetical response function for each experimental condition is constructed, based on the onset of this condition during the experiment convolved with the canonical HRF. It is only sensible to model all stimuli presented in an fMRI experiment separately if SOAs are not less than 2 sec (i.e. *event-related study design*; see section 3.2.1.4.).

The goal of the GLM estimation is to determine the regression coefficients (*parameter estimates* $\beta_1 \ldots \beta_p$ which usually represent the response amplitude, i.e. the magnitude of activation or its effect size) that fit the model to the data. The criterion for

this fit is the minimisation of the sum of the squared residuals by standard statistical criteria (ordinary or weighted least squares, maximum likelihood). The model estimation on the first level yields β -images for each regressor containing the parameter estimates, i.e. the estimated effect size of this variable at all voxels.

In order to draw a statistical inference about the magnitude of these effect sizes, a linear contrast vector has to be applied to the parameter estimates (e.g. [-1 1 0 0 0 ....] for a one-sided *t*-test comparing the first two of a number of conditions). The contrast vector *c* is multiplied with the β-images, rendering a *con*[trast]-image (effect size image). Statistical inference is done by thresholding the resulting SPM{*T*}-maps with a pre-defined α (see *2nd level* inference).

At the *2nd level* of analysis, the *con*-images of all subjects from 1st level estimation are tested in a *mixed-effects* group analysis. Here, standard statistical tests, i.e. ANOVA, one-sample *t*-test, linear regression/correlation etc. are applied.

Mixed-effect analyses on multi-session/subject fMRI data treat the session or subject-specific effect as a *random* variable, such that the observed activation is a mixture of *fixed* and *random* effects[2]. Inference is carried out at the second/group level and pertains to significant effects that are large in relation to between-session/subject variability. In contrast to that, *fixed-effect* analyses use models in which the interaction between the effect (e.g., activation) and session/subject is treated as a fixed variable and the effect is compared against within-session/subject error (as in a 1st level analysis).

[2] Whereas the levels of a *random* factor/variable are assumed to be random samples from a larger population, the values of a *fixed* variable are assumed to be always the same, i.e. measured without error (independent variables in an ANOVA or regression are mostly assumed to be fixed). A *fixed-effects ANOVA* refers to assumptions about the fixed variable and the error distribution for the variable, thus, results can be generalised only to the experimental values used in the study. A *random-effects ANOVA* makes inferences beyond the particular values of the independent variable used in the study, i.e. on the population where the values were drawn from. Thus, results can be generalised to other studies using other values of the variable, however, at the expense of less power (because random-effects analyses produce larger standard errors than fixed-effects models).

As on the 1st level of analysis, statistical inference is done by thresholding the SPMs resulting from linear contrasts. Basically, there are two types of inferences about a null hypothesis in neuroimaging (Friston, 2003):

(a) hypotheses concerning a pre-specified anatomical region. If the tested brain volume is restricted to *regions/volumes of interest (ROIs/VOIs)* according to a priori hypotheses about the involvement of brain regions in the process under investigation, the uncorrected *p*-value associated with the spatial extent of the nearest activated cluster in that region can be used for inference (Friston, 1997) (*cluster-level inference*, see below). However, it is also common practice to report corrected *p*-values (i.e., adjusted for multiple comparisons, see below) associated with the maximal height of the activation and constrain the search volume to the pre-specified region, i.e. to perform a *small volume correction, (SVC)* (Worsley *et al.*, 1996).

(b) hypotheses without anatomical constraints. Here, one has to account for the *multiple testing problem* in any case: as effects in neighbouring voxels tend to be highly correlated, multiple spatial comparisons (one for each voxel) cannot be regarded as independent and statistical thresholds have to be corrected for false positives (*Type I error*). The standard measure of Type I error is the probability of any Type I error, the *familywise error rate (FWE)*. As the standard Bonferroni-method controls for the FWE of activated voxels by correcting for thousands of t-tests (which are, moreover, not independent in adjacent voxels) it severely decreases the sensitivity. Alternative approaches have been developed specifically for functional neuroimaging, e.g. the *Gaussian random field (GRF)* theory (Worsley *et al.*, 1992) which controls for the FWE based on spatially extended regions (clusters) of activations in the data regardless of voxel number. The more recently developed *false discovery rate (FDR)* error metric describes the expected proportion of rejected hypotheses which are false positives, adaptive to the actual number of suprathreshold voxels in the data (Genovese *et al.*, 2002).

There are, moreover, different levels of inference in neuroimaging: (1) *set-level* inference decides whether the global pattern of activated regions (clusters) emerged by chance, based on how many clusters exceed a certain height of activation and *spatial extent threshold* (*k*). (2) *cluster-level* inference decides whether the extent of a cluster is emerged by chance. (3) *voxel-level* inference decides whether the height of activation of a single voxel arose by chance. Whereas the statistical sensitivity decreases from set- to voxel-level inference, the specificity of activation localisation increases.

3.2.1.4. Experimental design of fMRI studies

Setting up an appropriate experimental design for an fMRI study aims at isolating task-related changes in BOLD signal, i.e. experimental variance induced by the experimental manipulation, from signal changes that occur related to other non-interesting processes. The majority of study designs employed with fMRI more or less relies on the *cognitive subtraction* approach. Here, regional changes in BOLD signal related to one or several *experimental conditions* are compared with activity measured during one ore more *control conditions*, and one ore more *baseline conditions*, respectively. Information processing required by tasks and/or stimuli in the experimental condition(s) as compared to the control condition(s) is supposed to differ in the interesting aspect(s). During a baseline condition there are normally no specific task requirements, in attempt to induce a "resting" phase as a reference for any task-related signal changes, increases as well as decreases.

The simplest application of the subtraction logic is a *categorical study design*. Regional brain activity associated with a specific form of information processing (cognitive, sensory or motor) is sought to be identified by simply (or serially) contrasting regional activation changes related to an experimental condition with a control condition. On the level of statistical inference, comparisons between conditions are accomplished by

voxel-wise *t*-tests (see section 3.2.1.3.). However, the logic of the subtraction approach rests on the psychophysiological principle of "pure insertion", stating that cognitive processes can be added to an experimental situation without changing other processes required. This assumption, however, disregards that cognitive processes interact with each other. Thus, the neuronal activity induced by a certain cognitive process depends on the whole experimental context. Baseline activation against which task-related signal changes are evaluated is affected by every additional cognitive process as well.

Factorial designs also rest on the subtraction idea, however they account for interaction effects between different task-related activity changes. A factorial design comprises more than one independent variable/factor, and factor levels are completely crossed, i.e. each level of each factor is paired with every other level of every other factor. An example of a factorial design is the one employed in the present fMRI study (see section 3.3.). *Parametric designs*, furthermore, rely to a lesser degree on the subtraction logic, assuming that altering the load on one process does not change other component processes in the task. Parametric designs implement variation over several levels (at least three) over a process of interest, e.g. represented by task difficulty. The possibility to look for systematic linear or non-linear variations of regional activity across all levels of a variable renders control conditions obsolete, thus reduces the probability of false positives and activations due to confounding variables.

As fMRI generally is a contrastive method where task-related activation is evaluated in comparison to a baseline, it is generally important to set up an appropriate *baseline condition*. In fact, there is frequently substantial activation during those phases of an experiment where no explicit task has to be performed. These activations which can be due to mental imagery, rehearsal, eye movement etc. might severely reduce the sensitivity of a paradigm. Depending on the experimental hypotheses, the use of a high-level baseline

condition that is preferably similar to the experimental condition or even multiple baseline conditions which control for different possibly confounding factors may be advisable.

It is furthermore, desirable to enhance the sensitivity of a given design for the experimental effects and reduce error variance, i.e. raise the experimental variance. Higher experimental variance, on the one hand, can be achieved by optimising the parameters of an experimental design: (i) the *sampling rate*, or the resulting temporal resolution of fMRI, respectively can be virtually enhanced by *jittering* of SOAs, that is randomly shifting the phase onset of consecutive stimuli, and at the same time avoiding to synchronise onsets of stimuli with volume acquisition or using SOAs that correspond to a multiple of the TR. Jittered SOAs provide that hemodynamic responses to stimuli of different conditions will not sum up to a grand peak (as they overlap in rapidly following trials), but will rather lead to condition-specific temporal patterns and, in turn, higher experimental variance. (ii) *stimulus order*, moreover, has an impact on the magnitude of experimental effects.

In a conventional fMRI *block design*, similar stimulus events are presented to the subject with a fixed inter-stimulus interval of less than 2 sec, for e.g. a period of 15-60 sec. The different BOLD responses to the stimuli within a block do not add up linearly, but BOLD amplitude is attenuated after the first stimulus in a block, leading to a slight signal decrease over the course of a blocked presentation (Friston *et al.*, 1998b). After each block, a resting period of the same duration (or at least ca. 12-18 sec) has to be inserted, allowing the hemodynamic response to return to baseline. As BOLD responses elicited by single stimuli can not be separated from each other, block designs do only permit to analyse activation related to single stimuli.

Experimental effects obtained by block designs are markedly higher in magnitude than those obtained by *event-related* study designs. Here, stimuli of different conditions are normally presented in a randomised or pseudo-randomised order. To avoid overlapping

effects of adjacent events, fixed inter-stimulus intervals should not be below 2 sec. However, even shorter stimulus presentation rates (one trial per 2 s or less) have recently been proven feasible: in *rapid event-related* fMRI, jittered inter-stimulus/-trial intervals are used (see above). Event-related approaches permit to obtain correlates of neural activity that is related to single or averaged stimuli (belonging to one experimental condition). They are, however, not sensitive to tonic changes in activation.

Finally, several psycho(physio)logical factors have to be considered when opting for a block or an event-related design: whereas in a block design the stimuli within one block have to belong to the same stimulus type or experimental condition, stimulus order can be more flexibly chosen in an event-related design. This can help to reduce expectancy effects (cognitive sets), but on the other hand lead to undesirable learning of possible regularities within a pseudo-randomised stimulus order. Habituation due to repeated presentation of similar stimuli within a block might attenuate activation. Attention or vigilance might decline over the course of a long block of stimuli as well as over the course of a slow event-related stimulus presentation. Whereas an orienting reaction is potentially induced only by the first stimulus in a block, it may be elicited by each single stimulus in an event-related presentation. A critical advantage of rapid event-related designs is their comparability with approved paradigms from experimental psychology.

In general, block designs are most efficient in terms of induced experimental variance. There are, however, ways to benefit from the above described advantages of event-related designs, while at the same time achieving sufficient design effiency (Friston *et al.*, 1999; Josephs & Henson, 1999): if one is predominantly interested in detecting *main effects*, i.e. common averaged activation related to stimuli representing one experimental condition, longer SOAs (of 9 sec and longer) should be used. If *differential effects* are of highest interest, i.e. the difference in activation between different types of stimuli, shorter SOAs (even below 2 sec) should be employed. A trade-off between the sensitivity for main

and differential effects can be avoided by introducing *null events*, i.e. by occasionally omitting stimulus events in a sequence. This markedly improves the sensitivity of a rapid event-related design for main effects (and to a lesser degree also for differential effects; see the present fMRI study, section 3.3.).

3.3. Method of the present fMRI study

Participants

19 healthy individuals (10 females) aged 21 to 36 years (mean age: 25.2 years) were measured at the University Medical Center Hamburg-Eppendorf. All had no history of neurological disorder or head injury, normal or corrected-to-normal vision and were assessed as being right- handed according to the revised AHQ (see Annett, 1970, 1985). Subjects gave their informed written consent prior to the experiment to which purpose they were naive. They were paid for their participation. The study was in accordance with the Declaration of Helsinki (1964) and approved by the local ethics committee.

Stimuli

The stimulus material employed during fMRI corresponded to that used in the behavioural studies (chapter 2). Participants continuously watched a left hand resting on a white horizontal plane. To minimise eye movements, subjects were required to fixate a yellow cross that was placed on the stimulus' vertical midline and in equal Euclidian distance from both fingertips horizontally. The stimulus hand was presented in a mirrored orientation with respect to the subject's responding right hand. See Fig. 3.4 for an illustration of the stimuli.

A static picture of the left hand with the fingers slightly flexed served as a high-level visual baseline (Fig. 3.4). Stimulus conditions differed with respect to the presence or absence of (i) movement *per se* (i.e. movement of an object or a finger) or (ii) *animate* movement (i.e. movement of a finger). Four different types of picture sequences were presented as stimulus events, three of them presenting movement: (1) in a "finger movement" condition inanimate as well as animate movement was shown in that a finger moved up and down with a dot attached to the moving finger. (2) a "finger movement only" condition presented an animate up-and-down movement of a finger (with static dots visible). (3) a "moving dot" condition showed inanimate movement, i.e. a dot object moving up and down on a static finger. (4) in a "colour change" condition there was no movement present, but a static dot superimposed on a static finger changed its colour abruptly from red to green and back. Each event concerned either the index or little finger. Of note, this stimulus was different from the control stimulus presented as S1 in RT Experiment 2 (see section 2.3.).

To ensure that participants paid attention to the stimuli, a non-spatial oddball stimulus was presented that consisted of three parallel yellow lines superimposed on the static hand in the centre of the screen (see Figure 3.4). The use of an oddball condition was motivated by an fMRI pilot study in seven subjects where no oddball was introduced. Here, the first-level analysis revealed no or only weak activation of the pIFG and aIPL during the observation sessions. Subjects reported severe difficulties to maintain attention. The PET study by Elsner et al. (2002) is a positive example of an experiment where the use of a sensorimotor oddball condition did not adversely affect activation of the SMA by auditory presentation of learned "action effects".

Each picture sequence consisted of twelve frames and lasted approximately 400 ms (each single frame was presented for 33 ms).

Task

During the execution task, participants were instructed to lift the right index or little finger as fast as possible in response to the stimulus. During the observation task, subjects watched the same stimuli but responded only to the oddball stimulus. On appearance of the oddball, participants were required to lift the index, middle, ring and little finger of the right hand simultaneously. To ensure a constant cognitive set, participants performed the same task (execution, observation) throughout a single fMRI session. The task instruction was presented as a text ("Ausführung" or "Beobachtung") at the beginning of each fMRI session. Task instructions and training trials (10 per task) were provided outside the scanner prior to the fMRI measurements.

Design

A 4 x 2 factorial design was employed. Within-group factors were 'stimulus type' (finger movement only, moving dot, finger movement, colour change) and 'task' (observation, execution). Each participant underwent four fMRI sessions (two sessions per task) of approximately six minutes, separated by short breaks of approximately two minutes. The tasks alternated between consecutive fMRI sessions, and the order was counterbalanced across participants (execution-observation-execution-observation or reversed order; see Fig. 3.3B). All stimulus types were presented in a pseudo-randomised order during each fMRI session (see Fig. 3.3A), employing a rapid event-related design with a jittered stimulus-onset asynchrony of 3.4 – 4.4 sec. Each of the four spatial stimulus types (colour change, moving dot, finger movement, finger movement only) was presented 12 times in each session. Six stimuli were presented at the position of the index finger or little finger, respectively. Four oddball trials were added to each fMRI session. Furthermore, 12 null

events (400 ms-sequences showing the resting hand) were presented per session to improve the design's sensitivity for the main effect of stimulus type.

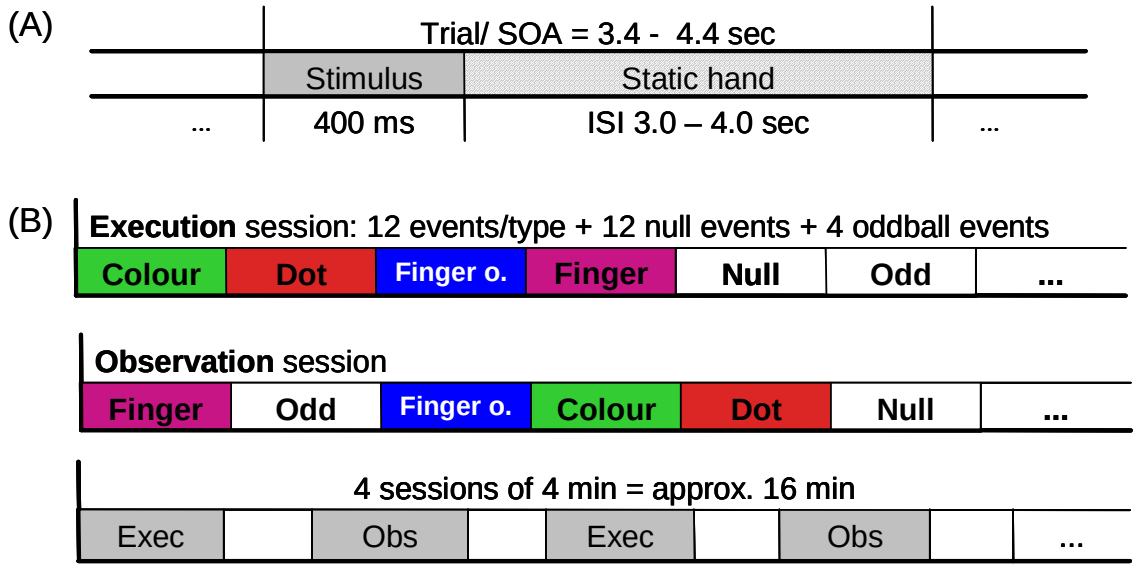

Fig. 3.3. Experimental design of the fMRI study. A: Timing of a single trial. B: Arrangement of stimulus events and sessions. Upper two beams: succession of stimulus events in the execution and observation sessions. For illustrative purposes, the different trial types within the fMRI sessions are not shown in the pseudo-randomised order in which they were actually presented. Lower beam: order of task-sessions in the experiment. Only one of two possible orders within the experiment is depicted.

