
Of men, monkeys, and machines.
Behavioral and neural correlates of goal understanding in humans and non-human primates

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By Aleksandra Kupferberg

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Munich,
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Supervisor: Prof. Dr. Stefan Glasauer
Second expert appraiser: Prof. Dr. Gordon Cheng
Third expert appraiser: Prof. Dr. Marco Iacoboni

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Systemic Neurosciences
LMU Munich

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List of abbreviations

AAL	Automated Anatomic Labelling
AIP, aIPS	Anterior Intraparietal Sulcus
ANOVA	Analysis of Variance
ASD	Autistic Spectrum Disorders
ATP	Adenosin Triphosphat
BA	Brodmann Area
BOLD	Blood Oxygen Level Dependent
DLPC	Dorsolateral Prefrontal Cortex
EEG	Electroencephalogramm
F5	Ventral premotor cortex in monkey
FDR	False Discovery Rate
fMRI	functional Magnetic Resonance Imaging
FOV	Field of View
FWHM	Full Width at Half Maximum
HRF	Haemodynamic Response Function
pIFG	Posterior Inferior Frontal Gyrus
IPL	Inferior Parietal Lobule
ISC	Intersubject Correlation Method
ITG	Inferior Temporal Gyrus
MFG	Middle Frontal Gyrus
MNI	Montreal Neurological Institute
MNS	Mirror Neuron System
fMRI	Functional Magnetic Resonance Imaging
MTG	Middle Temporal Gyrus
PFC	Prefrontal Cortex
PET	Positron Emission Tomography
PMC	Premotor Cortex
pSTS	Posterior STS
ROI	Region of Interest
RS	Repetion supression
SI	Primary Somatosensory Cortex
SII	Secondary Somatosensory Cortex
SMA	Supplementary Motor Area
SPL	Superior Parietal Lobule
SPM	Statistic Parametric Mapping
STS	Superior Temporal Sulcus
TE	Echo Time
TMS	Transcranial Magnetic Stimulation
TPJ	Temporo-parietal junction
TR	Repetition time

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Overview and summary

Over the past 15 years, neuroscientists and behavioral scientists have increasingly explored different constructs of social cognition such as intention understanding, morality, emotion processing and theory of mind[1]. The term social cognition is defined in various ways, but in the area of neuroscience it is often related to the capacity to understand other people and attribute intentions to them. Understanding the intentions of others and predicting their actions is the basis of social cognition and of high importance for any species living in groups because it is crucial for self-preservation and adequate social interaction. When observing someone, we automatically interpret her/his elemental movements in terms of goals, intentions, desires, and beliefs. This capacity emerges early on and is a basic precondition for the interpretation and prediction of actions of other agents. Apart from humans, the ability to understand intentions has been demonstrated in other social animals like apes [46,290], monkeys [36,218,249] and dogs [233]. However, the mechanism behind this ability is poorly understood. A series of experiments carried out in the last decade showed that the capacity to understand what others are doing from watching their movements is mediated, at least in part, by a specific mechanism called the mirror mechanism [240]. Mirror neurons becomes active when animals observe a certain action as well as when they execute the same action [107]. This mechanism is thought to map the sensory information describing actions of others onto the motor system of the observers, just as if they would perform the actions themselves [107].

In most studies on monkeys activity originating from the mirror neurons was recorded in the ventral premotor cortex (areaF5), and the inferior parietal lobe (area PFG and anterior intraparietal area, AIP) (for a review see [239]. Additional mirroring neuronal responses have been shown in primary motor cortex and dorsal premotor cortex [89,279] during reaching observation and in the lateral intraparietal area (LIP) during gaze following [258]. In humans, the areas that are supposed to belong to the mirror neuron system (MNS), i.e., respond to both action execution and observation, are located in the posterior inferior frontal gyrus (pIFG, congruent to the monkey F5), the premotor cortex (PMC) and the inferior parietal lobule (IPL) encompassing the AIP [210]. Additional mirror neurons, located in the supplementary motor area, and the hippocampus were shown by the single-neuron responses during execution and observation of actions in humans [199]. As mentioned earlier, the MNS is supposed to facilitate action understanding by internal simulation of other people’s actions. Thus, we might understand intentions of others by imagining ourselves in the other's position and simulating mental states (beliefs, desires, intentions) that we would possess if we were in the other's 'shoes' (“*simulation theory*”) [107,293]. Caused by this internal neuronal simulation during action observation, the perception of an action leads to simulative production of that action on the part of the observer, facilitating a similar action (motor

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[1] Theory of mind is the ability to attribute mental states and the awareness that other people have beliefs and desires different from one's own.

resonance) and interfering with a different action (motor interference). On the behavioral level, motor interference (MI) is seen as an increase of variance in one's own movement while watching an incompatible (incongruent) movement of a different person. MI is supposed to be the result of motor resonance, which has been shown to positively correlate with intention understanding [3,16,208].

This work consists of three studies. In the first study, I investigated what aspects in the appearance and movement kinematics of the observed artificial agent are required for triggering motor interference in human subjects by using a motion tracking method. In the following, I will refer to this study as MI-study. In the second study, by using functional magnetic resonance imaging (fMRI), I investigated whether MNS-activity can be modulated by goal-directed actions performed by non-biological agents (fMRI-study). Finally, in the third study, I investigated the flexibility of goal attribution capacity in non-human primates and its role in social learning. To this end, I tested the goal attribution capacity in marmoset monkeys by presenting them with inanimate previously unencountered agents. Since I used the preferential looking time paradigm for this study, I will refer to it as the looking times study. In the following, I will shortly explain the methods which I used in my studies and their main findings.

Previous studies emphasized that various features of the observed agent determine the degree of MI, but could not clarify how human-like an agent has to be for its movements to elicit MI and, more importantly, what 'human-like' means in the context of MI. Thus, it is not clear, whether the motor resonance and thus the motor interference require a tight match between one's own and the observed agent's physical features (presence of a body, head, face, extremities) and movement (smooth movement profile, natural joint configuration and movement velocity, capability of self-propulsion) to be triggered. Therefore, in the MI-study, I investigated in several experiments how different aspects of agent appearance, joint configuration (which determines the ability to move), and movement kinematics (variability of movement and movement velocity) of the observed agent influence motor interference. Participants performed arm movements in horizontal and vertical directions while observing videos of a human (i), a humanoid robot (ii), or an industrial robot arm with either artificial (industrial) (iii) or human-like joint configurations (iv). Both robots moved with a quasi-biological movement velocity. My results show that MI occurred for the observation of incongruent actions of the human agent, humanoid robot and industrial robot arm in human configuration (though, to a much smaller extent) but not for this arm in an unnatural joint configuration. Thus, my findings indicate that when observing inanimate agents, the ability to move in a human-like way (*motility* determined by the joint configuration) is more important than exhibiting other human-like features, like accurate biological velocity (since a quasi-biological movement velocity was sufficient), movement variability and human-like morphology.

The MI-study indicated some flexibility of mechanisms responsible for the motor resonance for non-goal directed movements in respect to appearance, movement velocity, movement variability and non-biological nature of the observed agent. To investigate whether motor resonance can also be demonstrated for goal directed movements of artificial agents and, more importantly to test whether the MNS activity is modulated by the artificial agent's goals, I designed an fMRI study. Previous studies that compared the activation of the MNS when observing artificial agents and humans have led to inconsistent results. Additionally, almost all previous studies only compared levels of MNS activation during action observation across agents (humans vs. robots) and did not test whether the activations are present if contrasting actions of artificial agents directed to different goals. Thus, in the fMRI study, I investigated whether MNS is involved in recognizing different action types and attributing goals/intentions to them when they were performed by an artificial agent. While being involved in intention detection task, the subject lying in the scanner observed videos depicting human and robotic grasping and pointing actions aimed at different object categories. The knowledge about the usage of the grasped object suggested different intentions in the following chain of motor actions. The debriefing after the experiment revealed that the subjects were able to attribute a certain intention to almost every robotic and human action. Further, I found that the bilateral IPL and the PMC differentiated not only between observation of action belonging to different action types, but also between the same action type (grasping or pointing) directed at different goals. This difference in activation that I have found for observation of both human and robotic agents indicates that MNS is involved not only in coding action types of artificial agents but also in coding their action goals, despite the fact that these agents are not presumed to have mental states. Thus, the MNS codes goals in the agent-independent manner.