Data acquisition

Stimulus delivery, recording and on-line processing of motor responses were controlled by a personal computer using Presentation software. Visual stimuli were back-projected by an LCD-beamer onto a screen inside the scanner that could be seen by the subjects via a mirror attached to the head coil. The screen was positioned at a distance of approximately 90 cm from the subjects' eyes. Thus, rectangular stimuli occupied a visual angle of ca. 10.7° diagonally.

Data acquisition

fMRI measurements

MRI data were acquired on a 3 Tesla whole body MRI scanner (Magnetom TRIO, Siemens, Erlangen, Germany) using a standard head coil (Bruker, Ettlingen, Germany). A T_1-weighted FLASH 3 D sequence was used for structural MRI of the whole brain (TR 15 ms, TE 4.92 ms, flip angle 25°, 192 slices, 1 mm slice thickness, 20% gap, 256 x 256 matrix) to exclude neurological abnormalities. To measure task-related changes in BOLD signal as an index of regional synaptic activity, functional images were acquired employing a T_2*-weighted single-shot gradient echo-planar imaging (EPI) sequence covering the whole brain (TR 2030 ms, TE 25ms, flip angle 90°, 35 transversal slices, 3 mm slice thickness, 33% gap, 64 x 64 matrix, 210 x 210 mm field of view, resulting in a 3.3 x 3.3 x 3.3 mm voxel size). The subjects' head position in the coil was stabilised with foam pads to minimise head movements. A total of 144 EPI volumes were acquired for each session along the transversal plane, including five dummy scans at the beginning of each to ensure steady-state magnetisation.

Behavioural responses

Participant's motor responses were registered by means of the custom-made light barrier device that was also used in the behavioural studies (chapter 2). The MR-compatible device was placed on the subjects's abdomen throughout the fMRI measurement. The participants' responses were quantified as RTs and errors as in the behavioural experiments.

Data processing and analysis

fMRI data

Image analysis was carried out using SPM2 (Wellcome Department of Cognitive Neurology, London, UK; www.fil.ion.ucl.ac.uk/spm) implemented in Matlab 6.5 (Mathworks, Sherborn, MA). The first five scans of each series were discarded to alleviate the scan equilibration effect. Images were slice-timed and realigned to the first image of the first session to correct for the effect of head motion across scanning time. Realigned images were spatially normalised using a representative brain (MNI series) as a template and 3rd degree B-spline interpolation and were finally smoothed using an isotropic Gaussian kernel of 12 mm FWHM to account for interindividual anatomical differences and to admit valid statistical inference at the group level (see section 3.2.1.2.).

All four sessions were entered into a 1st level single-subject analysis (see section 3.2.1.3.) within the context of the general linear model (Friston *et al.*, 1995b). The four fMRI sessions were modelled separately in each subject. Event-related BOLD responses were estimated voxelwise by modelling the onsets of each event as delta functions convolved with a synthetic HRF (Friston et al., 1998a). Separate regressors were entered into the design matrix for each of the four stimulus types (pooling stimuli indicating a movement of the index finger or little finger), for the oddball stimuli, for invalid events and for the six realignment parameters. A single event was considered invalid if there was either no response during the execution task or a subject responded to a stimulus (except for an oddball stimulus) during the observation task. Regression coefficients (parameter estimates) for all regressors were estimated using least squares within SPM2 (Friston et al., 1995b). To estimate relative BOLD signal increases in response to the different stimulus types and tasks, condition-specific effects were tested in each participant using the appropriate linear contrasts of the parameter estimates for the HRF regressors, resulting in a statistical parametric map (SPM) containing a *t*-statistic for each voxel.

Individual contrast images from the 1st level were raised to the 2nd level group analysis. They entered into a 2 x 4 factorial within-subjects ANOVA, including factors

'task' (2: observation, execution) and 'stimulus type' (4: finger movement only, moving dot, finger movement, colour change). The random effects analysis was corrected for potential non-sphericity of data.

Areas showing significant change in BOLD signal were identified using a voxel-level threshold of $p < .05$ corrected for multiple spatial comparisons according to the FDR method implemented in SPM2 (Genovese et al., 2002).

Functional activations were localised anatomically with reference to the cytoarchitectonic probability maps implemented in the anatomy toolbox in SPM2 (Eickhoff *et al.*, 2005) and the cytoarchitectonic and neuroanatomic *Talairach Daemon* (*TD*) database as incorporated in the *WFU Pickatlas* (v. 2.0; Maldjian *et al.*, 2003), also in SPM2.

On the basis of previous fMRI studies (Iacoboni et al., 2001; Iacoboni et al., 1999; Koski et al., 2003), a preferential neuronal response to finger movements was expected in the pIFG and aIPL. Given this a priori hypothesis, we applied small volume correction (SVC) for the left and right pIFG and aIPL to increase the sensitivity of the statistical analysis for these pre-defined regions. SVC was performed by centring up a sphere with a radius of 20 mm on the stereotactic coordinates which showed peak activation during the imitation of finger movements relative to the execution the same movements in response to static spatial cues as reported by Iacoboni et al. (2001, 1999) and Koski et al. (Koski et al., 2003). If a region was found to be activated in both fMRI studies, coordinates of peak activations in corresponding areas were averaged. Given the fundamentally bilateral organisation of the putative human mirror system (Aziz-Zadeh *et al.*, 2006), the left inferior parietal peak was also used to define the centre for SVC in the right hemisphere. The following coordinates were used as centre coordinates for SVC: x = -51, y = 11, z = 17 for left pIFG, x = 55, y = 11, z = 22 for right pIFG, x = -56, y = -29, z = 31 for left aIPL, and x = 56, y = -29, z = 31 for right aIPL (mean coordinate mirrored to the left

hemisphere). For all other brain regions, whole brain correction for multiple comparisons was performed.

Behavioural data

A one-way repeated-measurements ANOVA was calculated on mean RT and error rates from the execution sessions, with 'stimulus type' (4: finger movement only, finger movement, moving dot, colour change) as within-subject factor. Data obtained for the index and little finger was pooled in the ANOVA model. *F*-tests were corrected for non-sphericity. Planned comparisons (paired *t*-tests) were performed with *p*-levels adjusted for multiple comparisons.

Two participants had to be excluded from analyses as their over-all rate of behavioural errors exceeded the criterion of 10% for any stimulus-by-task condition or in total, respectively. Thus, 17 subjects (nine females; 21 to 36 years, mean age 25) were included.

3.4. Hypotheses

Assuming that simple finger movements specifically activate the human mirror neuron system, BOLD signal was expected to increase in the inferior frontal and inferior parietal cortex, and in the related superior temporal cortex, during both the imitation and observation of human finger movements. Increases should be present compared to the baseline as well as relative to the static and moving control stimuli.

As observation of animate movement is supposed to invoke the motor representation of the corresponding movement and make it available for execution instantaneously, we predicted that imitative responses to finger movements (irrespective of

whether combined with a moving dot or not) would be faster than responses to the other stimulus types.

We furthermore expected the stimuli involving movement as compared to static cues to lead to increased BOLD signal in higher order visual areas in the lateral temporo-occipital cortex: the V5/hMT-complex (Dumoulin *et al.*, 2000) that is known to process visual motion, and the extrastriate body area (EBA) which was found to selectively process human bodies and body parts, with even stronger response to moving stimuli (Downing *et al.*, 2001). As motor performance (i.e. limb movements) was found to modulate EBA activity (Astafiev *et al.*, 2004; Jackson et al., 2006), BOLD response should be more pronounced during imitation/execution compared with observation.

3.5. Results

Behavioural data

Errors

Over-all mean percentage of errors was 1.7 % (range 0.5 – 3.1 %). Only 0.5 ± 0.56 % of all trials (range 0.0 – 1.8%) were invalid (i.e. misses in execution trials or false alarms in observation trials) on average. This suggested that subjects did not experience difficulties in performing the task and kept attention to it. In line with that, the ANOVA revealed only a trend towards a main effect of stimulus type ($F(3,48) = 2.5$, $p = 0.078$). Error rates for the non-moving stimuli were numerically higher than those for the moving stimuli (mean error rate for colour change: 4.2 %, moving dot: 2.0 %, moving finger: 2.2%, moving finger & dot: 2.0 %). However, post hoc tests between stimulus types did not reveal significant differences.

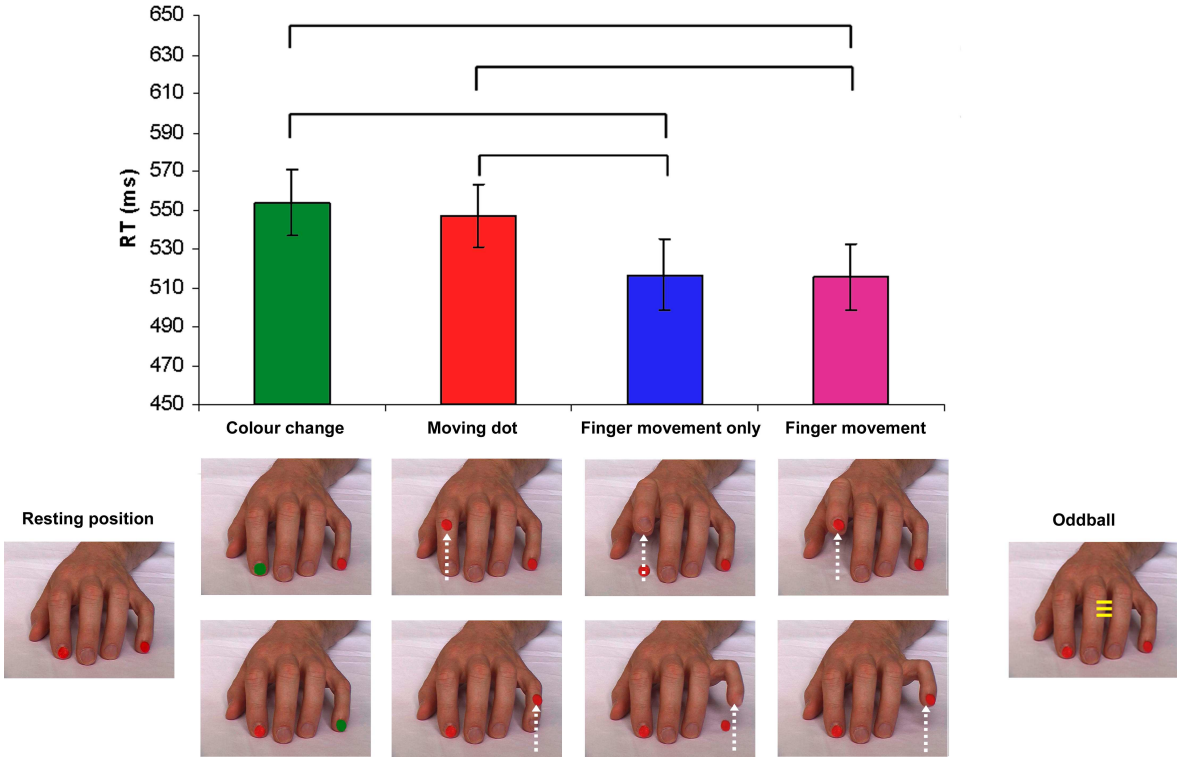

Fig. 3.4. fMRI experiment: Reaction times and picture stimuli. Upper part: Reaction time (mean ±standard error of mean) as a function of stimulus type during the observation-execution condition. Significant differences ($p < .001$) are indicated by brackets. Lower part: Visual stimuli presented during fMRI. Resting position (leftmost picture): a picture of a static left hand with red dots on the tip of the little and index finger was shown as a baseline condition. Four types of visuospatial stimuli (middle columns) were presented at the position of the index finger (top row) or little finger (bottom row): a colour change from red to green, a moving dot, a finger movement only with the dot remaining static, or a finger movement (from left to right). Each sequence consisted of 12 picture frames. The dotted arrows symbolise the upward movement. Occasionally, three horizontal lines were presented in the centre of the static hand as an oddball (rightmost picture).

Reaction times

In line with our hypotheses, there was a main effect of stimulus type ($F(3,48) = 21.2$, $p < .001$). As expected on the basis of previous studies (Brass et al., 2001a; Brass et al., 2000; Kessler et al., 2006), planned comparisons (Fig. 3.4) revealed that subjects were significantly faster at imitating animate movements (moving finger: 517 ± 65 ms.; moving finger & dot: 516 ms, ± 69.98) versus executing a response to a non-moving spatial cue (colour change: 554 ms, ± 70.01 ms). Imitative responses were faster to both a finger movement alone (mean difference: 37 ms, $t(16) = -5.7$, $p < .001$) and to a finger movement

with a dot attached (mean difference: 38 ms, $t(16) = -6.4$, $p < .001$). Moreover, imitation was faster than execution of responses to inanimate moving objects (moving dot: 547 ± 76.16 ms), whether participants imitated a moving finger only (mean difference: 30 ms, $t(16) = -4.7$, $p < .001$) or a combined finger & dot movement (mean difference: 31 ms, $t(16) = -5.4$, $p < .001$). There was no significant difference between responses to a moving dot and a static spatial cue (colour change). Responses to both types of finger movement stimuli were also matched in terms of mean RT.

fMRI data

Main effects of observation conditions

When the observation task was contrasted with the baseline (observation of a static hand), considering all stimulus types (except for the oddball), BOLD signal increase was found predominantly in occipital and temporo-occipital areas of both hemispheres. These comprised lower (BA 17/18) as well as higher order visual areas. Peak activations were located at the temporo-occipital junction (Fig. 3.5; Table 3.1), corresponding to coordinates reported for V5 (Dumoulin et al., 2000) and the EBA (Downing et al., 2001). Significant activations were also found bilaterally in the inferior parietal cortex, including the anterior intraparietal sulcus, in the inferior frontal cortex, and in the right superior temporal cortex (Fig. 3.5; Table 3.1). There was furthermore signal increase in the superior parietal cortex and the lateral part of the upper cerebellum bilaterally.

Table 3.1. fMRI experiment: Main effects of observation conditions. Local maxima within inferior fronto-parietal, superior temporal and temporo-occipital regions of interest showing significantly increased activation during the observation conditions versus the baseline. Small volume correction was applied for the bilateral posterior inferior frontal gyrus (pIFG) and the anterior inferior parietal lobule (aIPL). See text for centre coordinates. Whole brain correction was performed for all areas outside the pIFG and aIPL. A threshold of $p < .05$ was adopted, FDR-corrected for multiple spatial comparisons (cluster extent threshold ≥ 10 voxels), unless significance at an uncorrected $p < .001$ is indicated by an asterisk. In the table, frontal and parietal peaks are listed above the dashed line (SVC applied), temporal and occipital peaks are listed below (whole brain correction). Within each region, left hemisphere peaks are listed first. Peak coordinates for which effect size of changes in BOLD signal are illustrated in Fig. 3.6 are underlined.

Region	**Side**	**MNI-coordinates (mm)**			**Z-value**
		x	**y**	**z**	
Main effect of observation across all stimulus types					
Posterior inferior frontal gyrus	Left	-51	15	9	3.02
Posterior inferior frontal gyrus	Right	48	15	6	3.11*
Anterior inferior parietal lobule	Left	-54	-36	48	6.49
Anterior inferior parietal lobule	Right	60	-24	45	4.51
Posterior superior temporal gyrus	Right	69	-33	15	4.53
Inferior occipital gyrus	Left	-48	-72	-3	> 10.00
Inferior occipital gyrus	Right	57	-69	-3	> 10.00
Main effect of observation of a colour change					
Posterior inferior frontal gyrus	-	-	-	-	-
Anterior inferior parietal lobule	-	-	-	-	-
Posterior superior temporal gyrus	-	-	-	-	-
Inferior/middle occipital/temporal gyrus		-	-	-	-
Main effect of observation of a moving dot					
Posterior inferior frontal gyrus	Left	-57	18	0	3.06*
Posterior inferior frontal gyrus	Right	51	12	3	2.48*
Anterior inferior parietal lobule	Left	-54	-33	48	4.50
Anterior inferior parietal lobule	Right	60	-27	42	3.51
Posterior superior temporal gyrus	Right	69	-33	15	3.31
Inferior occipital gyrus	Left	-51	-72	-9	6.78
Inferior temporal gyrus	Right	57	-69	-3	6.68

Region	Side	MNI-coordinates (mm)			Z-value
		x	y	z	
Main effect of observation of a moving finger only					
Posterior inferior frontal gyrus	-	-	-	-	-
Anterior inferior parietal lobule	Left	-42	-39	39	3.35*
Anterior inferior parietal lobule	Left	-51	-33	48	3.05*
Posterior superior temporal gyrus	-	-	-	-	-
Inferior temporal gyrus	Left	57	-69	-3	6.76
Middle occipital gyrus	Right	-42	-69	0	6.11
Main effect of observation of a moving finger					
Posterior inferior frontal gyrus	Left	-60	15	3	4.26
Posterior inferior frontal gyrus	Right	48	18	6	3.85
Anterior inferior parietal lobule	Left	-57	-33	36	5.34
Anterior inferior parietal lobule	Right	57	-33	39	4.06
Posterior superior temporal gyrus	Right	66	-42	12	4.08
Middle occipital gyrus	Left	-45	-69	3	7.04
Middle temporal gyrus	Right	51	-66	0	7.72
Main effect (observation-execution) of responses to the oddball stimulus					
Posterior inferior frontal gyrus	Left	-39	3	12	> 10.00
Posterior inferior frontal gyrus	Right	51	12	3	> 10.00
Anterior inferior parietal lobule	Left	-45	-30	45	> 10.00
Anterior inferior parietal lobule	Right	63	-21	27	> 10.00
Posterior superior temporal gyrus	-	-	-	-	-
Middle temporal gyrus	Left	-51	-63	3	6.65
Middle temporal gyrus	Right	57	-51	3	7.30

A more detailed examination of the stimulus-specific activation patterns in the inferior fronto-parietal ROIs showed that a significant increase in BOLD signal in the pIFG was present only in one stimulus condition: when participants observed a finger movement the left and right pIFG (pars opercularis) were active (Fig. 3.5 and 3.6; Table 3.1). Observing a moving dot led to a trend activation of the same inferior frontal clusters ($p_{SVC} < 0.001$, uncorrected; Fig. 3.5; Table 3.1). However, neither the observation of a colour change nor

a moving finger alone increased regional activity in pIFG (even at an uncorrected threshold of $p_{SVC} < 0.01$).

Likewise, the aIPL was only activated by two stimulus types: both the observation of a finger movement and the observation of a moving dot led to a bilateral increase in BOLD signal in the supramarginal gyrus (Fig. 3.5; Table 3.1). When participants observed a finger movement only a trend activation was detectable ($p_{SVC} < 0.001$). Observing a colour change did not activate the supramarginal gyrus (even at a liberal threshold of $p_{SVC} < 0.01$, uncorrected).

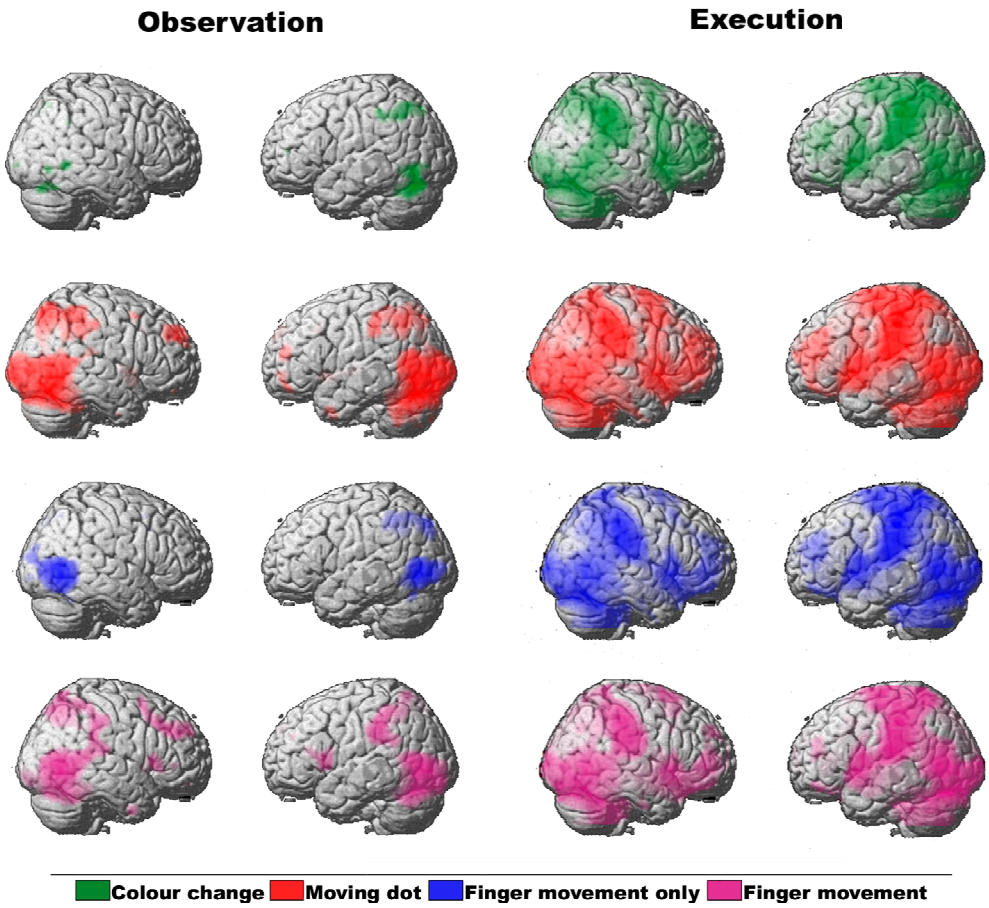

Fig. 3.5. fMRI experiment: Main effects of observation and execution conditions. Statistical parametric maps (SPMs) showing increases in BOLD signal at the group level during the different observation (two left columns) and execution (two right columns) conditions. For illustrative purposes, SPMs are superimposed on single subject surface renderings (SPM standard) and thresholded at $p < .001$, uncorrected for multiple comparisons. Each row of SPMs represents activations for one single stimulus type. The colour-coding of the SPMs is identical to the coding of the columns in Fig. 4.4 (reaction times) and Fig. 4.6 (effect size of BOLD signal change). From top to bottom: green = colour change; red = moving dot, blue = finger movement only, pink = moving finger.

An increase in BOLD signal in the right posterior superior temporal cortex was confined to the observation of a moving dot and a moving finger (Fig. 3.5; Table 3.1). When participants observed a colour change or a finger movement alone, there was, however, no increased superior temporal activity. Significant temporo-occipital activation in the V5/EBA region was present in all observation conditions (Fig. 3.5; Table 3.1).

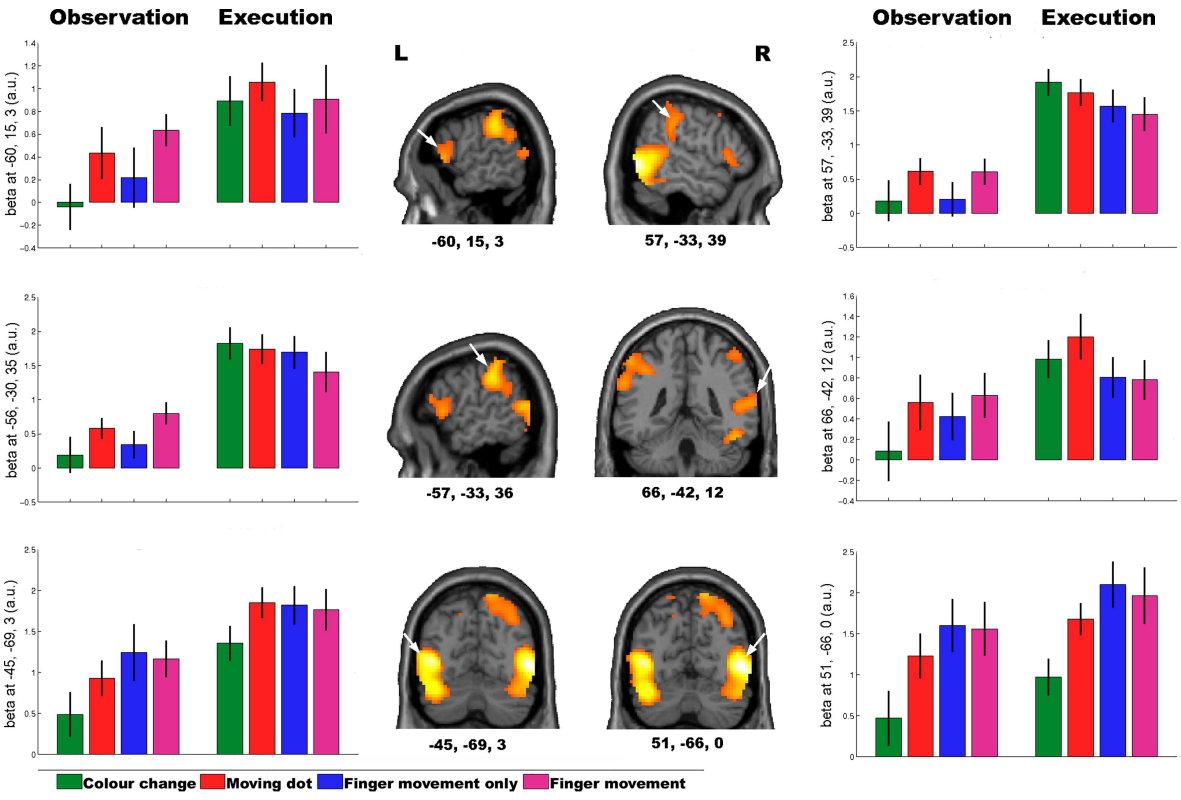

Fig. 3.6. fMRI experiment: Effect size of changes in BOLD signal during the observation and execution conditions. The columns depict the beta weight values/parameter estimates (group mean +/- standard error of mean) for the eight experimental conditions. The colour coding of the columns is identical to the coding of the columns in Fig. 3.4 (reaction times) and Fig. 3.5 (surface renderings of main effects). Left graphs: parameter estimates of left hemisphere peaks. Right graphs: parameter estimates of right hemisphere peaks. Middle panel: activations in regions of interest in the main effect of observing a finger movement ($p < .05$, FDR-corrected for multiple spatial comparisons; the corresponding peak activations are underlined in Table 3.1). Suprathreshold voxels are superimposed on sagittal or coronal sections (SPM standard), respectively. Left hemisphere peaks are shown in the left middle panel, right hemisphere peaks are shown in the right middle panel. Peak voxels in regions of interest are marked by white arrows. Activity profiles are given for a single voxel of peak activation each: left frontal operculum (top left), left inferior parietal lobule (middle left), left temporo-occipital junction (area V5/EBA; bottom left), right parietal operculum (top right), right superior temporal gyrus (middle right), and right temporo-occipital junction (area V5/EBA).

Main effects of execution/imitation conditions

When compared with the baseline condition, the execution/imitation conditions (Fig. 3.5; Table 3.2) elicited increased activity in occipital and temporo-occipital areas corresponding to those activated during observation. Peaks were located at the lateral temporo-occipital junction in V5 and the EBA. There was also widespread bilateral parietal activation, including the parietal opercula, the supramarginal gyrus, the intraparietal sulcus, the posterior superior parietal lobule and the precuneus. Activity in the frontal cortex was observed in the supplementary motor area (SMA), the hand area of the left primary motor cortex (frontal clusters clearly comprised the M1 region, although local activation maxima were mostly located more rostrally in the premotor cortex), the dorsal and ventral premotor cortex, and the prefrontal cortex of both hemispheres. Moreover, BOLD signal increased in the bilateral anterior insular cortex and, subcortically, in both hemispheres of the upper cerebellum, the caudal putamen and the thalamus.

Examining the stimulus-specific activation patterns in the inferior fronto-parietal ROIs revealed a stimulus-independent bilateral activation of the frontal opercular cortex, the ventral premotor cortex, the supramarginal gyrus and the parietal operculum (including the pIFG and aIPL, Fig. 3.5 and 3.6; Table 3.2). Activation in the inferior fronto-parietal cortex was comparable in magnitude for responses to the different stimulus types (Fig. 3.5; Table 3.2), regardless of whether participants observed a biological finger movement or not.

There was also activation of the posterior superior temporal cortex in all execution conditions. However, due to very extensive coherent clusters of suprathreshold activation (see Fig. 3.5), discrete peaks could not be identified within the superior temporal ROI.

Table 3.2. fMRI experiment: Main effects of execution conditions. Local maxima within inferior fronto-parietal, and temporo-occipital regions of interest showing significantly increased activation during the execution conditions versus the baseline. Small volume correction was applied for the bilateral posterior inferior frontal gyrus (pIFG) and the anterior inferior parietal lobule (aIPL). Whole brain correction was performed for all areas outside the pIFG, aIPL. A threshold of $p < .05$ was adopted, corrected for multiple spatial comparisons (FDR) (cluster extent threshold ≥ 10 voxels) unless significance at an uncorrected $p < .001$ is indicated by an asterisk. In the table, frontal and parietal peaks are listed above the dashed line (SVC applied), temporal and occipital peaks are listed below (whole brain correction). Within each region, left hemisphere peaks are listed first.

Region	Side	MNI-coordinates (mm)			Z-value
		x	y	z	
Main effect of observation-execution across all stimulus types					
Posterior inferior frontal gyrus	Left	-39	0	12	> 10.00
Posterior inferior frontal gyrus	Right	57	15	3	> 10.00
Anterior inferior parietal lobule	Left	-57	-21	21	> 10.00
Anterior inferior parietal lobule	Right	60	-33	39	> 10.00
Middle temporal gyrus	Left	-48	-66	3	> 10
Middle temporal gyrus	Right	54	-63	-6	> 10
Main effect (observation-execution) for responses to a colour change					
Posterior inferior frontal gyrus	Left	-39	0	12	> 10.00
Posterior inferior frontal gyrus	Right	48	15	3	6.37
Anterior inferior parietal lobule	Left	-57	-21	21	> 10.00
Anterior inferior parietal lobule	Right	66	-33	27	> 10.00
Middle temporal gyrus	Left	-48	-63	3	> 10
Inferior temporal gyrus	Right	57	-54	6	7.55
Main effect (observation-execution) for responses to a moving dot					
Posterior inferior frontal gyrus	Left	-48	6	3	> 10.00
Posterior inferior frontal gyrus	Right	63	15	12	5.60
Anterior inferior parietal lobule	Left	-57	-21	21	> 10.00
Anterior inferior parietal lobule	Right	66	-18	30	> 10.00
Middle temporal gyrus	Left	-45	-63	3	> 10.00
Inferior temporal gyrus	Right	54	-63	-6	> 10.00
Main effect (observation-execution) for responses to a moving finger only					
Posterior inferior frontal gyrus	Left	-39	0	9	> 10.00
Posterior inferior frontal gyrus	Right	60	15	3	5.86
Anterior inferior parietal lobule	Left	-57	-24	21	> 10.00
Anterior inferior parietal lobule	Right	69	-30	27	> 10.00
Middle temporal gyrus	Left	-48	-66	3	> 10.00
Inferior temporal gyrus	Right	54	-66	-3	> 10.00

Region	Side	MNI-coordinates (mm)			Z-value
		x	y	z	
Main effect (observation-execution) for responses to a moving finger					
Posterior inferior frontal gyrus	Left	-39	3	9	7.61
Posterior inferior frontal gyrus	Right	60	15	3	4.33
Anterior inferior parietal lobule	Left	-57	-24	21	> 10.00
Anterior inferior parietal lobule	Right	66	-30	24	7.26
Middle occipital gyrus	Left	-51	-72	0	> 10.00
Inferior temporal gyrus	Right	57	-69	-3	> 10.00
Main effect (observation-execution) for responses to the oddball stimulus					
Posterior inferior frontal gyrus	Left	-51	6	3	> 10.00
Posterior inferior frontal gyrus	Right	57	15	3	> 10.00
Anterior inferior parietal lobule	Left	-57	-27	36	> 10.00
Anterior inferior parietal lobule	Right	63	-21	27	> 10.00
Middle temporal gyrus	Left	-54	-66	-3	> 10.00
Inferior temporal gyrus	Right	57	-57	-6	> 10.00

In general, observation-execution led to a more pronounced activation of temporo-occipital and fronto-parietal regions than mere observation (Fig. 3.5 and 3.6).