In the third study, I tried to answer the question whether the goal attribution to inanimate agents which has been demonstrated in the first two experiments may have been shaped by evolution. To this end, I investigated goal understanding in common marmosets (*Callithrix jacchus*), which split from the human lineage ca. 40 million years ago. By testing goal attribution to previously unencountered agents I also wanted to investigate whether this capacity might be innate. In contrast to human children, who have the possibility to learn from experience with dolls from early childhood, the monkeys have never encountered any artificial agents before. Therefore, successful goal attribution to them would also point to the innateness of goal-attribution capacity. In addition, I assessed whether the perception of goal-directedness influences the marmosets' readiness to accept an inanimate entity as a model for social learning. If intention understanding was a precondition for social leaning from artificial agents in monkeys, it would indicate that the same might hold for the humans. By three preferential looking-time experiments, I first demonstrated that the marmosets attribute goals to a conspecific even when it is only seen in a video clip. I then demonstrated that the same effect holds when the observed agent was a monkey-sized quadruped robot, but not when a geometric box covered the same robot. Thus, the monkeys extended their capacity for goal attribution to previously unencountered agents, but only if the latter had conspecific-like features. Subsequent free choice trials revealed that the monkeys preferred the object which had been approached by the agent during the preferential looking-time experiment, but only if they previously had perceived its behaviour as goal-directed, i.e. in the case of a conspecific and the robot, but not of the geometric box. My results provide evidence that in non-human primates, the system for goal attribution does not require previous experience with a specific agent or agent-category, as long as it exhibits certain visual characteristics. This indicates that goal attribution capacity depends on certain morphological features and adds evidence to the proposition that it is innate. Furthermore, I demonstrated that goal attribution determines social learning in this species, since in the subsequent test, the monkeys tended to prefer the object previously chosen by the demonstrator and also spent significantly more time interacting with this object if they previously attributed intention to the agent.

Apart from investigating the mechanism of intention understanding, the secondary aim of this study was to test, whether in the future humanoid robots can be used in the area of neurorehabilitation and medical therapy. By conducting the fMRI study I tried to find an answer to whether we understand the actions of human-like robot agents using the same cortical and behavioral mechanisms that we use to understand other humans. The positive result indicated that human-like artificial agents might one day be used in therapy and as assistants to elderly people who are not used to modern-life technology. With the MI-study I aimed at clarifying what factors in the appearance and movement kinematics of robots are important to trigger the same kind of motor response as to a human agent during action observation. My findings indicated that actions of artificial agents with human-like morphology and smooth movements are simulated also on the behavioural (motor interference) level and in case of non-goal directed movements. The importance of human-like motility over human-like features further indicates that for certain medical interventions, like observational therapy aimed at improving the function of the paretic hand, the robots do not necessarily need to possess a human-like body with a head and two limbs. Instead, it is sufficient if the robot moves its limbs in human-like fashion even if it lacks detailed human-like features (like a palm with fingers). Further, I showed that although the movements of the robots should be smooth enough, the movement variability and biological velocity are less important. Finally, the preferential looking-times study indicated the importance of certain morphological similarities of artificial agents with conspecifics. I therefore suggest that robots with basic human features (like human body, head and limbs) are better suited for social interaction and learning scenarios than robots with industrial appearance.

1 Introduction

In a nutshell, this dissertation builds a bridge between the neuroscience of social cognition, animal behavior and humanoid robotics with three aims. The first aim was to investigate the agent's properties which facilitate motor resonance during dyadic interaction. The second aim was to test whether during observation of goal directed movements we simulate them in an agent independent manner. The third aim was to investigate on what agent cues goal attribution capacity depends in non-human primates and whether it is required for simple forms of social learning.

In the introduction, I will provide a brief overview of how all three disciplines could profit from my findings and present the reader with the state of the art literature and general concepts relevant for this work. The possible applications of the results will be in assessment and therapy of impairments of social cognition and in designing humanoid robots for neurorehabilitation and medical therapy.

In the following, I would like to explain in more detail the cortical mechanisms of action understanding and provide examples for potential applications of my findings.

1.1 Intention understating as fundamental building block of social cognitions

In recent years, the interest in research on the neural correlates of social cognition has been growing fast. Social cognition is defined as the ability to construct representations of the relations between oneself and others [1] and is based on mental operations that underlie social interactions. These operations include perceiving, interpreting, and generating responses to the intentions, dispositions, and behaviors of others [123]. Thus, the definition of social cognition is broad and refers to many scientific disciplines depending on the emphasis of the investigated function. In social psychology, social cognition includes moral reasoning and formation of attitudes [173]. In developmental psychology, the investigation of social cognition has focused most frequently upon the study of "theory of mind" (ToM) [104], which is the ability to attribute mental states to other people and the awareness that other people have beliefs and desires different from one's own [225]. In neuroscience, social cognition is defined more narrowly as the ability to perceive the intentions and dispositions of others [28]. This ability allows animals to interact with one another – a matter of survival not only for individuals but also for the species as a whole. In contrast to many animal species, humans do not just interact with conspecifics socially, but also engage with them in complex collaborative activities such as making a tool together, preparing a meal together, building a shelter, playing a cooperative game, collaborating scientifically, and so on. These collective activities require intention understanding and the capability to predict the behavior of other individuals. Therefore, inferring others' intentions and being able to understand and predict behavior of other people is a crucial aspect of social cognition.

Although intention understanding feels rather automatic and effortless to us, the complexity of this process becomes obvious in people with neuropsychiatric disorders. Many of these disorders are developmental in nature and include impairment of emotion processing and intention understanding – two processes which are closely related and most likely function in a highly integrated fashion. Impairments of these building blocks of social cognition can lead to various mental illnesses such as Autistic Spectrum Disorder (ASD) [140], schizophrenia[123,298], depression [255], posttraumatic stress disorder (PTSD)[2], amyotrophic lateral sclerosis (ALS)[3] [60], psychopathy [83] and social phobia [272]. On the other hand, William's syndrome [216], a genetic disease, has been associated with hypersociabililty [12], so that the individuals with WS seem driven to greet and interact with strangers. ASD is a complex developmental disability that causes deficits in social interaction, verbal and non-verbal communication, and might lead to restricted and repetitive behaviours [302]. Subjects with ASD have an impaired ability to attribute mental states to others (that is, to have a theory of mind) [146], impaired face and emotion processing, deficits in joint attention abilities and attributing mental states [129]. Autistic children have deficits in the processing of biological motion of point-light displays [15], whereas children with Williams syndrome have intact face recognition [216] and were shown to have intact processing of biological motion [160]. If social cognition deficits are determinants of daily functions, tasks designed to study these functions in the laboratory (as the ones used here) might one day used as a form of assessment of the efficacy of interventions on these patients.

1.2 The Mirror Neuron System as the mediator of intention understanding

When we see other persons act, we do not just recognize and categorize their actions, we frequently even imagine the reason behind the actions of the agents; there is evidence that adults encode actions in terms of their outcomes [143]. However, since the same motor act may lead to different outcomes, attributing intentions goes beyond recognizing the motor act as such [130,264]. Thus, intention understanding is a multi-layer process involving different levels of action representation, which spans from the motor intention that drives a given chain of motor acts to the propositional attitudes like beliefs, desires and so on. Hence, monitoring the properties of a prehensile movement (motor intention) conveys different cognitive intentions of the actor toward the object depending on the context: touch, use, move, drop or throw. But how does the intention understanding work on the neuronal level?

It has been argued, that in humans and non-human primates, the mirror neuron system (MNS) facilitates action understanding through neural simulation of action [148,153,240]. In monkeys, single-neuron recordings showed that mirror neurons discharge both when a monkey executes a specific object-directed action and when it observes another individual performing the same motor act (see Figure 1a). Thus, it is supposed that during action observation we get into the mental shoes of the people whom we observe [107] (simulation). The simulation theory has gained support from a number of recent experiments. By means of

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[2] PTSD is characterized by recurrent and invasive trauma-related memories, increased fear responsiveness, and increased physiological reactivity to trauma-related stimuli.