Differential effects of stimulus types

According to the main objectives of the study, finger movement-specific increases in BOLD signal in inferior fronto-parietal human mirror neuron areas were assessed. In contrast to the hypotheses, no brain area showed stronger BOLD signal increase for a finger movement (finger movement or finger movement only) relative to the moving control cue (moving dot). Even the application of SVC to maximise the sensitivity the analysis for activation of the pIFG and aIPL yielded no preferential regional signal increase during the observation or the execution task.

Moreover, the observation or imitation of a finger movement (finger movement or finger movement only) did also not elicit a stronger signal increase in the pIFG or the right

aIPL relative to the non-moving control cue (colour change). Application of SVC revealed a left hemisphere peak in the aIPL only when contrasting the observation of a finger movement with the observation of a colour change (peak difference at x = -66, y = -33, z = -27; Z = 3.61). Contrasting the observation or execution of a finger movement only with a colour change yielded a bilateral increase in BOLD signal in the lateral temporo-occipital cortex, covering the EBA and the area V5.

To obtain the neuronal correlate of the observed RT effects, regional changes in BOLD signal during imitative responses to both types of finger movements (moving finger and moving finger & dot) were contrasted with those during motor responses to both control cues (moving dot and colour change). In contrast to our hypotheses, there was no preferential activation of inferior fronto-parietal mirror neuron areas with the imitation conditions. Application of SVC for the pIFG and aIPL also yielded no regional differences. Lowering the threshold to an uncorrected threshold of $p < .001$ yielded only trend activation outside of the ROIs, located at the right temporo-occipital junction (covering area V5 and the EBA).

The reverse contrast (control cues – finger movements; see Fig. 3.7), however, yielded trend increases in BOLD signal (significant at an uncorrected p-level of .001) with the control cues relative to the finger movements in the anterior insular cortex in both hemispheres (peak difference at x = -36, y = 18, z = 9; Z = 4.24, and x = 36, y = 27, z = 0; Z = 3.58), bilateral clusters in the posterior intraparietal sulcus (peak difference at x = -27, y = -57, z = 48; Z = 3.55, and x = 30, y = -60, z = 42; Z = 3.32), activation of the anterior cingulate cortex (peak difference at x = 12, y = 21, z = 36; Z = 3.28), as well as activation of the right ventral premotor cortex (peak difference at x = 45, y = 6, z = 33; Z = 3.89) (Fig. 3.7). The left insular and the right ventral premotor peak were located within the pre-defined frontal ROIs, however they actually did not belong to the pIFG.

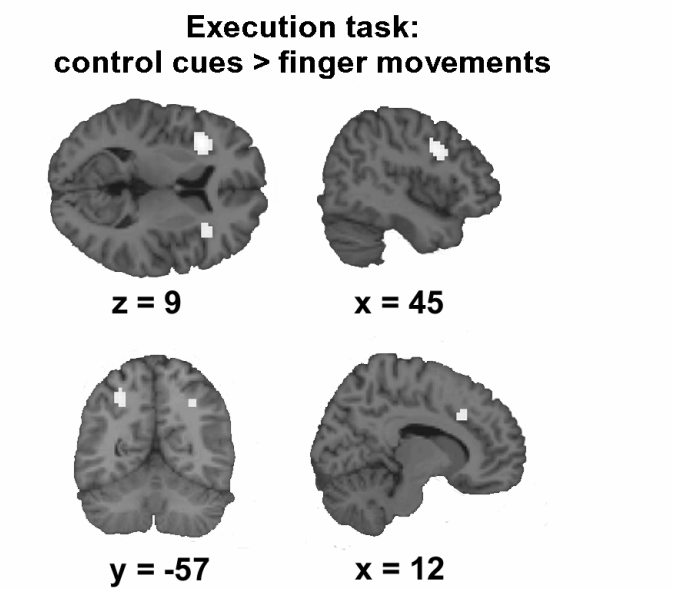

Fig. 3.7. fMRI experiment: Responses to both control stimuli (a colour change or a moving dot) compared with imitative responses to finger movements (finger movement or finger movement alone). Statistical parametric maps (SPMs) showing increases in regional BOLD-signal with the control stimuli relative to the finger movements. Voxels activated during the execution task are superimposed on transversal, sagittal, and coronal and sections, respectively ($p < 0.001$, uncorrected for multiple comparisons). Adapted from Jonas et al. (2007) © 2007 Elsevier Science.

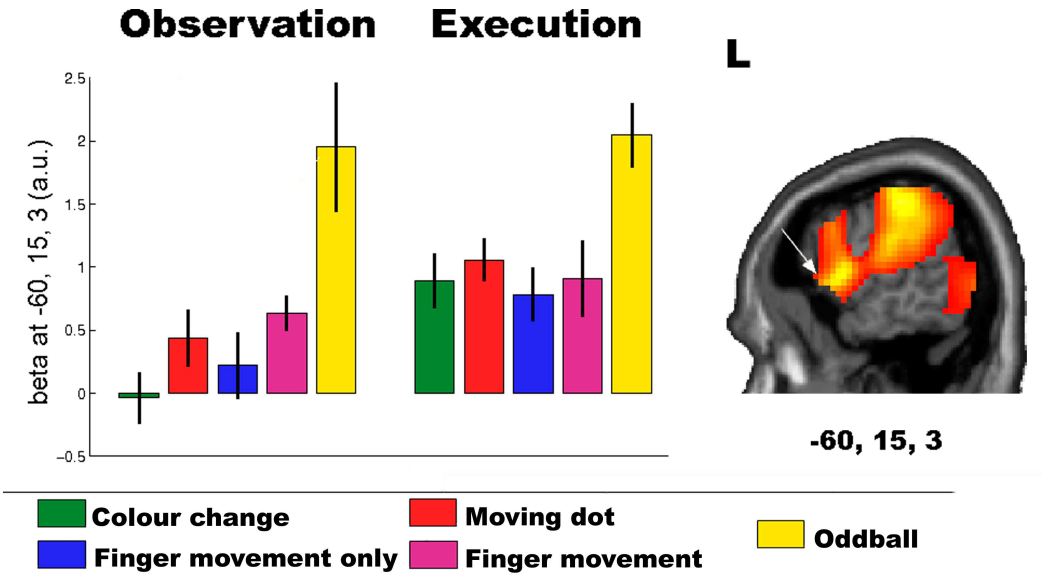

Fig. 3.8. fMRI experiment: Parameter estimates (group mean ± standard error of mean) of the activation maximum in the left frontal operculum. Left part: bar plots showing beta weight values (group average) for the inferior frontal peak in all eight experimental conditions (visuospatial stimuli) plus the oddball conditions. The peak voxel is taken from the main effect of observing a finger movement ($p < .05$, FDR-corrected for multiple spatial comparisons; the corresponding peak activation is underlined in Table 1). Parameter estimates for the observation and the execution task which correspond to the same stimulus type are filled with the same pattern. Right part: Main effect of the oddball. Results of a one-sample t-test for both oddball conditions observation and execution are shown. Activated voxels are superimposed on a sagittal section ($p < .001$, uncorrected for multiple comparisons).

None of the differential linear contrasts yielded a preferential activation of the pSTS for the observation or imitation of finger movements relative to the control cues (or vice versa).

After including the oddball trials in the second-level ANOVA, we found that the oddball condition produced a prominent bilateral activation of the pIFG and aIPL during the OBS and EXE task (Table 3.1 and 3.2). Parameter estimates revealed that the generation of a motor response to the oddball resulted in a stronger increase in BOLD signal in the inferior fronto-parietal cortex than any other experimental condition (Fig. 3.8).

3.6. Discussion

Behavioural results

In agreement with previous studies on imitation of simple intransitive finger movements that used static spatial control stimuli (e.g. Brass et al., 2000), participants were faster at imitating a finger movement than at responding to a non-imitative static control cue (a colour change). Moreover, imitative responses were also faster than responses to a dynamic-spatial control stimulus, i.e. a dot that moved "biologically" along the same trace as the moving finger. This confirmed the results of RT Experiment 1 and 2 (chapter 2), as well as the behavioural findings from a recent MEG study conducted by my colleagues in Düsseldorf (Kessler et al., 2006) where two of the presently used picture stimuli were employed in a two-alternative choice reaction task (combined finger-dot movement and moving dot). To re-iterate, these findings altogether demonstrate that the RT advantage for imitative responses is actually not due to the unspecific movement component per se that is present in imitative cues (finger movements) as well as in non-imitative dynamic stimuli (moving dot). Furthermore, in line with RT Experiment 4 (chapter 2) the present study

again demonstrates that the behavioural effect is not attributable to differences in perceptual salience between the imitative and the control stimuli: a combined finger-dot movement and a less salient isolated finger movement yielded the same RT advantage in comparison to control cues, while RTs to the two imitative stimuli were virtually identical. Likewise, a "redundancy gain"-like effect, due to the presence of multiple simultaneous targets (here: finger plus moving dot) was ruled out as an explanation for the RT advantage. Moreover, statistical comparisons between total error rates in the different stimulus conditions showed that speed-accuracy trade-off was not a problem.

The facilitation of responses following the observation of biological finger movements is compatible with the concept of a direct matching or AOEM mechanism for simple intransitive finger movements in humans (Iacoboni et al., 1999).

fMRI results

Imitation

Contrary to expectations, the faster responses to imitative cues were not paralleled by an increased activity in fronto-parietal mirror neuron areas, or in the related superior temporal cortex. Although spatially compatible (specular) imitation of simple intransitive finger movements consistently activated the pIFG, the aIPL and the pSTS, imitative movements elicited no extra-activity in these areas relative to non-imitative movements cued by the control stimuli. Thus, results are at variance with previous fMRI results that demonstrated specific "mirror activity" in putative mirror neuron areas of the inferior fronto-parietal cortex, and related activation of the pSTS, during imitative finger movements (Iacoboni et al., 2001; Iacoboni et al., 1999; Koski et al., 2003).

The preferential activation of the inferior frontal and parietal areas was interpreted as reflecting a direct matching of observed and executed movements during imitation, with

respect to motor or somatosensory information, respectively. Related superior temporal activation, on the other hand, was attributed to an interaction between higher-order visual descriptions of the to-be-imitated movement and reafferent copies of motor plans sent back from the inferior frontal mirror or direct matching area (Iacoboni, 2005a, 2005b; Iacoboni & Dapretto, 2006). However, taking into account the lack of a corresponding "mirror activity" in the present study and the recent behavioural findings of Bertenthal et al. (2006) raises the question to what extent AOEM processes actually contributed to imitation in the present study: using basically the same simple intransitive finger movement stimuli as Brass and colleagues (2001a, 2000) the authors tested the priming effects of common spatial coding and automatic imitation in combination, in opposition, and independently of each other (see section 4.2.1 for more details). The series of experiments provided converging evidence that automatic imitative response tendencies in fact contribute to facilitation of motor responses relative to a baseline. However, the facilitative effect of imitation was in fact smaller than the effect of spatial compatibility of stimuli and responses.

The contribution of stimulus-response mapping based on common spatial coding to specular imitation of finger movements might have been even enhanced relative to direct matching by the presently employed stimuli and design: the intermingled presentation of two spatially compatible imitative stimuli with two also spatially compatible non-imitative cues during continuous task performance, the use of very closely matched imitative and non-imitative cues, and the presentation of finger movements and control cues at relatively more lateralised positions than in previous studies, i.e. index – little finger as opposed to index-middle finger (see Iacoboni et al., 2001; Iacoboni et al., 1999; Koski et al., 2003). Although the imitative and non-imitative stimuli were matched for spatial SRC to control for its effects on RTs, a positive interaction between the priming effects related to direct matching and common spatial coding in trials requiring imitative responses cannot be

excluded: the priming effect of spatial compatibility might have been stronger for imitative than for non-imitative cues. Starting from the facilitation of imitative responses, it is reasonable to assume that the finger movement stimuli employed in the present fMRI study were processed differently from non-imitative cues. Direct matching processes (automatic imitation) or an interaction between direct matching and common spatial coding might have made the internal motor program more readily available than in the motor control conditions. Due to the specific processing of human body movement, imitative cues might have been also less ambiguous with respect to response selection than non-imitative cues.

Acknowledging that direct matching and spatial compatibility are confounded in specular imitation, associated neuronal activity consequently can reflect both mechanisms. This interpretation applies to previous imaging studies (Iacoboni et al., 2001; Iacoboni et al., 1999; Kessler et al., 2006; Koski et al., 2003; Koski et al., 2002) as well as to the present experiment employing a two-alternative choice reaction task that required visuospatial processing, spatial-to-motor mapping as well as shifts in spatial attention to lateralised cues. Since participants responded with their right hand while a left-hand stimulus was presented, the observed finger movements were always spatially compatible with the required motor response. In fact, the fMRI study by Koski et. al (2003) demonstrated a preferential neuronal response in the fronto-parietal mirror neuron areas for specular imitation compared with anatomical imitation, though both types of imitation involve direct matching of the observed and executed movement. Koski et al. attributed the differential increases in BOLD signal in inferior frontal and posterior parietal areas to a stronger engagement of the human mirror neuron system in direct matching of observed and executed movements during specular as opposed to anatomic imitation. However, the findings of Bertenthal et al. (2006) clearly favour the interpretation that the stronger activation of the inferior frontal motor area with specular relative to anatomic imitation was an effect of spatial compatibility between finger movement stimuli and motor

responses, or an effect of an imitation-specific interaction between spatial compatibility and direct matching of observed and executed movements. One has to keep in mind that the inferior frontal and parietal ROIs are first and foremost motor-related cortical areas, and secondly supposed to contain mirror neurons, i.e. to form core regions of a human mirror neuron system.

Regarding the task-related pattern of regional changes in BOLD signal, our findings are compatible with the assumption that response mapping based on common spatial coding and direct matching processes contributed to response facilitation: whereas there was no preferential response of inferior fronto-parietal mirror areas or the pSTS when contrasting regional BOLD responses to finger movements with BOLD responses to control cues, a cluster in the right lateral temporo-occipital cortex showed a trend towards a stronger activation with imitative responses. The activation comprised a compound cluster covering both area V5 and the EBA, which is in line with previous reports of a partial overlap of the EBA with area V5 in individual subjects (Downing et al., 2001). However, the maximum was nearer to localisations reported in studies on the EBA region (Astafiev et al., 2004; Downing et al., 2001) as compared to average coordinates published for the V5 region (Dumoulin et al., 2000). Although strict functional validation of the EBA is usually done by an initial localizer session comparing responses to the perception of body parts with responses to object perception, the pattern of activation observed in our study is in good agreement with the functional properties attributed to the EBA area: firstly, consistent activity throughout all conditions reflects the area's essential capability of recognising the presented hand as a human body part. Secondly, responses to moving fingers and also moving dots were much stronger than responses to the static hand, which is also in line with previous findings on enhanced responses in EBA (and V5 as well) for moving as compared to static human bodies and objects (Downing et al., 2001). Thirdly, we found

larger signal increase in the EBA during execution than during observation, corresponding to previous results which suggest modulation of activity in this region by movement planning and execution (Astafiev et al., 2004; Jackson et al., 2006).

Given its differential response to moving versus static human bodies and the influence of observers' actions, it has been discussed if the EBA might also be connected to a human mirror neuron or a direct-matching system, respectively. As suggested by Astafiev et al. (2004) and Jackson et al. (2006), the role of the EBA might be extended from visual processing of body parts to planning and execution of limb movements. By creating an "interpersonal registration", i.e. automatically mapping the visual representation of another's body to the body of the perceiver, which can then be used for motor planning, the EBA could provide initial input for a larger mirror system. Therefore, the increased activation of the right lateral temporo-occipital cortex with imitative cues in the present study might represent a neuronal correlate of direct matching.

On the other hand, the weaker response of the intraparietal sulcus, the anterior insula, anterior cingulate cortex, and right ventral premotor cortex to imitative cues as compared to non-imitative stimuli may be a neuronal correlate of common spatial coding. It is possible that the spatially compatible finger movements were more efficiently processed with respect to their spatial properties than the control stimuli, leading to a lower metabolic demand in the above areas.

Likewise, an interpretation in terms of a substantial contribution of common spatial coding in specular imitation of intransitive finger movements might also apply to the results of a recent companion MEG study (Kessler et al., 2006). Here, basically the same task and part of the stimuli as in the present fMRI experiment were used, having participants imitating a combined finger-dot movement or responding to a moving dot. Though an analysis of long-range synchronisation revealed no qualitative differences between finger and dot

movements in terms of the involved cortical areas, there was increased synchronisation during imitation of finger movements in a widespread network of brain regions, including the left ventral premotor and bilateral posterior parietal cortex. Observed RT advantages for imitation correlated with a relative increase in synchronisation of left ventral premotor cortex with right posterior parietal cortex and right temporal pole. Referring to previous fMRI studies on imitation (Iacoboni et al., 2001; Iacoboni et al., 1999; Koski et al., 2003) we considered direct matching processes mediated via premotor and parietal mirror neuron areas, in interaction with the temporal cortex, the basal ganglia and other motor areas (cerebellum, sensorimotor cortex) as a reasonable neuronal correlate of the observed behavioural advantage. However, re-considering the locations of the identified power sources, findings also are indeed compatible with a dominance of spatial stimulus-response mapping during imitation of finger movements: many of the sources were located in the right hemisphere and have been traditionally linked to visuospatial processing and attention (Behrmann *et al.*, 2004), rather than to processing of imitative stimuli exclusively. The temporal pole, the posterior cingulate cortex, and the medial portion of the right dorsal premotor cortex, showed no imitation-specific activation in previous studies and are not considered to be directly related to the human mirror neuron system. According to the given centre coordinate, the posterior parietal source might be best characterised as being located in the right intraparietal sulcus. The ventral premotor region, is the only of the identified sources which clearly constitutes a human mirror neuron region. Thus, the stronger synchronisation of the ventral premotor and the intraparietal area with imitative responses might indicate a functional interaction between the visuospatial network (as represented by the right intraparietal sulcus) and the AOEM system (as represented by the left ventral premotor region).

Observation

The mere observation of a simultaneous finger-dot movement activated the left pIFG, the aIPL bilaterally as well as the right superior temporal gyrus. However, the observation of the same intransitive finger movement without a dot attached was not sufficient to induce resonance activity in the inferior fronto-parietal nodes of the human mirror neuron system. These fronto-parietal regions also showed no stronger BOLD response during observation of finger movements relative to the moving control stimuli. When the observation of finger movements was contrasted with a static control cue, only the left aIPL was activated.

It is worth to point out that previous neuroimaging studies diverge concerning the extent to which the inferior frontal and parietal regions respond to the mere observation of intransitive movements. As mentioned above, the observation of simple intransitive finger movements activated inferior frontal mirror regions but failed to activate the aIPL (Iacoboni et al., 1999; Koski et al., 2003). Moreover, neuronal activation in the pIFG during the observation of simple intransitive finger movements did not exceed the activation produced by the observation of static visuospatial cues (Iacoboni et al., 1999).

In accordance with our results, two fMRI studies found no consistent activation in left pIFG during the observation of intransitive hand and foot movements (Jackson et al., 2006) or finger and face movements (Leslie et al., 2004). Positron emission tomography (PET) revealed inferior frontal activation when subjects observed pantomimes of object-directed actions but not during observation of meaningless intransitive hand movements (Decety et al., 1997).

Other neuroimaging studies underscore the importance of an action goal for the activation of the frontal mirror node. Johnson-Frey et al. (2003) demonstrated that observation of the achieved goal of a prehensile action is already sufficient to activate inferior frontal gyri, even in the absence of a dynamic movement. Koski et al. (2002) found a bilateral activation of the pIFG during imitation of a finger movement pointing towards a

visible goal (i.e. red dots presented on the surface below the fingers) as compared to a movement without an explicit goal. These findings are in agreement with the firing behaviour of mirror neurons in area F5 of the macaque's brain which are not activated unless an action is directed toward a visible or occluded object that was previously seen (Umiltà et al., 2001). However, the inconsistent response of the human mirror neuron system to intransitive movements cannot be interpreted as evidence that the mirror neuron system in humans is also exclusively tuned to object-directed actions.

Indeed, resonance activity in the inferior frontal and parietal ROIs could be detected in the present study during the mere observation of a moving finger. However, mirror activity was present only with the most salient type of finger movement stimulus, i.e. when a dot was attached to the moving finger, but not when the finger movement was presented in isolation (with the dot remaining static). It is commonly accepted that stimuli that are perceptually more salient automatically attract more visuospatial and motor attention. In turn, this may have a substantial impact on the magnitude and pattern of task-related activation in inferior frontal and parietal motor areas due to top-down processes. This issue has been ignored in previous studies on the mirror neuron system so far and has to be addressed systematically in future research.

Methodological considerations

First, it is worth to note that the present study was obviously sufficiently powered. Despite the lack of motor resonance in putative mirror neuron areas during the observation of an intransitive finger movement in isolation, activation of the pIFG and aIPL during the observation of combined finger-dot movement shows that the experimental procedure was sensitive enough to detect performance-unrelated motor resonance phenomena in these ROIs. Signal increase was detectable although the baseline condition, i.e. the observation

of a static hand (with static dots), against which the main effects of the different stimulus types were evaluated was rather strict in comparison to the one-coloured background used by Iacoboni et al. (2001, 1999) and Koski et al. (2003).

Regarding these studies, several modifications of the experimental design were introduced to minimise the influence of non-specific effects on mirror activity in the pIFG and aIPL. In previous fMRI studies, only one type of cue was presented during a single block, and consecutive blocks were separated in time by a period of rest without any stimulus presentation. The blocked imitation of finger movements might have produced an "imitative set" resulting in a condition-specific increase in BOLD signal during observation-execution of finger movements. However, reaction times in the present fMRI study revealed that the pseudorandom presentation of cue types did not corrupt the behavioural advantage for imitative cues. Thus, the absence of "mirror activity" in the pIFG and aIPL cannot be explained by a failure of imitative cues to prime the motor response.

The introduction of an oddball in our study is another deviation from previous studies. The oddball was associated with a motor response which differed from the responses required in all other conditions, in that it was more complex (lifting of all fingers vs. a single finger) and far less frequent. Although the oddball stimuli were quite rare as compared to the experimental conditions (ratio of 3:1), it is possible that the motor significance of stimuli might have been affected in the observation runs. In contrast to that, the imitation conditions should not have been influenced by the oddball conditions, as subjects were always prepared to respond in all trials. Most important, it is not reasonable to assume that the oddball affected motor preparedness differentially in different stimulus conditions during observation, thus levelling out latent mirror effects in inferior fronto-parietal areas. Furthermore, the markedly stronger response of the pIFG to oddball as compared to other stimuli, even in the execution task, can be regarded as a proof that the

activation of this motor related ROI did not show a ceiling effect due to tonic activation which would have rendered it impossible to detect differential “mirror” effects.

In order to match the stimuli as closely as possible, hand- and dot-objects were present in all stimulus types. When participants responded to the stimuli, they responded to a dot in most of the cases during the execution task, regardless of whether the dot was moving or not or whether it was attached to the fingernail of a moving finger: (i) a moving dot, (ii) a finger movement with a dot attached, (iii) a colour change of a dot, i.e. in virtually 75% of the experimental trials. Thus, one may argue that participants might have focused their attention always on the dot, as an efficient strategy to optimise their responses. As a consequence, the finger movement itself would have been attended less than the dot. This might explain the lack of differential activations in the inferior frontal and parietal regions showing a signature of “mirror”-activity. However, behavioural results clearly argue against this assumption, as responses to the isolated moving dot were significantly slower than responses to the isolated moving finger.

Finally, it remains open to what extent our synchronisation analyses on imitation on the basis of MEG measurements and the present analysis of fMRI-measured BOLD contrast are directly comparable. Comparative studies indicate that hemodynamic and electrophysiological measures rather complement each other: whereas fMRI measures hemodynamic changes that reflect the metabolic demand generated by neural activity, electric and magnetic evoked responses are affected by the synchrony of neural activity (see Hari *et al.*, 1997). Thus, hemodynamic signals might reflect primarily late event-related responses that can be modulated by feedback connections, while early MEG response may even be generated by a small set of neurons that fire in synchrony but generate a minimal metabolic demand. For example, Furey *et al.* (2006) in their study on attentional modulation of perception of faces and houses, revealed that cortical responses

as measured with fMRI versus MEG were divergent in a time window from 0 to approximately 200 ms after stimulus onset, but corresponded afterwards: attention (to faces versus houses) strongly modulated the face-selective fMRI hemodynamic responses in fusiform cortex, inferior occipital and superior temporal sulcal cortex as well as later category-related MEG responses. However, attention had no effect on an early face-selective cortical MEG response. This suggested that the category-related hemodynamic responses in fusiform cortex were due primarily to the late responses measured with MEG, with little contribution of the early MEG response in essentially the same locations.

In our MEG analysis (Kessler et al., 2006), an early synchronisation network with connections peaking prior to 300 ms after stimulus onset was supposed to mediate the RT advantage for imitative response. Furthermore, the correlation between the amount of synchronisation between the left premotor region, the right intraparietal sulcus and right temporal pole with the RT advantages for the imitation of biological movements was observed also in an early time window (100-250 ms after stimulus onset). Thus, event-related differences in BOLD signal change might have failed to capture early and transient differences in inter-regional synchronisation which could be detected by MEG. Finally, one has to keep in mind that the MEG method has a much lower spatial resolution as compared to fMRI. Thus, the localisation of the power sources cannot be considered equivalent to peak activations detected with fMRI.

In conclusion: adopting the view that both observation and imitation of human movement are strongly influenced by context factors which favour specific bottom-up processes and top-down strategies, different experimental procedures might lead to different processing of the perceived movement (c.f. Williams et al., 2006). Consequently, factors beyond “animacy/biologicity” affected our results, especially spatial compatibility of stimuli and responses and stimulus salience. In contrast to the observation of transitive action, the mere

observation of simple intransitive may not be “by default” sufficient to elicit task-related changes in BOLD signal in fronto-parietal human mirror neuron areas. Likewise, the imitation of intransitive finger movements does not necessarily lead to “mirror activity” in these areas when compared to observation-execution of matched visuospatial control stimuli. It can be proposed, instead, that the processing of finger movement stimuli is strongly influenced by experimental context factors as the adopted design (even-related vs. blocked stimulus presentation) and the exact correspondences versus differences between significant features of experimental and control stimuli (e.g. corresponding spatial characteristics vs. different “biologicity/animacy”). Behavioural and imaging data suggest a more tenuous and variable involvement of AOEM in the behavioural advantage for imitation of simple intransitive finger movements than previously assumed.

4. General discussion

After providing a summary of the behavioural and neuroimaging results presented in this dissertation (section 4.1.), I will make the attempt to draw some general conclusions on observation-execution of biological movement starting from these and related findings. Hypotheses concerning the cognitive processes which may underlie behavioural effects of observed on executed biological movement will be discussed in section 4.2.1. Section 4.2.2. deals with the role of the human mirror (neuron) system in the neural network underlying observation-execution of biological movement. Finally, proposals concerning possible functions of a link between movement observation and execution will be considered (section 4.3.).

4.1. Results of the present studies

The results of the present series of four behavioural experiments (chapter 2), demonstrating automatic effects of observed biological finger movements, are well in line with a number of previous findings on response priming by human body movements (for reviews see Blakemore & Frith, 2005; Brass & Heyes, 2005). The use of simple intransitive human finger movements as stimuli allowed for assessing effects of observed biological movement independent from influences of real or virtual objects, as in transitive actions (Bekkering et al., 2000; Buccino et al., 2001; Wohlschläger & Bekkering, 2002). Furthermore, the specificity of effects for animate movements was evaluated in comparison with strictly matched control cues, controlling for spatial and kinematical stimulus characteristics. Two-alternative choice RT experiments, using single-stimuli (RT Experiments 1 and 4) and priming/cueing paradigms (RT Experiments 2 and 3), revealed effects of observed on executed finger movements, comprising immediate as well as delayed effects and their temporal dynamics.

Summed up, the observation of an intransitive finger movement automatically elicits an imitative response tendency in the perceiver. This response tendency leads to a facilitation of a corresponding (i.e. the same) response if released immediately (as observed in the single-stimulus RT experiments, and in the fMRI study). However, if the response has to be withheld by the participant due to the requirements of the situation or task (i.e. in the present S1-S2 experiments) facilitation turns into an inhibition of the congruent response. Paralleling effects of non-biological priming stimuli, the time course of facilitation and inhibition induced by biological movement is also influenced by expectancies regarding the occurrence of the go-/instructive stimulus. In the present priming studies, no facilitation of congruent responses (PP) was observed. Inhibition of congruent finger responses was consistently present with a short SOA of 533 ms. In contrast, a facilitation of incongruent responses was obtained with an SOA of 1200 ms only in the second but not in the first priming study. Re-focused motor preparation after the initial period of response inhibition might be responsible for the lack of this "secondary" facilitation phenomenon in the second priming study. Motor preparation might have been drawn away from the fingers' target orientation with increased likelihood of S2 to appear, i.e. at the 1200 ms interval when it constituted the longest SOA in the first priming study.

A two-alternative choice reaction task paralleling the single-stimulus RT experiments also was used in combination with event-related fMRI. Task-related regional changes in BOLD signal during observation and execution of simple intransitive finger movements were contrasted with perceptual and motor control conditions presenting spatially and kinematically matched control cues.

Contrary to previous fMRI studies, the behavioural advantage for immediate responses to single finger movement stimuli was not accompanied by a preferential "mirror activity" in inferior frontal and parietal human mirror neuron areas in the present fMRI

experiment. A trend activation observed in the right lateral temporo-occipital cortex might be interpreted as a correlate of direct matching. However, increased activation of the posterior intraparietal sulcus, the anterior insula, anterior cingulate cortex, and the right ventral premotor cortex with non-imitative motor responses relative to imitative responses also indicates a more efficient (thus less energy-consuming) spatial processing of imitative as compared to non-imitative stimuli.

4.2. General conclusions

4.2.1. Processes underlying behavioural effects of observed biological movements

The present studies permit conclusions with respect to the effects of very simple, intransitive movements. Of note, some authors proposed a distinction between the processes underlying visuomotor transformation of different types of biological movement:

Rizzolatti et al. (2002) distinguished between “low-“ , and “high-level resonance mechanisms”, according to which type of sensory code elicits resonance activity in those motor-related areas where either *movement forms* or *action goals* are coded. Low-level resonance, on the one hand, was supposed to be an effect of the *form* of an observed biological movement (i.e. its kinematical aspects). “Response facilitation”, defined as a selective enhancement of motor responses that are already in the imitator’s repertoire (c.f. Byrne, 1994), was assumed to be a behavioural manifestation of such low-level resonance. High-level resonance, on the other hand, was supposed to rely on the representation of the *goal* of an action (e.g. grasping an apple). Observed actions which differ in kinematical characteristics but accomplish the same goal would all activate the same action/goal code. High-level resonance was assumed to underlie the phenomenon of “true imitation”, in the sense of learning a new behaviour and precisely reproducing the movements that lead to the perceived behavioural goal (c.f. Byrne & Tomasello, 1995). In contrast to the low-level

resonance mechanism, the purpose of high-level resonance during imitation was assumed to be action understanding (see section 1.3.). According to how Rizzolatti et al. (2002) defined the term “goal”, i.e. to indicate the aim of a transitive action in which the effectors interact with the external world, the RT effects observed in the present experiments would be interpreted as response facilitation due to low-level resonance mechanisms. Accordingly, they would not imply that participants achieved the internal description of an action goal (i.e. recognised it as such) and used it to organise their behaviour.

Based on behavioural interference effects that are specific to observed biological movement (e.g. Brass et al., 2001a; Craighero et al., 2002; Kilner et al., 2003) and on neurophysiological studies on the human mirror system, Blakemore and Frith (2005) proposed at least three levels of “mirroring” processes: at the lowest level (i) automatic “motor contagion” arises from the observation of any animate movement, irrespective of whether it is object-related or not. Motor contagion is supposed to lead to imitative response tendencies. The resulting effects are assumed to be responsible for facilitation and interference effects. At the next higher level of mirroring processes (ii), transitive actions are processed. Finally, at the highest level of mirroring processes (iii), the intentions of movements are mirrored.