[3] ALS involves the progressive degeneration of upper and lower motor neurones.

functional magnetic resonance imaging (fMRI) [30,31], transcranial magnetic stimulation (TMS) [8] and electroencephalography (EEG) [70], it has been demonstrated that observation of human action gives rise to matching motor activation in the observer. Likewise, during hand action observation, there is a significant increase in the motor-evoked potentials from the hand muscles which are involved in performing such a movement [94]. The congruency between visual and motor properties of mirror neurons indicates that when we observe an action performed by others, a “potential motor act” is evoked in our brain that is identical (or at least similar) to that which would be spontaneously activated when we plan the execution of that same action. However, although in the latter case this act would be translated into an overt series of movements, in the former it would remain a motor representation of that goal at its potential stage. Based on this representation, we automatically attribute the intention to the action which appears to be most compatible with the object, the actor, our prior knowledge and the context. But now let us look at the anatomical bases of intention understanding.

1.2.1 The anatomy of the Mirror Neuron System

The mirror neurons were first discovered in the premotor area, F5, of the macaque monkey [106,293]. Later, they were found in the area PF [99] and the anterior intraparietal area (AIP, see Figure 1b). Both AIP and PF belong to the inferior parietal lobe (IPL). The neurons located in the superior temporal sulcus (STS) have only visual properties (responding to body movements) and are not active during action execution [238].

The three cortical areas: STS, area PF and area F5, are reciprocally connected. Thus, the area PF of the inferior parietal cortex is reciprocally connected to the area F5 [186] (see [164] for a review). The area F5, on the other hand, is connected with area F6 (the pre-supplementary motor area), with the area F5 and the prefrontal cortex [241]. The prefrontal cortex is connected with the AIP [241]. Both area PFG and the AIP receive higher-order visual information from the cortex located inside the STS [20]. The AIP also receives connections from the middle temporal gyrus (IT), located in the temporal lobe [20]. This input could provide the parietal areas, which are suggested to play a role in intention understanding [99], with information concerning object identity. On the other hand, the frontal inputs control the selection of self-generated and stimulus-driven actions according to the intentions of the observed agent [105].

Although MNS was originally discovered during recording of responses of single neurons in the monkey [238], there is a growing body of evidence from noninvasive neurophysiological techniques and brain imaging studies that a similar MNS-based action observation-execution matching mechanism is also present in humans [122]. Most of these studies have shown that in humans, as in the monkey, the mirror circuit is formed by three main regions: the inferior section of the precentral gyrus (premotor cortex, PMC), the posterior part (pars opercularis, po) of the inferior frontal gyrus (pIFG) and the inferior parietal lobule (IPL) including the cortex located inside the anterior intraparietal sulcus (aIPS) [238] (see Figure 2). Based on over 200 fMRI studies investigating social cognition, another meta-analysis [210] also demonstrated that the MNS areas with motor and visual properties are most often found in the parietal lobe (aIPS), IFG and the premotor cortex (see Figure 3).

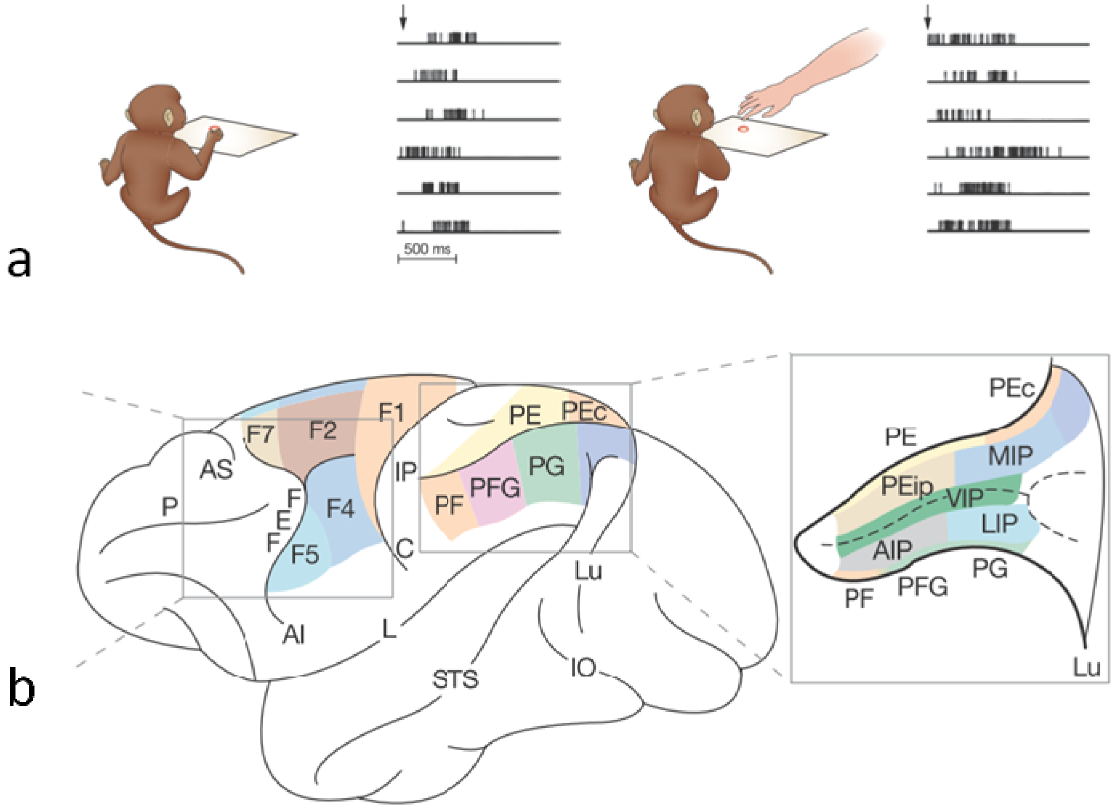

Figure 1: Activity of a mirror neuron and cytoarchitectonic map of the monkey cortex. a) Activity of a mirror neuron recorded from the area F5. The neuron discharges both when the monkey grasps an object and when it observes the experimenter grasping the object. b) Lateral view of the macaque brain. The areas of the parieto-frontal circuit containing mirror neurons are the ventral premotor cortex (area F5), area PF and the anterior intraparietal area (AIP). The parieto-frontal circuit receives high-order visual information from areas located inside the superior temporal sulcus (STS). Figure was adopted from [243] with permission from the publisher.

Additional cortical areas (such as superior parietal lobule, SPL) have also been occasionally found to be active during action observation and execution [111,124]. Although it is possible that their activation is due to a mirror mechanism, it is equally possible that it reflects motor preparation [243]. Single-neuron data from monkeys showing that these areas are involved in covert motor preparation [73] or are activated when volunteers observe proximal arm movements directed to a particular location in space, support this interpretation [96]. Neurons in the superior temporal sulcus (STS) also respond selectively to biological movements [104,126] and the posterior part of the STS region is recruited by relatively low level processes such as observation of biological motion [154]. A different function attributed to the STS is higher level operations such as social inferential processing in tasks involving theory of mind reasoning and mentalizing [252]. Since this region has no motor properties, it is not part of the mirror system in a strict sense.