Blakemore and Frith used the distinction between intransitive and transitive movements to explain systematic errors that were observed in behavioural studies on imitation in children (Bekkering et al., 2000; Wohlschläger *et al.*, 2003). On the one hand, children show a preference for mirror (specular) imitation. If a model in front of a child moves its right hand to the left across the midline, the child will imitate the movement with its left hand, also crossing the midline. However, if the model’s movement has an obvious goal, e.g. to pick up an object on its left with the right hand (crossing the midline), the child in front of the model will pick up the object on its right with the right hand (avoiding to cross the midline). Blakemore and Frith regarded these imitation errors in children as

resulting from the combination of two processes: (i) motor contagion that primes the motor system to reproduce the observed movement, and (ii) affordance that primes the motor system of the observer to interact efficiently with the object. As adapted from Gibson (Gibson, 1966), the concept of object affordances indicates parameters for motor interaction that are signalled by sensory cues without the invocation of high-level object recognition processes.

According to Blakemore and Frith's view, the behavioural effects observed in the present experiments would be regarded as effects of motor contagion. Like the concept of AOEM, motor contagion comprises an automatic activation of the motor representation of an observed movement.

In contrast, automatic effects of observed objects would be interpreted as resulting from object affordances. There is behavioural evidence that visual properties of objects related to actions have an influence on different parameters of movement execution, i.e. RTs and kinematical properties (Craighero *et al.*, 1999; Craighero et al., 1996; Edwards et al., 2003). Visuomotor priming of grasping actions was shown even for observed drawings of hand action irrelevant objects (Craighero et al., 1996). In an object interference task conducted by Wohlschläger and Bekkering (2002), subjects were required to imitate downward movements of the left or right index finger. In one condition, the observed finger touched one of two dots on a table either ipsi- or contralaterally. In a second condition, the same movements had to be imitated in the absence of target objects. It turned out that the presence of dots significantly reduced the onset of required ipsilateral finger movements and increased the use of the wrong finger when contralateral movements were required. Wohlschläger and Bekkering inferred from their results that human imitation behaviour is driven by objects. Relating their behavioural findings to neurophysiological evidence, they further hypothesised that the mirror neuron systems in monkeys and humans

are functionally and anatomically equivalent, and that human imitation is based on a human mirror neuron system.

Furthermore, associating these findings with the above described “contra-/ipsi-“ errors in children’s imitative behaviour, Wohlschläger and Bekkering concluded that the recognition of a movement or action is strongly affected by its effects. They proposed that imitation entails representing an observed action as a set of goals (or *action effects*; see also section 1.3.). However, according to their view, goals are not confined to objects, but can also be positions in space, agents, movement paths, or other salient features (such as an open versus closed hand). One feature (i.e. the main goal) always wins over other features as far as accuracy is concerned. This main goal then automatically activates the motor program that is most strongly associated with its achievement. Consequently, mirror neuron-based imitation in humans would not be restricted to transitive movements.

Therefore, contrary to the view adopted by Rizzolatti (Rizzolatti et al., 2002) and Blakemore and Frith (Blakemore & Frith, 2005), the imitative behaviour required by the subjects in the present studies might have implied “higher level” mirroring or resonance processes as well. Although the to-be-imitated movements were intransitive, participants might have represented the selection of the correct effector (i.e. finger) and the accurate reproduction of the movement path as goals of their imitative responses.

Apart from the question which level or type of mirroring process was elicited by the presently employed intransitive finger movements, the observed automatic effects of intransitive movements can be attributed to a mechanism which automatically (pre-) activated or primed the motor representation corresponding to the observed movement.

Using different spatially and/or kinematically matched control stimuli (i.e. lateralised colour change vs. moving dot) allowed for excluding potentially confounding

factors which are not specific for a biological movement but may also be present in inanimate visual stimuli:

importantly, the behavioural data altogether indicated that the general movement component is not the crucial factor to which effects can be attributed. This is even more evident in the behavioural results of the fMRI study, showing that the animation of the dot object does not lead to response facilitation relative to motor responses to a static object (that changes its colour).

Furthermore, according to the behavioural results of RT Experiment 4 and the fMRI study, it is unlikely that the mere difference in stimulus salience between the (original) finger movement (where a dot is attached to the fingernail) and the moving dot or the colour change caused the RT advantage. However, a confound of stimulus salience and factors "biologicity" or "animacy" may actually be present in every behavioural and neurophysiological experiment that contrasts observed human body movement with other visual stimuli. Obviously, the human brain processes biological movement as a special category of motion (see Blakemore & Decety, 2001; Giese & Poggio, 2003). Consequently, a higher capacity of animate movement to draw attention might well be responsible for a more efficient processing of this type of stimulus as compared to any other type. The putative evolutionary background of the human brain's sensitivity to biological movement is discussed further in section 4.3.

Behavioural effects of finger movements were evaluated against effects of visual control stimuli that were also spatially compatible with responses. Thus, differential effects relative to spatially compatible control stimuli can not be attributed to spatial stimulus-response compatibility per se. Nonetheless, there is evidence that response facilitation by observation of intransitive finger movements, as evaluated to a baseline, can be to a considerable part a function of spatial compatibility of movement stimuli and

corresponding responses. Adapting the SRC set-up of Brass et al. (2000; see section 1.4.), Bertenthal et al. (2006) systematically assessed the contribution of automatic imitative response tendencies and spatial compatibility to facilitation and inhibition of responses. In a first experiment with spatially compatible stimuli (left-hand finger movements and symbolic cues) and responses (right-hand finger movements instructed either by the imitative or the symbolic stimulus) they were able to replicate automatic effects of observed finger lifts on reaction times of executed finger movements. There was a facilitation of congruent and an inhibition of incongruent finger movements, even when responses were instructed by the symbolic cue. However, when opposing effects of spatial compatibility and imitation in substituting the left-hand stimulus by a right-hand stimulus, the overall automatic effect of the spatially incompatible imitative stimulus (as evaluated with respect to a baseline) was reduced to one third of the effect induced by the original spatially compatible imitative stimulus. Moreover, the spatially incompatible imitative stimulus induced only facilitation of congruent responses, whereas the spatially compatible finger movement led to both facilitative and inhibitory effects. To assess the influence of the intention to imitate, the authors conducted a third experiment where participants were instructed to either imitate only, i.e. respond to the observed finger movement either with the identical finger, or match the observed and executed finger movement spatially. This rendered either the spatial or the imitative characteristics of the finger movement stimulus the irrelevant stimulus dimension. Both irrelevant stimulus dimensions exerted an effect on RTs, however, the overall effect was significantly larger when the spatial dimension was irrelevant as compared to when the imitative dimension was irrelevant.

As already considered in section 3.6., these findings may lead to the conclusion that in previous studies (e.g. Brass et al., 2000) as well as in the present experiments not only direct matching/AOEM, but also spatial stimulus-response mapping operated during visuo-motor transformation of observed finger movements into imitative responses. Actually, the

results of Bertenthal et al. (2006) suggest a very strong effect of the spatial component on imitative responses. Moreover, these findings offer a reasonable explanation for the human tendency towards imitation in a mirrored rather than in an anatomically correct mode, which is especially marked in early childhood (Bekkering et al., 2000): whereas specular imitation includes both direct matching of observed and executed movements as well as spatial compatibility, anatomical imitation does not involve spatial compatibility.

Based on the results of a series of simple RT experiments, Brass et al. (2001a) hypothesised that the singular properties of biological movement and its concurrently existing unspecific spatial properties induce qualitatively different processes: in the first study, participants executed pre-instructed finger movements (either a finger lift or a finger tap) in response to finger movement stimuli (showing either a finger lift or tap). In a second experiment, a square moving up or down on a one-colour background with identical kinematics and amplitude as the finger lift or tap was introduced as a second type of go-stimulus. The main results of the first two studies were (i) a general RT benefit for responses to finger movements as compared to moving squares, (ii) a compatibility effect i.e. shorter RTs for finger movements which were executed in response to compatible as compared to incompatible stimuli, (ii) an interaction between the type of go-stimulus (finger vs. square movement) and compatibility: only the observation of a compatible finger movement led to an RT advantage relative to an incompatible movement. Moreover, (iii) as revealed by analyses of RT-quintiles, compatibility effects for responses to finger movements increased with increasing RT. In experiment 3 participants responded either to the original finger movement stimuli or to stimuli which had been flipped upside down. The results confirmed that the reduction of the compatibility effect for responses to moving squares was not just due to the perceptual differences between square and finger stimuli: the movement type (lift vs. tap) contributed more to the observed compatibility effect than the movement direction in space (up vs. down). On the basis of the ideomotor theory (see

section 1.3.) and the above results, the authors proposed two ideomotor components or mechanisms which control action execution and mediate the influence of observed onto executed action: (a) a fast working movement direction component related to the spatial-dynamic action properties, i.e. classical SRC, (b) a slow working movement type component related to more complex properties of action, i.e. ideomotor compatibility. Whereas the direction component is activated by both a moving finger and a moving square, only human body movement is capable of activating the ideomotor component. This is because only with a finger movement there is a match between the perceived event and the representation of what the subject intends to do (i.e. the anticipation of the sensory consequences of the planned action).

Generalising Brass et al.'s assumptions to the present behavioural findings, both finger movements and moving dots might have activated the spatial-dynamic component, whereas only finger movements were capable of additionally inducing the ideomotor mechanism. In other words, common spatial coding (alias SRC) and AOEM (alias the ideomotor mechanism) might have positively interacted in observation and specular imitation of intransitive finger movements in the present studies. The intermingled presentation of spatially compatible imitative stimuli with also spatially compatible non-imitative cues during continuous task performance, the use of very closely matched imitative and non-imitative cues, and the presentation of finger movements and control cues at lateralised positions might have even enhanced the relative contribution of spatial SRC, especially in the fMRI study where a number of control stimuli were used. It is conceivable that, due to the additional impact of direct matching, the spatial characteristics of the finger movement stimuli were processed more efficiently than those of non-imitative stimuli. As a result, motor programs of responses might have been more readily available with imitative stimuli, or, alternatively, imitative cues were less ambiguous with respect to response selection than non-imitative cues. Such an assumption would be in line with a

facilitation of responses to spatially compatible biological finger movements as compared to other spatially compatible cues, as observed in the present experiments. Furthermore, the assumption of a more efficient, less energy-consuming processing of biological movement would be in line with the observed decrease in BOLD signal with non-imitative as compared to imitative stimuli in areas engaged in visuospatial processing.

Moreover, an interaction of direct matching and common spatial coding in the processing of finger movement stimuli would be readily compatible with the results of the present priming/cueing experiments: the S1-S2 studies revealed general effects of attentional orienting in space that were induced by observed finger movements and control stimuli as well, and modulations of priming effects that were specific to finger movement stimuli.

Trying to draw general conclusions with respect to the processes underlying effects of observed biological movements, spatial compatibility between stimuli and response seems to be a very influential factor in observation-execution of intransitive movements. According to Wohlschläger and Bekkering (2002), the reproduction of the exact movement path is represented as the (highest) goal in imitation of movements that do not involve interaction with an object. If an individual attempts to correctly reproduce kinematical characteristics of a movement, visuo-motor processing of spatial characteristics is consequently one of the most crucial aspects. In an experimental set-up with intermingled presentation of several visual stimuli with similar spatial properties, the influence of spatial processing might be even enhanced. Extending on these ideas, visual concordance or similarity between observed and executed movements might be far more important in the case of intransitive as compared to transitive movements. The latter are possibly rather (by default) represented in terms of an efficient interaction with the external world than in terms of their exact spatial-dynamic movement parameters. Consequently, the similarity

between human body movements and control conditions presented in an experimental situation would potentially have a higher impact on visuo-motor processing of intransitive as compared to transitive movements. These considerations lead to the hypothesis that direct matching/AOEM processes are qualitatively different with different types of biological movement, and might thus be sensitive to the influence of different context factors, e.g. spatial stimulus characteristics versus object affordances.

4.2.2. The role of the human mirror neuron system in observation-execution of biological movements

Starting from results of neuroimaging studies on imitation of intransitive and transitive movements (see section 1.5.), Rizzolatti and colleagues (Rizzolatti & Craighero, 2004; Rizzolatti et al., 2001) proposed that imitation of actions which are already present in the imitator's motor repertoire is mediated by a direct matching mechanism in human mirror neuron areas, especially in the pIFG. The mirror neuron system is considered to be involved in all stages of imitation, i.e. (i) the retrieval of an elementary movement (i.e. its internal sensory and motor representation) which is already achieved by observation (initially a link is made to the internal sensory anticipation, then the motor representation is re-activated), (ii) the construction of a sequence of elementary movements, and (iii) the fine tuning/modification of the movement or sequence of movements (Rizzolatti et al., 2001).

On the basis of single-cell recordings in macaque monkeys and functional brain imaging studies in humans, Iacoboni (2005a, 2005b; Iacoboni & Dapretto, 2006) furthermore proposed that the inferior frontal, inferior parietal and superior temporal cortex form a "core circuit" for imitation in the human brain. Within this network, the STS is supposed to

provide inferior parietal mirror neurons with a high-level visual description of the to-be-imitated movement. Visual information and somatosensory and motor information provided by the inferior parietal area reaches the inferior frontal mirror neurons, where the goal of the action is coded. Reafferent copies of the motor commands providing the predicted sensory consequences of the planned imitative movement are sent back to the STS. Here, a matching between the motor commands and the actual visual description of the observed action occurs. In an iterative monitoring process, the motor plan for imitation is adjusted until a sufficient congruence between the perceived movement and the motor plan is achieved. In other words, the STS creates an *inverse model* for the imitative action which input is the visual description of the desired sensory state (i.e. the percept of a self-produced action that is identical to the observed action), and which output or prediction is the motor command. The STS furthermore creates a *forward model* for imitation which input is the reafferent copy of the motor command from fronto-parietal mirror areas, and which predicts the sensory consequences of the planned imitative action. If the inverse-forward model pair predicts the selection of an efficient motor output, then a low error signal will be generated in the forward model, and the model pair will be reinforced.

While Iacoboni and colleagues (Iacoboni, 2005a, 2005b; Iacoboni et al., 1999; Koski et al., 2003), in line with Rizzolatti and Craighero (2004), suggested that a direct matching mechanism in frontal and parietal human mirror areas mediates imitation of even very simple intransitive movements, other authors have emphasised that the human mirror system distinguishes between different types of biological movements:

Blakemore and Frith (2005) proposed a mirror system that is extending beyond the commonly accepted cortical mirror neuron system. Within this enlarged mirror system, hierarchically organised “mirroring” processes (see also section 4.2.1.) are assumed to be mediated by different neural substrates: the authors suggested that only object-directed

actions have the property to induce “mirroring” or “resonance” phenomena in the mirror neuron system, because this system is hard-wired to transitive action as are mirror neurons in the monkey’s area F5. On the other hand, the neuronal system underlying low-level effects of motor contagion, i.e. response facilitation and interference induced by the observation of any animate movement, is assumed to have different functions than these mirror neurons.

Blakemore and Frith’s suggestions are in line with an earlier proposal by Rizzolatti and colleagues (Rizzolatti et al., 2002; but see Rizzolatti & Craighero, 2004). Till then, the authors assumed that parietal and frontal mirror neuron areas become active only if a task requires action understanding, which encloses the recognition of action intentions and the inference of action goals. If a task, however, does not require action understanding, then non-mirror regions are activated, including areas in the inferior and superior parietal lobule and other motor centres such as the precentral gyrus and the cerebellum (Decety et al., 1997; Grèzes et al., 1998; c.f. Rizzolatti et al., 2002). According to Rizzolatti et al. (2002), only transitive actions have a goal, are meaningful for this reason and sufficient to drive the high-level resonance mechanism mediated by frontal and parietal mirror neurons. Because every transitive action consists of individual movements, the observation of a transitive action should also activate the low-level resonance mechanism located outside the mirror system. Intransitive movements, however, which were classified as meaningless by Rizzolatti et al. (2002), would not be sufficient to elicit high-level resonance in mirror neurons. Assuming this, the lack of a preferential activation of inferior frontal and parietal areas during the observation and imitation of simple intransitive finger movements in the present fMRI study would be due to the fact that the employed movements did not have an explicit goal, i.e. there was no interaction with a target object. On the other hand, one might adopt a more abstract definition of an action goal as proposed by Wohlschläger and Bekkering (2002). According to the task instruction, the responses made by the subjects

had to accomplish a defined goal, i.e. to respond as quickly as possible, select the correct finger and make a movement that is identical to the observed movement. Assuming this, one would have expected mirror areas that are tuned to goal-directed action to respond also during observation-execution of the presently used intransitive finger movements.