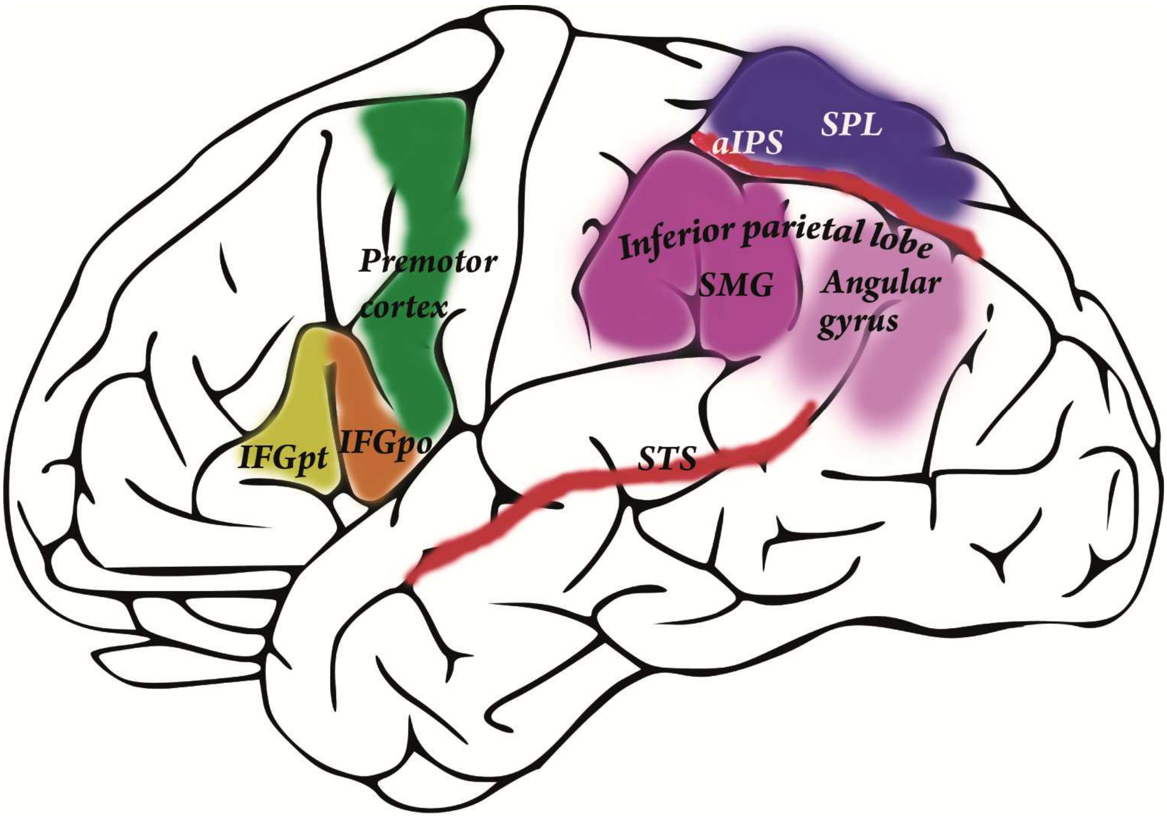

Figure 2: Lateral view of the human brain with coloured areas representing the human MNS. The MNS consists of the pars opercularis the inferior frontal gyrus (IFGpo), the premotor cortex, the superior parietal lobe (SPL) the inferior parietal lobe (IPL) consisting of the supramarginal gyrus (SMG) and angular gyrus, as well as anterior intraparietal sulcus (aIPS). The superior temporal sulcus (STS) provides the MNS with visual input (like the area IT in the monkey brain) but has no motor properties.

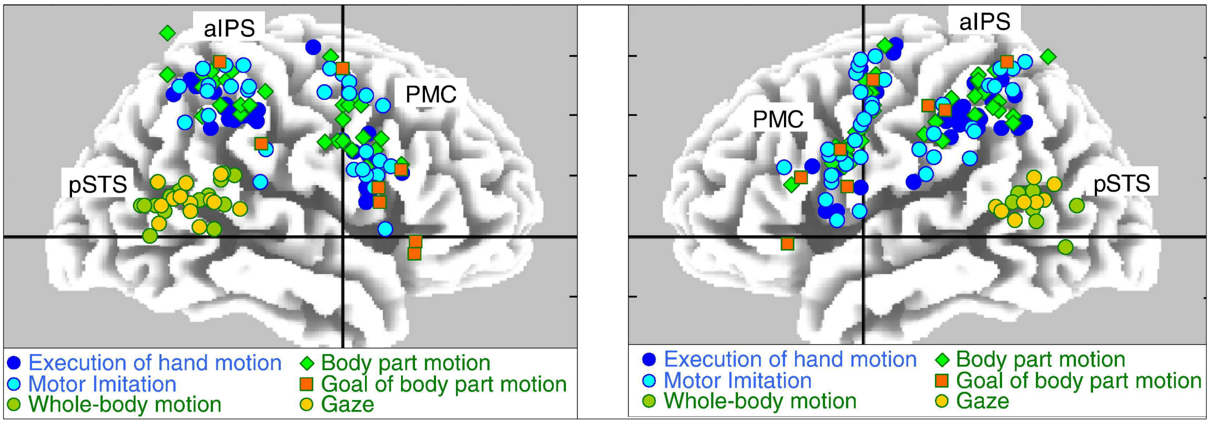

Figure 3: Brain regions revealed by fMRI-studies investigating action execution and observation. Every circle represents the hypothesized anatomical localization of mirror neurons in one of the studies. All studies were taken from an earlier meta-analysis on social cognition by [211] and updated by including fMRI studies on mirror neurons and social cognition located by searches in PubMed and Science Direct in the period between April 2007 and August 2008. Figure adopted with permission from [210].

Analogous to the monkey MNS, a similar pattern of connectivity between premotor areas and inferior parietal lobule has also been shown in humans, both directly [248] and indirectly [147,149]. In addition, a sequential pattern of activation in the human MNS has been demonstrated during action-observation (for details see [205]). The premotor node of mirror system is somatotopically organized [30]. Thus, observation of motor acts done with different effectors determines activation of specific parts of it so that leg, hand, and mouth movements are represented in a medial to lateral direction of the premotor cortex.

1.2.2 **Neurons with mirroring properties outside the classical MNS**

Single-subject fMRI analyses have recently provided evidence that other cortical areas, which lie outside the classical MNS (for example, the primary and secondary somatosensory cortices and the middle temporal cortex) also become active during action observation and action execution [111]. A recent study showed that the mirror neuron system in humans extends beyond the ventral premotor cortex and inferior parietal lobe traditionally associated with the MNS [199]. The authors inserted electrodes in the medial wall (cingulate cortex, supplementary motor area (SMA and pre-SMA) and the medial temporal lobe (amygdala, hippocampus, parahippocampal gyrus and entorhinal cortex) of the patients' brain. Although these brain areas are not classically associated with mirror neurons, in line with what previous fMRI experiments have suggested [111], the authors found mirror neurons in the SMA, the hippocampus and parahippocampal gyrus and the entorhinal cortex. This indicated the existence of mirror neurons in many brain regions. Additionally, the authors reported evidence for the existence of inhibitory neurons, which might help us understand how we perform motor simulations without moving our body.

Another recent analysis used combined results from 125 fMRI papers to document the areas which were associated with mirror neurons apart from classical MNS-areas [196]. Although the main revealed areas were BA 44 (21% of the studies), BA 7 (27% of the studies), BA 9 (38% of the studies), BA 6 (40% of the studies) and BA 40 (48% of the studies) which belong to the classical MNS, further significant clusters of activation encroached upon 34 separate Brodmann areas and revealed regions such as the primary visual cortex, cerebellum and parts of the limbic system (see Table 1). Another recent meta-analysis of MRI studies investigating observation and imitation of actions showed that MNS-areas additionally encompassed the dorsal PMC, SMA, posterior MTG, and V5 [57]. Further, neuroimaging studies in both humans [111,112,113] and monkeys [93,235] demonstrated overlapping activity for the generation and the perception of hand actions also within the somatosensory and motor cortices. The activation in these areas might result from the fact that the classical mirror neuron studies are unable to measure exclusively mirror neuron activity. Some of the areas which do not belong to the "core MNS" are likely to be involved in processes of visual recognition (primary visual cortex for example), visual motion perception, working memory, movement planning, and movement execution (in the case of imitation), which are all integral components of fMRI tasks.

BA	Region	N	BA	Region	N	BA	Region	N
1	SI	1	18	V2	5	38	Temp. Pole	1
2	SI	12	19	V3	10	39	IPL	7
3	SI	11	20	ITG	2	40	IPL	60
4	MI	13	21	MTG	9	41	pSTG	4
5	SPL	4	22	STG	19	42	pSTG	3
6	PM	59	24	vaCingulate	4	43	Post-, precentral	4
7	SPL	34	28	Entorhinal	1	44	IFG, pars opercularis	26
8	SFG	2	31	pCingulate	4	45	IFG, pars triangularis	23
9	IFG	48	32	daCingulate	5	46	DLPF	15
10	SFG	4	34	aEntorhinal	1	47	Orbital frontal cortex	7
13	Insula	29	36	Parahippocampus	1		Cerebellum	13
17	V1	3	37	Fusiform gyrus	15		Other	26

Table 1: Regions associated with the mirror neuron system. These regions were found in meta-analysis of studies which investigated the MNS [196]. Abbreviations: BA-Brodmann area, N: Number of studies which found a certain region; da: dorsal anterior; p: posterior; DLPF: dorsolateral prefrontal cortex; ITG: inferior temporal gyrus; SFG: superior frontal gyrus.

1.2.3 **Features of mirror neurons**

Although the monkey area F5 includes also the canonical neurons, which respond to the presentation of an object [241], the mirror neurons do not fire in response to a simple presentation of objects, including food [243]. Most of them do not respond or respond only weakly to the observation of the experimenter performing a motor act (for example, grasping) without a target object [106,171].

A number of fMRI studies in humans show that, similar to monkeys, the information about the goal of the observed motor acts can be encoded with different degrees of generality. Some mirror neurons (strictly congruent mirror neurons) fire when the observed and executed motor acts are the same or at least very similar (for example, grasping with precision grip). For these neurons (about 30% of mirror neurons) ‘‘corresponding’’ seems to mean an action that achieves a similar goal and that involves the same motor details [163]. In contrast, broadly congruent mirror neurons, making up about 60% of all mirror neurons, fire when the observed motor act has the same goal as the executed motor act (for example, grasping), but can be achieved in a different way (for example, with both precision and whole-hand grips) [240]. For such neurons, ‘‘corresponding’’ means ‘‘having the same goal.’’ Together, strictly and broadly congruent mirror neurons could therefore represent both what another individual did, and how he did it [278].

Mirror neurons in the F5 of the monkey brain may also fire in the absence of visual information describing the motor act of the experimenter only if the sound of an action is present (such as ripping a piece of paper) [167]. Thus, the neurons fired also if the monkey saw the experimenter’s hand disappear behind the screen and knew that behind a screen there was an object [293]. The neuronal activation therefore underpinned the coding of the goal of the motor act of the other individual, regardless of the sensory information that described that motor act. Likewise, in humans, it was shown that listening to the sound of hand and mouth motor acts alone activated the parieto-frontal mirror network [110]. This activation was somatotopically organized in the left premotor cortex and was congruent with the motor somatotopy of hand and mouth actions.

A recent study provided compelling evidence that in monkeys most of the motor neurons in F5 encode motor acts (that is, goal-related movements, such as grasping) rather than movements (that is, body-part displacements without a specific goal, such as finger flexion) [292]. Thus, when monkeys were trained to grasp objects using two types of pliers: normal pliers (which require typical grasping movements of the hand), and ‘reverse’ pliers (which require hand movements executed in the reverse order), F5 neurons discharged during the same phase of grasping in both conditions, regardless of whether this involved opening or closing of the hand. However, in contrast to monkeys, whose MNS has been shown to react only to the sight of goal-directed actions, in humans, motor system also “resonates” in response to intransitive movements, including those without any obvious meaning. The initial evidence for this mechanism was based on the transcranial magnetic stimulation (TMS) experiments which indicated that the observation of other’s movements results in activation of the muscles involved in the execution of those movements [94,274]. In a more recent study, motor-evoked potentials in response to TMS were recorded from the right *opponens pollicis muscle* in participants observing an experimenter either opening and closing normal and reverse pliers or using them to grasp objects [58]. The observation of moving tools (that is, opening and closing the pliers without grasping anything) activated the cortical representation of the hand movements involved in the observed motor behavior, whereas the observation of the tool grasping action activated a cortical representation of the observed motor goal, no matter what individual movements were involved. Due to this feature of goal matching during action observation, the human MNS can resonate even if the person who observes the action does not have body parts with which the acting agent performs the action [113]. Indeed, it has been shown that two aplasic individuals who were born without arms and hands showed an activation of parieto-frontal mirror circuit (that was active during their movements of the feet and mouth) when observing hand motor acts that they have never executed but the motor goals of which they could achieve using their feet or mouth.

1.2.4 **Brain regions associated with goal understanding**

There is evidence that parietal mirror neurons are involved in encoding of not only the observed motor acts but also of the entire action of which the observed motor act is part. Thus, when monkeys performed motor acts embedded in grasping, the inferior parietal lobule (IPL) neurons showed markedly different activations when this grasping act was part of grasping for eating than grasping for placing [99] (see Figure 4a, b). Likewise, when monkeys saw the experimenter who grasped the objects with either the intention to place it to the mouth or into the container, the majority of the IPL neurons were differently activated depending on the final action to which the observed motor act belonged (see Figure 4c, d). This finding indicates that, in addition to describing what the observed individual is doing (for example, grasping), IPL mirror neurons also enable the observer to explain why the individual is performing the action.

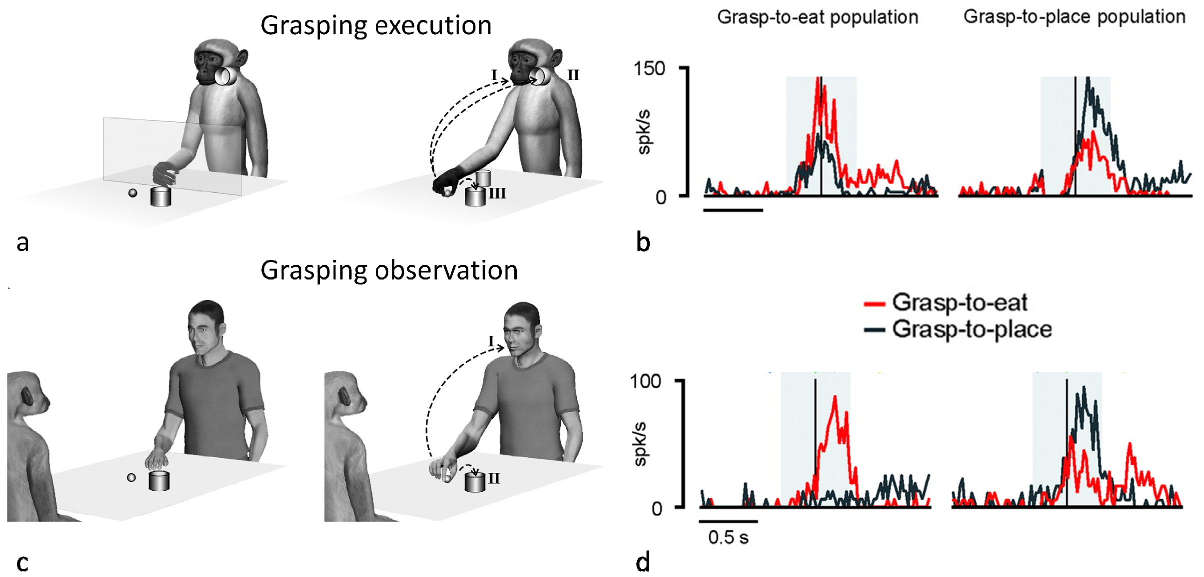

Figure 4: Activation of the parietal mirror neurons in monkeys depending on the goal of grasping. In their study, Fogassi et al. presented the monkeys with 2 tasks: grasping execution and grasping observation [99]. During action execution, the animals had to grasp a food pellet and put it either into their mouth (line I in 4a) or inside a container (line II in 4a) The mirror neurons coding eating showed higher firing rates around the time of grasping followed by eating relative to grasping followed by placing (b). During observation of according grasping acts performed by an experimenter (c), the activity of the mirror neurons which coded eating was also modulated by the particular action context: it was higher when grasping was followed by eating relative to grasping followed by placing an object (d). In the trials in which the container is present, the experimenter puts the food in it. When the container is not present, the experimenter eats the food. So, the container was the contextual cue for the monkey to code the grasp as grasp-to-eat or grasp-to-place. Modified figure adopted from [19] with the permission from the publisher.