The previous neurophysiological literature seems to be quite consistent regarding activation of the putative human mirror neuron areas during observation and imitation of transitive actions (see Rizzolatti & Craighero, 2004). However, regarding simple intransitive finger movements, behavioural and neuroimaging data suggest a more tenuous and variable involvement of the human mirror system in observation and imitation (see section 3.6.). Imitation-specific activation of the pIFG during observation-execution of intransitive finger movements varied across previous fMRI studies that used intransitive finger movements. On the one hand, two studies performed by the same group (Iacoboni et al., 1999; Koski et al., 2003) reported a relative increase in BOLD signal with imitative responses in left pIFG, aIPL, and the anterior intraparietal region. MEG (Kessler et al., 2006) showed that the imitation of intransitive actions was associated with time-dependent increases in inter-regional synchronisation within a large-scale functional network that, with the exception of a left ventral premotor region, consisted of cortical and subcortical areas that were not clearly located within human mirror areas. Finally, the present study as well as a recent fMRI study by Williams et al. (2006) found comparable neuronal activation with responses to imitative and non-imitative cues, but did not show a preferential response of the pIFG or aIPL to finger movement imitation.

Moreover, previous results are not conclusive regarding the extent to which the inferior frontal and parietal putative mirror regions respond to the mere observation of intransitive movements (see section 1.5.). In accordance with the results of the present fMRI experiment, two fMRI studies found no activation in left pIFG during the

observation of intransitive hand and foot movements (Jackson et al., 2006) or finger and face movements (Leslie et al., 2004). A series of experiments performed by one research group found that the observation of simple intransitive finger movements activated inferior frontal mirror regions but failed to activate the aIPL (Iacoboni et al., 1999; Koski et al., 2003). Furthermore, the magnitude of neuronal activation in the pIFG during finger movement observation did not exceed the activation produced by the observation of static control cues (Iacoboni et al., 1999), as opposed to an execution task.

One can conclude that observation and imitation of intransitive movement does not inevitably elicit a pattern of cortical "mirror activity" in premotor or parietal regions. However, simple intransitive movememts that are easy to execute constitute the first movements that newborns are able to imitate (Meltzoff & Moore, 1977). Therefore, if resonance of mirror neurons or regions is *essential* for imitative behaviour, as implied in the model of a core circuit for imitation proposed by Iacoboni (2005a, 2005b), then these circuits should be also recruited in imitation and observation of intransitive movements. Neurophysiological findings rather point out that mirror neurons *can* be involved in observation-execution of intransitive movements.

It is conceivable, as already acknowledged in chapter 1, that evolutionary processes might have led to a less specialised mirror system in humans as compared to monkeys. To account for the more complex demands on human behaviour, it is reasonable to assume that the processing of observed human movements is also substantially influenced by the specific context or situation in which it is embedded. Moreover, one can imagine that phylogenetic evolution from monkey to man did not only affect functional properties of the inferior frontal and parietal areas that are proposed to be homologue to areas F5 and PF in the monkey. According to the more complex demands on the human brain, a greater influence of inter-regional connections to other brain areas is reasonable.

Within such a mirror system, responses to simple intransitive movements might be even more capable of being influenced by experimental or situational context factors than resonance phenomena in response to object-directed actions (see also 4.2.1.). This might explain why findings concerning the responsiveness of fronto-parietal human mirror neuron areas to observation and imitation of intransitive movements seem to be less consistent than findings regarding transitive action. One might speculate that in a hierarchy of action goals as proposed in the goal-directed theory of imitation (Wohlschläger et al., 2003), the efficient interaction with an object, probably coded as an action goal in human mirror neuron areas (Rizzolatti et al., 2002), might be more robust against the influence of task instruction etc. than the reproduction of an intransitive movement. However, this hypothesis has not been tested systematically so far.

Recent research brought forward hypotheses about the role of mirror neurons in human imitative behaviour (see section also 4.3.) which emphasise the interplay of motor resonance in mirror neurons and cognitive and visuo-motor processes that are mediated by areas outside the putative mirror regions. Meltzoff and Decety (2003) suggested that mirror neurons indeed serve imitation, but imitation requires more than resonance between neural codes for action observation and execution. They assumed that the intention to imitate requires the individual to attribute goals and intentions to the observed movements. Consequently, biological movement is observed differently, according to the specific top-down strategies employed in an imitation situation. These cognitive strategies, which are influenced by factors as task instructions and control conditions in an experimental setting, are associated with frontal lobe function.

Williams et al. (2006) drew parallel conclusions from studies on imitation in autistic spectrum disorder patients and healthy subjects: they proposed that the mirror neuron system serves imitation function as a result of being embedded in a broader system of neural components. In more complex imitation situations (i.e. more complex than the

simple intransitive finger lifts employed in the study by Williams et al.), this system could contribute to the analysis of perceived movement and even to higher, social cognitive functions (see also section 4.3.). Visuomotor learning processes, associating previously learned motor actions with different visual stimuli, might rely on dorsal premotor and dorsolateral prefrontal cortex (Toni & Passingham, 1999). Temporo-occipital regions and the lingual gyrus might serve processing of visual movement: Astafiev et al. (2004) and Jackson et al. (2006) suggested that the role of the EBA might be to provide an automatic "interpersonal registration" as an initial input for a larger mirror system, i.e. to match the visual representation of another's and the perceiver's body (see section 3.6.). The present fMRI results support this hypothesis only in part, as activation of the temporo-occipital cortex was indeed stronger with the execution than with the observation task. Though, differential contrast did not reveal higher signal increases with finger movements as compared to control stimuli, i.e. no specific "mirror" pattern.

Furthermore, an important role of other motor-related areas in imitation has been discussed by Miall (2003) and Kessler et al. (2006). Their considerations extended on the account by Iacoboni (2005a, 2005b) who proposed the cortical core circuit to implement inverse as well as forward models. Miall (2003) proposed that the cerebellum might actually play a crucial role by providing the necessary motor parameters for the selection of an inverse model (during movement observation) and of a forward model (during later imitation/execution). Moreover, Miall assumed that the posterior parietal cortex rather than the ventral premotor region would actually be the critical interface between inverse and forward models due to its functional multimodality (i.e. visuo-spatial; sensori-motor). Although the temporal resolution of BOLD-fMRI is not sufficient to draw conclusions about the role of brain areas in inverse versus forward models, nonetheless, the present fMRI results support the assumption that the cerebellum might be important in movement observation and imitation: during the observation and the execution task, there was signal

increase in the upper cerebellum bilaterally. However, the cerebellum was not differentially active with observation/imitation of finger movements as compared to control stimuli. Kessler et al. (2006) performed a synchronisation analysis on MEG data recorded during imitation of simple intransitive finger movements. Taken together, their data implied (i) an early synchronising subnetwork specialised on observation-execution matching for biological movements, and (ii) a later synchronizing subnetwork that is most likely related to the control of imitation performance. The ventrolateral premotor cortex as well as the basal ganglia participated in the early subnetwork, the diencephalic areas possibly by selecting suitable motor programs that match the stimulus. The ventrolateral premotor cortex was found to be also involved in the later subnetwork, together with the right temporal pole and the posterior parietal cortex. The latter two regions were supposed to constitute important junctions for the integration of information from different sources in imitation tasks that are controlled for the movement component (i.e. as used by Kessler et al. and in the present studies) and involve a certain amount of spatial orienting of attention. Contrary to Miall's proposal, the cerebellum only seemed to play a role for the instantiation of the appropriate forward model in this imitation task. The data suggested a stronger involvement of diencephalic areas (i.e. the basal ganglia) at an early stage, which would encompass the selection of an appropriate inverse model. However, the authors also pointed out that the importance of the cerebellum might increase with more complex movements. Both the cerebellum and the caudal putamen were active during the execution task in the present fMRI study. This finding, though, does not allow to differentiate between the above hypotheses. Kessler et al.'s (2006) data furthermore indicated that the PPC indeed plays a crucial role during the early integration of perceptual and motor-related information, yet the vPMC seems to be more important for the transition between perception and action.

Taken together, especially experiments on observation-execution of simple intransitive finger movements indicate that imitation does not by "default" coincide with resonance in putative human mirror neuron areas. Although on the behavioural level, an RT advantage for imitative responses to finger movements is consistently reported across studies using different designs and control stimuli (see chapter 2), measures of correlated regional increases in BOLD signal are obviously influenced by the employed experimental protocol: a blocked (e.g. Iacoboni et al., 1999) as compared to an even-related stimulus presentation (as in the present fMRI study) might facilitate a cognitive set that enhances an imitation-specific increase in BOLD signal in fronto-parietal mirror neuron areas.

In contrast, reducing unspecific effects of perceptual salience on neuronal activity in fronto-parietal mirror areas by using equally salient and spatially as well as kinematically matched control stimuli (i.e. biologically moving objects) might also attenuate condition-specific differences in BOLD signal increase in these regions.

If observed and executed movements are spatially compatible as in specular imitation common spatial coding contributes to task-related changes in BOLD signal. Favouring spatial stimulus-response mapping through the use of similar spatial compatible control stimuli in an event-related experimental protocol, as in the present fMRI study, may further reduce imitation-specific activation in fronto-parietal mirror neurons areas.

This higher context-specificity of inferior fronto-parietal mirror activity during observation-execution of intransitive as compared to movements might be due to the fact that these two types of biological movement induce different kinds of mirroring processes. Whereas in intransitive movements primarily spatial-dynamic properties might lead to resonance of motor-related brain areas, effective interaction with objects might be predominantly effective in transitive actions. According to Rizzolatti et al. (2002) and Blakemore and Frith (2005), AOEM in intransitive movements would not comprise resonance of human mirror neurons (as in monkeys). However, assuming that even the

reproduction of kinematical movement characteristics can form a goal in imitation of movements (Wohlschläger & Bekkering, 2002), observation-execution of intransitive movements might involve activation of human mirror areas. In this respect, one might hypothesise that the goals implied in intransitive movements are represented in inferior parietal rather than in inferior frontal mirror areas. However, as laid out above, there is no conclusive evidence so far concerning an interaction between types of biological movement (transitive, intransitive) and mirror activity in frontal versus parietal areas. Here, mirroring or direct matching of the goals implied in intransitive movements might be more sensitive to specific characteristics of the observed movement and the situational context as well, leading to a more variable activation of inferior frontal and parietal mirror areas. As implied by the results of the present fMRI study, an enhancement of spatial visuo-motor transformation processes through the choice and mode of presentation of control conditions might attenuate imitation-specific resonance of mirror areas.

4.2.3. The role of the learning in observation-execution of biological movements

Finally, there is no evidence that the human mirror neuron system might be *dedicated* to imitation, i.e. that imitation was the function which favoured its evolution. In line with this, Rizzolatti et al. (2001) proposed that the purpose of the mirror neuron system is not imitation but action *understanding*. The fact that macaque monkeys do not show the capacity to imitate (Visalberghi & Fragaszy, 2001) even though they have mirror neurons might be regarded as another argument supporting this notion. However, the possibility of important functional changes during phylogenetic evolution from monkey to human remains. A human mirror system might even have evolved independently. Moreover, during the ontogeny of a human individual, its environment might make demands on its

brain that enforce the development of mirror neurons with more imitation-relevant functional properties than in a monkey.

In line with these considerations, generalist theories of imitation (e.g. the ideomotor theory and the common coding approach; see section 1.3.), assuming that imitation depends on general mechanisms of associative learning and motor control rather than on a special purpose mechanism, imply that the properties of mirror neurons are not innate. They rather suggest that mirror neurons acquire their properties through general learning mechanisms in the course of an individual's development (c.f. Brass & Heyes, 2005).

In line with that, a crucial role of learning mechanisms has been proposed for the mirror neuron system of the monkey: an initial visuo-motor link between the motor representation of an action as coded by premotor neurons and the corresponding visual action description as represented by temporal and parietal neurons might be established through an association between the motor command, the execution of the movement and the sight of an the monkey's own effector. This observation-execution match that is originally acquired in the first-person perspective then becomes progressively generalised to other's actions by experience (Rizzolatti & Luppino, 2001). Oztop and Arbib (2002) suggested a more elaborate model of how the mirror neuron system might learn the right associations between the classification of a monkey's own transitive movements and the movements of others: according to the "hand-state hypothesis", the basic functionality of monkey F5 mirror neurons is to elaborate appropriate feedback for opposition-space-based control of manual grasping of an object. The authors propose that mirror neurons first evolved to augment *canonical*[1] F5 neurons by providing visual feedback on the hand-state, i.e. on the relation between the shape of hand and the shape of the to-be-grasped object.

[1] Canonical neurons are another class of visuo-motor neurons coexisting with mirror neurons in the monkey area F5. They are active during execution of goal-directed actions and, unlike mirror neurons, respond to the mere sight of a manipulable object (see Rizzolatti et al., 1999).

The hand state encompasses data to determine whether the motion and preshaping of a moving hand conform to the grasp that is appropriate for the object's affordances. This code will work for how well another monkey's hand is moving to grasp an object, and it will work also for observing how the monkey's own hand is moving to grasp, allowing self-observation to train the system.

The finding that mirror neurons for tool use can develop during ontogeny in the monkey's ventral premotor cortex can be regarded as supporting the notion that the mirroring properties of mirror neurons are rather acquired than innate (Ferrari *et al.*, 2005).

Of course, the hand-state hypothesis can not explain how visuo-motor neurons might be trained to respond to intransitive movements that a human individual observes in another. However, corresponding associative mechanisms of visuo-motor learning might work in the human brain.

Results of behavioural studies that investigated the role of learning in human imitation have been broadly supportive of the assumption that the cortical connections mediating motor activation by action observation are formed through experience, rather than being innate.

Heyes *et al.* (2005) showed that automatic imitation (e.g. facilitation of hand opening or closing by observation of the corresponding gesture) can be abolished by a brief period of training. The training consisted of 72 incompatible trials, i.e. performing hand opening while observing hand closing and vice versa, 24 hours before testing. In contrast to participants who had received compatible training, the participants who had received incompatible training did not show a significant RT difference between compatible and incompatible trials in the test procedure. This finding suggests that the incompatible training, on the one hand, established inhibitory links between visual and motor representations of corresponding hand actions (opening–opening, closing–closing),

slowing responses on compatible trials by counteracting the effects of already existing excitatory links.

Recent behavioural findings by Press et al. (2005) corroborate the assumption that visuomotor priming of hand movements depends on cortical links established through associative learning, rather than on innate connections. As stimulus generalisation is a ubiquitous feature of associative learning, one would expect non-biological movements to elicit priming effects to the extent that they resemble the human movements observed during acquisition of the cortical connections which mediate priming. In line with this prediction, behavioural responses to compatible robotic stimuli were faster than responses to incompatible robotic stimuli. However, the compatibility effect was smaller as compared to that elicited by human stimuli. The behavioural results obtained in the present priming studies, comparing effects of real finger movements and "biologically" moving objects, might as well be interpreted in this way.

Furthermore, functional imaging studies demonstrated an influence of learned expertise in performing specific movements on task-dependent changes in BOLD signal during observation and imitation of these movements. In an fMRI study by Calvo-Merino *et al.* (2005), experienced capoeira dancers showed stronger activation in the premotor, parietal and pSTS regions when observing capoeira movements than when observing ballet movements, whereas ballet experts showed stronger activation in the same areas when observing ballet movements than when observing capoeira movements. Haslinger *et al.* (2005) tested professional pianist and musically naive controls during observation of piano playing and control movements (serial finger-thumb opposition). The pianist showed stronger motor activation than the control subjects when observing piano playing, however, the two groups did not differ when observing the control stimuli.

Moreover, physiological findings support the notion that imitation originally depends on experience of owns ones, rather than others', actions, which would be also in

line with the associative learning mechanism proposed for mirror neurons in the macaque monkey (Rizzolatti & Luppino, 2001). Using TMS, Maeda et al. (2002) showed greater facilitation of MEP size during observation of intransitive finger movements when the movements were presented in "self" or "first person" perspective (facing out from the observer) as contrasted with movements present in the "other/third person" perspective. There is, so far, no evidence that priming effects of observed on executed movements differ depending on the whether priming stimuli are presented in the first- or third-person perspective (c.f. Vogt et al., 2003). However, given the massive exposure to other people's movements in everyday life, the experience with body parts in both perspectives is likely to result into strong visuo-motor associations for both perspectives.

Finally, there is a controversy regarding the question whether newborns are actually able to imitate facial gestures or not (c.f. Heyes, 2001). If it was true that newborns can imitate facial gestures prior to having seen their own faces, this would not fit easily the assumption that observation-execution links are not innate but rather learned through experience with ones' own actions is. Based on the assumption of an inborn imitation capacity, Meltzoff and Moore (1997) proposed a special purpose mechanism for infant facial imitation (*active intermodal mapping*, AIM). According to this model, the visual representation of the movement that is observed with the intention to imitate is actively converted in to a supramodal representation which can be directly compared with the proprioceptive feedback of the infants' self-produced movements.