A recent experiment using electromyography[4] suggested that similar to monkeys, in humans there is an organization of chained motor acts underlying intention understanding [59]. In this experiment, children were asked to observe the experimenter who grasped a piece of food and brought it to his mouth (see Figure 5a) or grasped an object and placed it into a container (see Figure 5b). During execution of grasping actions, the mouth-opening muscle was active more strongly when grasping for eating than for grasping for placing (see Figure 5c). Interestingly, the researchers recorded an activation of the mouth-opening muscles during observation of the reaching and grasping phases only when grasping preceded eating the food but not when they preceded placing the food to a different location (see Figure 5d). This activation indicates the capacity of the child’s motor system to predict the experimenter’s intention. It seems that, as soon as the action starts, the entire motor program for a given action is activated. This motor representation is identical to that which the observer himself would activate if planning the same action [242].

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[4] Electromyography is a technique for evaluating and recording the electrical activity produced by skeletal muscles.

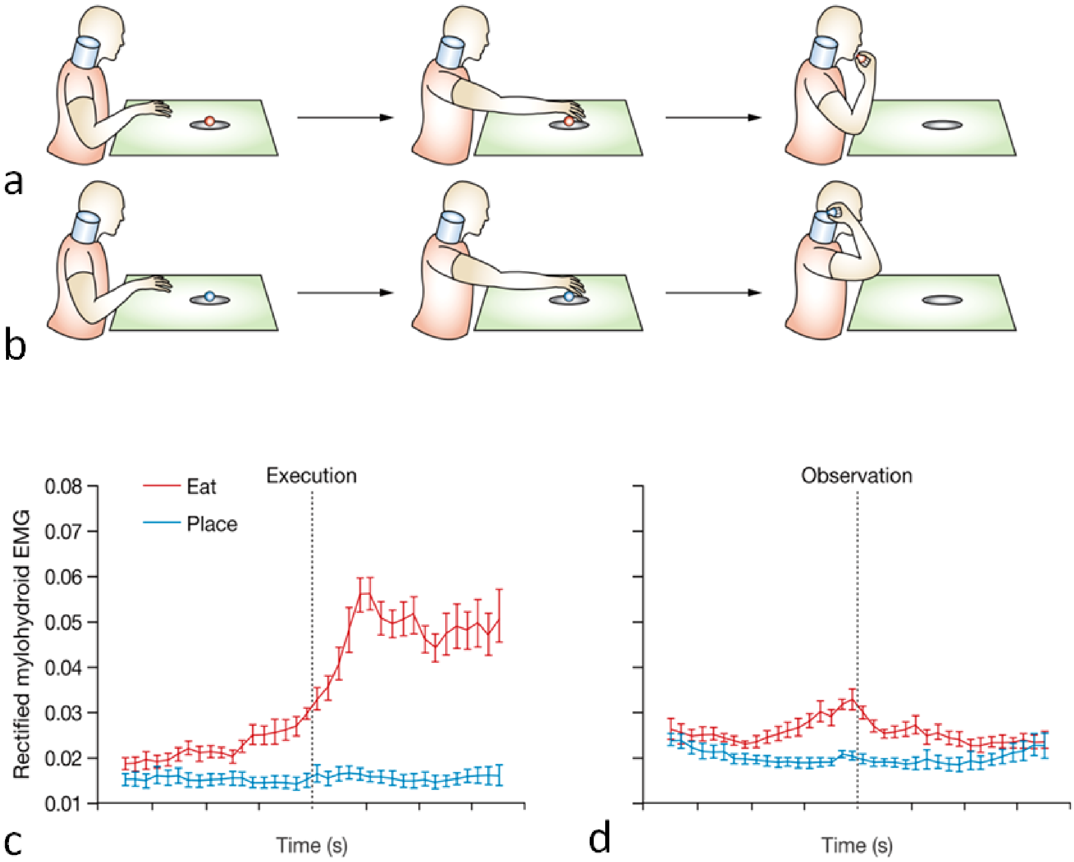

Figure 5: Motor behavior of the mouth-opening muscles during action execution and observation. The figure 5a and 5b depict the schematic representation of two grasping tasks directed at different goals. The individual reaches for an item on a plate and either brings it to his mouth or puts it into a container placed on his shoulder. The figure 5b shows the time course of the rectified electromyographic activity of the mouth-opening muscle during the execution (left side) and observation (right side) of the ‘bringing-to-the-mouth’ action (red line) and of the ‘placing’ action (blue line). All curves are aligned with the moment of object lifting from the touch-sensitive plate (time = 0). Figure was adopted from [243] with permission of the publisher.

Thus, the motor knowledge and experience allow us to recognize the intentional meaning of the motor acts we observe both when they are performed singly and when they are part of motor chains. In this latter case, their meaning is no longer determined solely by the specific goal-centeredness of a single motor act, but offers the goal-centered representation which describes the intentional meaning of the whole action.

1.3 Is the goal understanding capacity innate?

The evolution of social cognition predicts mechanisms for cooperativity, altruism, and other aspects of prosocial behavior, as well as mechanisms for coercion, deception and manipulation of conspecifics. The former are exemplified in the smallest groups, in the bond between mother and infant; the latter in the largest groups by the creation of complex dominance hierarchies.

1.3.1 **Development of goal understanding in infancy**

Ontogenetically, the understanding of others' intentions develops gradually. Already 6- to 9-month-olds infants manifest an early sensitivity to goal-directedness and appear to be biased toward interpreting humans' reaching behavior as goal-directed [77,116,142,194,224,266]. Woodward (1998), for example, showed that even in the first half-year of life infants encode goal-directedness over spatiotemporal properties of the human reaching gesture [304].

Most studies have shown that infants younger than nine month attribute goals only to humans [142] and agents with a certain degree of human-likeness such as humanoid robots [161]. Thus, no intention attribution is possible to boxes [161], claws/rods [142,304], mechanical devices [194], or geometrical shapes [77]. However, one study has shown that 6.5-month-old infants were able to attribute a goal to a moving inanimate box if it slightly varied its goal approach. This suggested that morphological identification of agents is not a necessary precondition of goal attribution in young infants and that the single most important behavioural cue for identifying a goal-directed agent is variability of behaviour [79]. In consent with this finding, by means of near infrared spectroscopy, an action execution and observation matching system was demonstrated already in 6-month-old human infants [259]. In contrast to adult participants, the sensory–motor cortex of infants (but not that of adults) was also activated during the observation of a moving object on a TV screen, indicating that during the early developmental stages even non-biological moving objects can activate the MNS.

For investigating goal attribution in infants older than nine months of age, most studies agree that infants are able to attribute intentions to both morphologically familiar and unfamiliar inanimate agents [10,77,116,157,172,224,262]. Finally, at 12 months of age, infants have been shown to attribute goals even to geometrical shapes [116].

Based on these findings, some researchers argue that the early form of the intention understanding capacity is an innate brain function, which is triggered by specific morphological and behavioral cues such as faces and eyes [9,51,157], biological motion [9], self-propulsion [180,224,226], or contingent and reciprocal interactions with other agents [157,158]. Thus, according to these researchers, no prior experience with the agent should be required if certain morphological cues are present [9,77,116,180,224,226]. In contrast, some other researchers argue that goal attribution is not innate but instead is first learned through experience with human agents by forming associations between observed actions and their target and later gradually extended to less human-like agents [194,197,282,304].

Therefore, it is still unclear whether the capability to attribute intentions is innate and based on certain cues, or whether it develops with experience and can be extended to other agents. Further, in case of the first, it is not clear exactly which cues (e.g. presence of a body with a head, biological motion, monkey shape and size, ability to manipulate objects) a familiar or an unfamiliar entity must exhibit in order to be perceived as an intentional agent.

1.3.2 Goal understanding in non-human primates

Traditionally, researchers claim that in contrast to humans, who are thought to understand others by means of their capacity to “read mind” [222], all other animal species just read behavior [221,223]. Relying on many situations from the past experience, they can predict the actions of others if the same situation arises again by extraction of procedural rules from observable environmental regularities [295].

However, the view of primates simply as “behavior readers” has been challenged by studies showing that chimpanzees have been observed doing things that would seem to require more than just an understanding of surface-level behavior, like, for example, tactical deception [43]. Also rhesus monkeys prefer to steal food lying in front of the human experimenter when he does not see it (his gaze is turned to a different direction) in comparison to the condition when the experimenter is visually aware of food presence. This indicated that rhesus monkeys seem to understand the relationship between seeing and knowing [98].

There is evidence that at least some primates perceive the actions of others in terms of goals. Similar to results obtained with human children, experiments using the Woodward habituation paradigm [249] (see section section 3.3.1 for details about the paradigm) found that monkeys expect that people will reach for the object after gazing at it. Using the preferential looking time paradigm, Rochat, et al. recently investigated the ability of macaque monkeys to predict goal-directed actions of others [245]. Her results indicated that macaque monkeys, similarly to the nine to twelve-month-old human infants, detect the goal of an observed motor act and, according to the physical characteristics of the context, construe expectancies about the most likely action the observed agent will execute in a given context.

Further, chimpanzees [46,290], rhesus monkeys [245], capuchin monkeys [218], cotton-top tamarins [249] and common marmosets [40] show sensitivity to the intentional structure of behavior. The evidence that primates understand the goals of others comes also from the studies of social learning, which have shown that when apes see a novel action, they do not try to simply copy it in all details, but try to reach the same goal (goal emulation) [215]. Similar to human children who imitate others’ actions ‘rationally’ by copying a demonstrator’s action when that action is freely chosen, but less when it is forced by some constraint [114], enculturated chimpanzees also imitate rationally and therefore show some understanding of the rationality of others’ intentional actions [41].

In contrast to cooperative contexts (when experimenter’s goal was to share food with the chimpanzee), in which primates performed poorly by failing to understand what others know on the basis of where they are looking [222], other data obtained in competitive contexts show that when competing for food, chimpanzees perform much better [134]. Another study reported that chimpanzees do not simply react to the outcome of the human’s behavior, but consider the reason why the human failed to give them food [46]. Thus, when chimpanzees interact with a human experimenter who “fails” to give them food, they tend to produce begging behaviours more often and leave the room later than if the human is unwilling to give them food (for example teasing them). A similar experiment in capuchin monkeys has shown that the monkeys remain in the testing area longer when the experimenter is unable to give them food than if he is teasing them [218].

Not only understanding goal-directedness, but also seeing is an early sign of intentionality. By 12- to 14-months, infants follow an adult’s gaze around a barrier [157]. Indeed, all primate species tested so far visually co-orient with conspecifics or humans [247], including common marmosets [35,37], indicating an understanding of what the agent sees.

1.4 Role of goal understanding for social learning

It has been proposed that learning by imitation requires the observer to not just bring about the result of the model's action by repeating the bodily movements that another individual has performed, but also to understand that the model intended to bring about the goal by that behaviour [45,178,280,282]. The perception of actions as goal-directed rather than in terms of physical properties in monkeys might be a necessary precondition not only for understanding intentional actions and attributing mental states to agents [108] but also for later development of human imitative learning. Thus, it might provide the basis for cultural learning [282].

An intimate link between intentional understanding and social learning has been demonstrated in one to one and a half year olds. Meltzoff et al. showed that 18-months olds correctly inferred and copied the goal of an unsuccessful action [194]. However, the infants did not copy the failed action but instead completed the action which was intended by the actor. Interestingly, they did not imitate the same actions in case of being performed by a mechanical device. The same pattern was present in 15- [158], but not in 12-months olds [11]. Furthermore, 14- and 18-months olds differentiate between intentional and accidental actions and copy only the former ones [53], and 12- and 18-months olds copy actions in terms of goals [54] and do so in the most rational way [114]. Finally, results from a recent study [267] indicate that action observation and execution rely on a shared code starting in infancy since the infants become better in a certain task after watching a solution performed by an experimenter.

1.5 Motor interference - a tool for investigating motor resonance during action observation

Since the tendency to anthropomorphise humanoid robots is natural, it is important to analyze what morphological and behavioural features of a robot facilitate the human-machine interaction in social scenarios and which features have less influence on making this interaction intuitive.

Although the quality of interaction between humans and humanoid robots has been investigated by some studies (e.g. [88,144], mostly, questionnaire-based subjective judgments were used for this purpose [17,82,118]. A possibly objective tool, which is based on the phenomenon of *motor interference*, has been developed only recently [166]. In the following, I will describe this phenomenon in detail since it will be used in my investigations.

As stated earlier, by using fMRI it has been shown that observation of an action leads to activation of the corresponding motor areas in the human premotor cortex [30,31]. On the behavioural level, this phenomenon has been supported by the finding that during hand action observation, there is a significant increase in the motor-evoked potentials from the hand muscles that would be used for performing such a movement [94]. Thus, a part of the central motor systems becomes activated during the observation of action (motor resonance). However, what happens when we attempt to perform an action while observing a qualitatively different (incongruent) action? In this case, the motor program (or representation) associated with the observed movement interferes with the outgoing motor output for the intended movement.

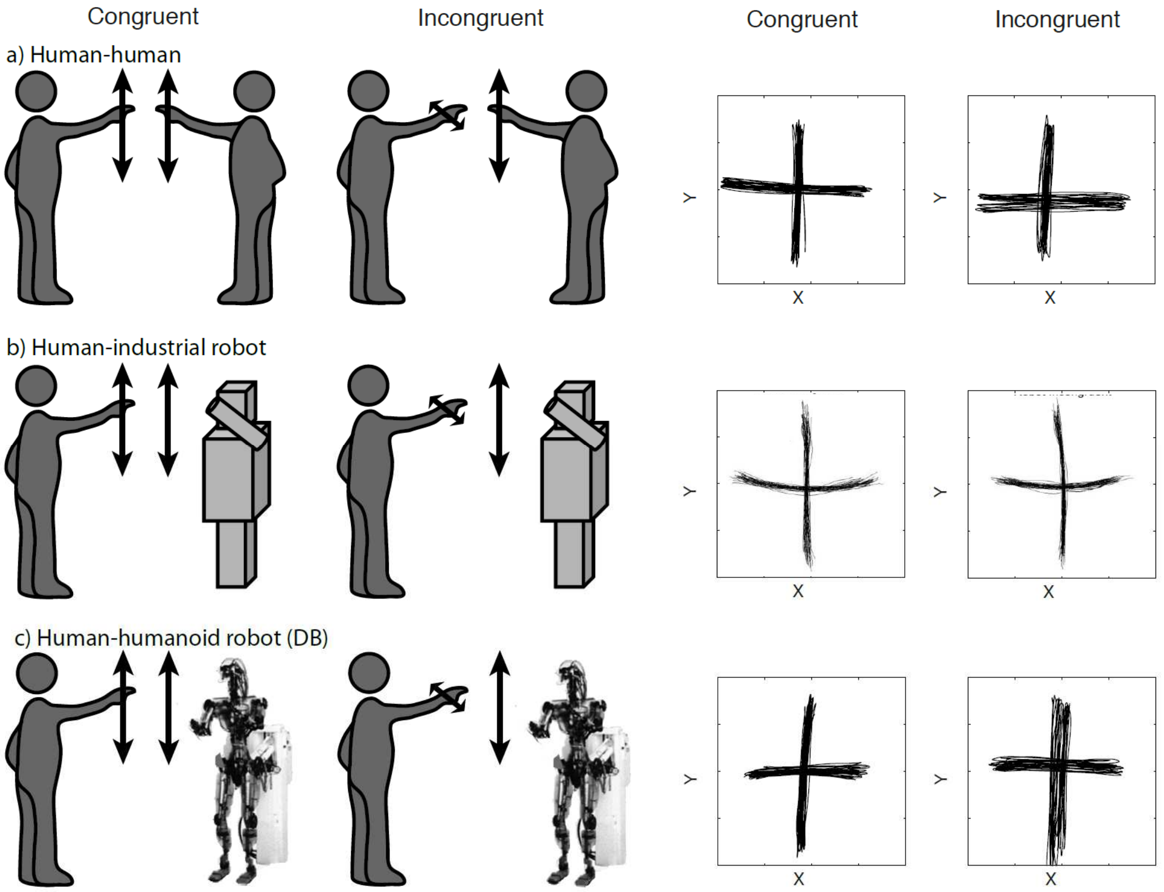

Figure 6: Setup and results of previous studies investigating motor interference. Left: experimental conditions. Right: examples of movement trajectories of the observing subjects. a) Observation of incongruent movements performed by a human subject leads to MI [166]; b): video observation of a an incongruent movement performed by a robot arm does not lead to MI [166]; c) observation of an incongruent movement of a humanoid robot elicits MI [212]. Figure was adopted from [174] with permission of the publisher.