4.3. Why are observation and execution of biological movement linked to each other?

Apart from the issues of *how* (section 4.2.1. and 4.2.3.) and *where* (section 4.2.2.) observation and execution of biological movement are linked to each other, it is also worth asking *why* the human brain employs this way of information processing. In other words,

what advantages convey automatic effects of observed movements in others on the motor system of an individual?

From an evolutionary perspective, it might be very important to optimally perceive actions of biological agents (Premack & Woodruff, 1978) to generate the appropriate reaction to potential prey, enemy or mate as fast as possible. As the movement of an animate entity is one of the most important visual cues to identify it as animate (Schultz et al., 2005), phylogenetic evolutionary processes may have favoured the development of neuronal structures in the brain designed to specifically identify and react to characteristics of biological agents. However, evidence for basically unconscious mechanisms as discussed above, i.e. behavioural priming by observed biological movement or shared brain activations for movement observation and execution, does not exclude the possibility that processes which require more intentional control in the young individual become increasingly "automatised" during ontogeny.

Behavioural and neurophysiological studies suggest that the observation of human biological agents is more effective in generating motor activation than compared with any other type of stimulus. The perception of a specific biological movement interferes more with the execution of an incongruent movement when it is performed by a person than when it is performed by a robotic agent (Castiello et al., 2002; Kilner et al., 2003; Press et al., 2005; see section 2.1.). Similarly, neuroimaging studies indicate stronger motor activation or resonance while observing human movements than while observing movements of a robotic or "virtual" agent, or even biomechanically impossible human movements (Costantini et al., 2005; Perani et al., 2001; Tai et al., 2004; see section 1.5.).

It seems that observing biological movement optimally prepares the human motor system to act out the perceived movement. In fact, imitative response tendencies have been noted in studies of normal and pathological behaviour: during development, infants and

small children very often spontaneously imitate others. Involuntary imitative actions with explicit emotional or vegetative components (so-called “hot” actions as smiling or yawning) are also common in adults. These automatic tendencies may be socially relevant by contributing to the coordination of people’s behaviours, cooperation, and the development of affiliative tendencies (Dijksterhuis & Bargh, 2001).

Inappropriate overt manifestations of imitative response tendencies have been observed as *imitation behaviour* in patients with lesions to the fronto-medial prefrontal cortex or lateral prefrontal cortex (De Renzi *et al.*, 1996; Lhermitte *et al.*, 1986) or as *echopraxia* in patients suffering from the Gilles de la Tourette syndrome (Leckman *et al.*, 2001).

However, in everyday life adult and healthy people do not constantly tend to confuse observed movements with their own intentions and spontaneously imitate every movement they observe in a conspecific. There also is an important difference between infant behaviour and so-called *release behaviour* that can be observed in birds (Thorpe, 1963): typically, if one bird in a flock starts wing flapping, then the other birds repeat the observed movement. In contrast, imitative behaviour in infants is not simply due to response release, as it can be delayed by using a pacifier and is emitted subsequently when the response becomes possible (Meltzoff & Moore, 1977). Consequently, healthy humans are able to store the evoked response and to control its emission. There have to be dedicated mechanisms which prevent us from acting out putative response tendencies. These mechanisms, on the other hand, may be defective in patients showing imitation behaviour or echopraxia.

Using fMRI, suppression of imitative response tendencies automatically elicited by movement observation (i.e. an instructed movement had to be executed during observation of an incongruent movement) has previously been shown to activate anterior fronto-median cortex and right temporo-parieto-occipital areas (Brass *et al.*, 2005; Brass *et al.*, 2001b).

These are similar to those which have shown to be involved in distinguishing self- from etero-generated imitative action (Decety *et al.*, 2002), determining self-agency (Farrer *et al.*, 2003; Farrer & Frith, 2002) and perspective taking in action (Ruby & Decety, 2001). Thus, there seems to be a dissociation between brain regions responsible for the inhibition of imitative response tendencies and prefrontal regions known to be engaged in inhibition of proponent response tendencies per se, as are active in go/no go-tasks for example (e.g. de Zubicaray *et al.*, 2000).

Moreover, spinal mechanisms might also play a role in inhibiting overt repetition of observed behaviour: Baldissera (2001) demonstrated that H-Reflexes recorded from hand flexors increased in size during observation of finger extension (hand opening) and were depressed during observation of finger flexion (hand closing). The reverse was found for recordings from extensors.

Obviously, the existence of a very close link between observed and executed movement has costs, i.e. it can interfere with the execution of observer's current motor plans and also lead to socially inappropriate behaviour if not held at bay by dedicated inhibitory mechanisms. What advantages, however, might an AOEM mechanism have?

One proposal has been based on the assumption that the human mirror neuron system, in contrast to that of the monkey, codes also for intransitive movements that can form an action, rather than only for actions proper. It has been hypothesised that the evolution of such properties might account for the human capacity to learn by imitation, in contrast to nonhuman primates and apes (c.f. Visalberghi & Fragaszy, 2001). If a single elementary movement that is already present in the individual's motor repertoire has to be copied, then the activated representation can be readily used for reproduction. In imitation of a novel, complete action, however, i.e. "true imitation" (see Byrne & Tomasello, 1995), mirror neurons would decompose the movement into its constituting motor elements (see

Rizzolatti et al., 2001). The original sequence would then have to be re-constructed first before the motor output could be fine-tuned for reproduction. This recombination process has been proposed to essentially constitute learning by imitation and to be also a function of the mirror neuron system (Buccino et al., 2004b). Of note, the core circuit for imitation would not be sufficient to implement imitation learning. This form of imitative behaviour would rather require large-scale interaction between core mirror areas and other neural networks (Iacoboni & Dapretto, 2006). In line with this, the results of an fMRI study on observation, imitation and non-imitative execution of guitar chords (Buccino et al., 2004b) were interpreted as evidence that inferior parietal and ventral premotor mirror regions also subserve core processes in imitation *learning*. The authors concluded from their data, that the rostral inferior parietal lobule and the ventral premotor cortex represent the circuit that translates the observed action into their motor representations by motor resonance of contained mirror neurons. Additional activation of the anterior mesial cortices during the delay period between the observation and the execution phase in an imitation condition (where subjects observed a model performing a guitar chord and imitated the chord later) relative to a non-imitative execution condition (where the subjects observed a moving guitar neck and freely chose the chord they executed later) was interpreted as reflecting the selection of appropriate motor acts for subsequent execution. This activation was considered to represent an organising mechanism that guides the selection and recombination of motor elements in the frontal and parietal mirror regions.

Furthermore, it has been proposed that the “mirroring” of observed movements might facilitate communication (Rizolatti & Arbib, 1998), empathy (Carr *et al.*, 2003) and also so-called “theory of mind” functions (Gallese & Goldman, 1998; Jeannerod, 2001).

Theory of mind function would involve, on a lower level, the understanding of other people’s intentions from their actions. On a higher level, it would even comprise

understanding other people's minds. According to the "simulation theory of mind reading" (c.f. Gallese & Goldman, 1998) the attribution of mental states to other people is achieved by adopting their perspective and simulating their states (i.e. predicting/retrodicting their intentions by pretend states, respectively) by one's own mechanisms. As proposed by Gallese and Goldman, the capacity to simulate other people's mental states might have evolved from an AOEM system whose neural correlate are premotor mirror neurons. The internal imitation of other people's actions would trigger an action representation from which the underlying goals and intentions could be inferred on the basis of what our own goals and intentions would be for the same action. Thus, the mirror system would allow the observer to "get into the mental shoes of the target" (Gallese & Goldman, 1998).

However, the suggestion that imitation constitutes a core cognitive process required for the development of social cognitive ability (Meltzoff & Decety, 2003), including a theory of mind function, also implies that imitation actually requires more than resonance between neural codings for action observation and execution in a human mirror neuron system. Macaque monkeys have mirror neurons, but neither show a theory of mind ability nor evidence of imitation (Visalberghi & Fragaszy, 2001). Therefore, for a human mirror neuron system to serve an imitation function, either further cognitive abilities are required, or the system itself must have undergone evolutionary modification in some way. As stated above, Meltzoff and Decety (2003) proposed that imitation is also influenced by the attribution of goals and intentions, and a means for representing self–other relations.

Impaired imitative skills in infancy, on the other hand, may reflect a neurological deficit that could account for autistic syndromes. It has been proposed that in autistic spectrum disorder both social cognition and imitation might be affected by a dysfunction of the mirror neuron system (Iacoboni & Dapretto, 2006; Williams et al., 2006; Williams *et al.*, 2001). As concluded from their recent fMRI findings on imitation of finger movements in

autistic spectrum disorder patients and healthy controls, however, Williams et al. (2006) proposed that the mirror neuron system serves imitation function embedded in a broader system of neural component. Within such a large-scale network, the right temporo-parietal junction might be specifically associated with theory of mind function (e.g. Castelli et al., 2000).

5. Summary

Behavioural as well as neurophysiological data support the notion that the execution of human body movements and the perception of the same movements in other individuals are closely linked.

Automatic effects of observed movements on movement performance have been attributed to a common coding of movements in the perceptual and motor domain, enabling an action observation-execution matching (AOEM) mechanism that directly maps a perceived movement onto its internal motor representation. Common activation of a set of motor-related brain areas during both the observation and execution of biological movements is supposed to constitute the neural correlate of the AOEM mechanism. Specifically, inferior frontal and inferior parietal cortical areas are reported to constitute core regions of a human “mirror (neuron) system” that serves AOEM.

In a series of four two-alternative choice reaction time (RT) experiments, the present dissertation provides evidence for imitative response tendencies following observed simple intransitive finger movements. Using single-stimuli paradigms in RT Experiments 1 and 2 aimed at investigating immediate effects of observation on execution of corresponding finger movements. Priming/cueing (S1-S2) paradigms were employed in RT Experiments 2 and 3 to reveal delayed effects of an observed finger movement (S1) on the execution of a subsequent imitative movement (that is instructed and prompted by a second finger movement stimulus S2). Defined stimulus onset asynchronies (SOAs) of S1 and S2 were introduced to explore the time-course of effects. Strictly matched salient control stimuli were used in all behavioural studies, i.e. “biologically” moving objects that controlled for spatial and also kinematical stimulus characteristics. This permitted demonstration of

priming effects which were specific to the observation of real human body movement, and not attributable to the unspecific inherent motion component.

It was hypothesised that AOEM should generally facilitate responses to an animate finger as compared to an inanimate dot in all experiments. In the context of the S1-S2 paradigm, attentional orienting was expected with inanimate and animate movements, as both occurred spatially lateralised. AOEM processes, however, should only be induced by biological finger movement stimuli, leading to a specific modulation of effects of S1-finger movements.

Accordingly, results of single-stimuli experiments yielded immediate facilitatory effects of observed on executed finger movements. Priming/cueing experiments revealed delayed facilitatory and inhibitory effects of observed biological finger movements on subsequently executed finger movements. Patterns of effects depended on SOAs of S1 and S2.

Findings suggest that the observation of a biological movement leads to a transient activation of its internal motor representation. A facilitation of the corresponding response becomes manifest provided the resulting response tendency can be released immediately. Otherwise, facilitation rapidly turns into an inhibitory effect. Both movement-specific and unspecific facilitatory and inhibitory effects are similarly affected by temporal expectancies regarding the occurrence of the instructive/go-stimulus.

An event-related functional magnetic resonance imaging (fMRI) study was conducted in order to investigate the neuronal correlates of the immediate facilitatory priming effects of biological movement obtained in the present single-stimulus RT experiments. This experiment followed-up on previous fMRI studies which reported a preferential activation of putative human “mirror areas” in the inferior frontal and parietal cortex during imitation of intransitive finger movements as compared to motor control tasks. Task-related changes

in regional BOLD signal during the mere observation and imitation of simple intransitive finger movements were contrasted with the observation of control stimuli and the execution of finger movements in response to these control cues, respectively. The employed two-alternative choice reaction task paralleled the task required in the single-stimulus RT studies. To control for unspecific effects, different salient control stimuli were matched to finger movements with respect to either spatial or both spatial and kinematical properties (paralleling the behavioural studies). Event-related, intermingled presentation of different stimulus conditions in single trials was used to minimise neuronal activity related to cognitive sets.

Assuming that finger movements specifically activate the human “mirror system”, BOLD signal was expected to increase in the inferior frontal and inferior parietal cortex during both the imitation and observation of human finger movements. Increases should be present compared to the baseline as well as relative to the static and moving control stimuli. Due to AOEM, imitative responses to finger movements were expected to be faster than responses to other stimulus types.

In accord with previous and present behavioural results, participants were faster at imitating a finger movement than at performing the same movement in response to a static or a moving control stimulus. However, contrary to previous fMRI findings, the behavioural advantage was not paralleled by a difference in regional activity of inferior fronto-parietal “mirror areas” during the imitation/execution task. Moreover, during pure observation, BOLD signal in putative mirror areas was increased only when the finger movement was made more salient by attaching an object to it.

Thus, the present results lacked a functional signature of inferior fronto-parietal “mirror activity”. It was hypothesised that the specific experimental situation enhanced the relative contribution of common spatial coding of stimuli and responses to the observation-execution of intransitive finger movements, as compared to expected AOEM processes.

This might have been favoured by the intermingled presentation of closely matched finger movement and control stimuli which were all spatially compatible with required responses, and which occurred in lateralised locations. In line with that, the finding of an increased activation of the posterior intraparietal sulcus, the anterior insula, the anterior cingulate cortex, and the right ventral premotor cortex with motor responses to control stimuli relative to finger movements might indicate a more efficient spatial processing of biological finger movements as compared to control cues.

Taken together, the present behavioural and neurophysiological results suggest that AOEM or “mirroring” processes might differ qualitatively between intransitive and transitive movements. Whereas mirroring processes in motor-related brain areas induced by intransitive movements might rely primarily on spatial-dynamic properties of the movement, mirroring of transitive movements might rather be based on representations of the interaction between effectors and (objects in the) external world. Consequently, visuo-spatial and dynamic stimulus characteristics seem to have a higher impact on visuo-motor transformation processes during observation-execution of intransitive as compared to transitive movements. Moreover, a potentially higher interference between specific context factors of an observation/imitation situation and mirroring/AOEM processes which are elicited by intransitive movements might lead to a more variable engagement of inferior frontal and parietal “mirror (neuron) areas” in visuo-motor transformation of intransitive as opposed to transitive movements.

6. References

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7. Appendix

7.1. Abbreviations

AIP	anterior intraparietal area
ANOVA	analysis of variance
AOEM	action observation-execution matching
β	vector of parameter estimates
B_0	direction of the main magnetic field (*z*-axis) in MRI
B_1	direction of the radiofrequency pulse (*x*,*y*-plane) in MRI
c	vector of contrast weights
$CMRO_2$	cerebral metabolic rate of oxygen
(r)CBF	(regional) cerebral blood flow
e	vector of residuals
EEG	electroencephalography
EPI	echo-planar imaging
EXE	execution
fMRI	functional magnetic resonance imaging
FDR	false discovery rate
FWE	familywise error rate
FWHM	full-width-at-half-maximum
GLM	general linear model
GRF	Gaussian random field
H^1	hydrogen
HF	radiofrequency
HRF	hemodynamic response function
IFG	inferior frontal gyrus

IM	ideomotor theory
IOR	inhibition of return
IPL	inferior parietal lobule
M1	primary motor cortex
MEG	magnetoencephalography
MEP	motor evoked potential
MNI	Montreal Neurological Institute
MRI	magnetic resonance imaging
hMT	human (visual) motion area
OBS	observation
P	predictor variables/regressors
PET	positron emission tomography
PMd	dorsal premotor cortex
PMv	ventral premotor cortex
PP	positive priming
PPC	posterior parietal cortex
ROI	region of interest
RT	reaction time
S1	first/priming stimulus
S2	second/target stimulus
SII	somatosensory cortex
SMA	supplementary motor area
SNR	signal-to-noise ratio
SOA	stimulus onset asynchrony
SPM	Statistical Parametric Mapping
SPM{*T*}-map	image of *t*-values

SRC	stimulus-response compatibility
(p)STS	(posterior) superior temporal sulcus
SVC	small volume correction
T_1	relaxation time of longitudinal magnetisation
T_2	relaxation time of transversal magnetisation (idealised)
T_2*	relaxation time of transversal magnetisation (effective)
TE	echo time, between excitation and signal readout in MRI
TR	repetition time, between two excitations in MRI
TMS	transcranial magnetic stimulation
V5	visual (motion) area 5
VOI	volume of interest
X	design matrix
Y	vector of measured data

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