Thus, caused by the internal neuronal simulation during action observation, the perception of an action leads to simulative production of that action on the part of the observer, facilitating a similar (congruent) action and interfering with a different (incongruent) action (motor interference) [24,152,229]. The first phenomenon is called *motor resonance*, the second –

motor interference. While motor resonance becomes obvious in mimicking actions of our interaction partners (e.g. the contagion of yawning), motor interference (MI) can be observed as an increase of variance in our own movement trajectory while watching an incompatible movement either face-to-face or in video [166] (see Figure 6a). A recent study [133] has shown not only interference, but also facilitation effects when observing congruent movements (see Table 5).

Motor interference influences not only the trajectory of the observer's movements but also his/her reaction times. Research on visuomotor priming has shown that responses to human body movement (e.g. a video image of a hand opening) are faster and more accurate when they involve execution of the same movement (e.g. hand opening) than when they involve execution of an alternative movement (e.g. hand closing) [72,275]. Similarly, if the subjects are instructed to perform a finger tapping in response to a visual signal depicting finger tapping (compatible) or lifting (incompatible), the reaction time to initiate the prepared finger movement is significantly slowed down when the stimulus is incompatible [24].

Individuals automatically mimic many different aspects of their interaction partners, including speech patterns, facial expressions, emotions, moods, postures and gestures [67]. Even one-month-old infants have been shown to smile, stick out their tongues, and open their mouths when they see someone else do it [193]. The main function attributed to motor resonance is action understanding, since mirroring the actions of others might help to understand what another person is doing [240] and why he/she is doing it [148]. Thus, simulating another person's actions might allow humans to make predictions about the mental states of others based on the mental states and behaviours that they experience themselves while mimicking others [25]. The higher degree of movement synchronization (chameleon effect) between interaction partners is generally regarded as a sign of higher degree of mutual rapport, involvement and togetherness [67,285]. For example, people change their breathing when observing other people making effortful actions [213] as if preparing to make such actions themselves. Students in a small class often exhibit the same postures as their instructor and other classmates [13]. A recent study investigating unintentional synchronization of rocking frequencies of pairs of participants sitting in rocking chairs has revealed that subjects unintentionally adopted the same rocking frequency when they had visual access to each other [236]. Surprisingly, subjects moved in synchrony even after the researchers manipulated the natural rocking frequency of the chairs. Further, behavioral synchrony during a dyadic interaction has been shown to lead to an increase of attention to the interaction partner and thus enhanced memories about his appearance and his utterances [187]. Finally, in psychotherapeutic counseling, congruent limbs movements of the therapist and the client have been shown to be significant contributors to the attributions of rapport [285].

When talking about the link between the MNS, motor resonance and motor interference, it needs to be considered, that at least in monkeys, mirror neurons respond only to object-directed actions (e.g. a hand grasping an object) and not to movements (e.g. a hand moves in the absence of an object to grasp) [240]. Thus, although in humans motor resonance can also be triggered by non-goal-directed movements, this effect might be increased when observing goal-directed movements. Evidence for this account comes from a recent study which has shown that MI in the observer’s movements was modulated by presence and absence of goals in horizontal and vertical arm movements of the observed agent [23]. The authors could show an additional increase of MI if two red dots were added on the observed video sequence at the level of endpoints of the actor’s arm movements, such that they represented targets for the observed movement. Additionally, Capa et al. [49] has performed an experiment to test whether MI results from the activation of the MNS. The authors have investigated MI in two groups of subjects who watched incongruent movements. However, only one group received a brief visuo-motor practice phase of the observed incongruent action. The authors suggested that in case that MI arises from activity in the mirror system, this effect would increase when the observer received prior practice with the observed movement, because visuo-motor experience should increase motor resonance with the observed movement by strengthening excitatory links between its visual and motor representation. In contrast, if motor interference only reflects the adjustments to synchronize with the observed movement, increasing the visuo-motor experience with that movement should facilitate its perception and synchronization and thus reducing the MI effect. As expected, prior action observation induced a larger motor interference in participants who had practiced the observed action supporting the mirror neuron account for the emergence of MI.

Nevertheless, the system underlying MI during non goal-directed movement observation might be distinct from the goal-sensitive mirror neurons described in the monkey premotor cortex since in humans the resonance arises from any kind of movement and is not restricted to goal-directed actions. Possibly, human goal-sensitive mirror neurons are part of a much wider ‘mirror’ system, which has a number of levels.

1.6 Factors which influence goal understanding

The simulation theory indicates the necessity of morphological similarity with other agents for intuitive understanding of other’s actions since the observed actor should have the same motor constraints and morphological features as the observer (the "like me" hypothesis [194]). Therefore, it seems reasonable that the closer the match between the observed action and the observers’ own sensorimotor representations, the more efficient the simulation will be. Thus, the process of simulation reduces the possible range of actors, whose intentions the observer might be able to simulate. But how closely has an artificial agent to resemble the human and what other human-like features does he have to have to engage the MNS? Also, does an agent need to be biological in order to be perceived as being intentional?

1.6.1 Agent appearance

In children, several studies show that the simulation cannot take place when the observed action cannot be transformed to the own body of the infants, as in case of geometrical shapes. The lack of goal attribution when interacting with mechanical devices [194], or claws [142,304] suggests that interaction with a machine fails to activate the same mechanism that codes human motor behaviour; direct matching cannot therefore occur. However, although the tested artificial agents do not have mental states, infants have been shown to attribute goal-directedness to them, if they exhibit similar motor constraints and morphological features as humans (the "like me" hypothesis). Thus, as stated earlier, in contrast to geometrical shapes [161], mechanical devices [194] and claws [142,304], a human-like shaped agent (e.g. a humanoid robot) might enable isomorphic mapping of its actions to the observer's body [161] and thus enable goal attribution towards those agents.

A recent study has shown that the tendency to build a model of another person's mind linearly increases with its perceived human-likeness [170]. This study investigated how the increase of human-likeness of interaction partners modulates the participants' brain activity. Subjects were playing a computer game (the prisoners' dilemma game) against four different game partners: a regular computer notebook, a functionally designed Lego-robot, the anthropomorphic robot BARTHOC Jr. and a human[5]. The results clearly demonstrated that neural activity in the medial prefrontal cortex as well as in the right temporo-parietal junction linearly increased with the degree of "human-likeness" of interaction partners. The more the respective game partners exhibited human-like features, the more the participants engaged cortical regions associated with mental state attribution. Further, in a debriefing questionnaire, participants stated having increasingly enjoyed the interactions most when their respective interaction partners displayed the most human features and accordingly evaluated their opponents as being more intelligent.

However, do we need a fully anthropomorphic synthetic robotic agent or is a certain degree of human form realism sufficient for social acceptance of robots? In 1978, the Japanese roboticist Masahiro Mori has made an interesting discovery: the more humanlike his robots became, the more people were attracted to them. However, if a robot became too lifelike, suddenly people were repelled from it [198]. In his theory called "The Uncanny Valley" Mori suggests that a high degree of human likeness might also cause a negative effect. The uncanny valley theory states that as a robot increases in humanness, it becomes more susceptible to failures in its functionality and design and can cause the feeling of uneasiness. This results from the fact that the more human-like the robot appears, the higher are the expectations of people interacting with it. The "uncanny valley" hypothesis predicts, for example, that a prosthetic limb covered with skin-coloured rubber, which imperfectly, albeit extremely closely, reproduces the texture and the motion of real limbs, would be more repulsive than a less realistic limb with a mechanical appearance. Recently, Hiroshi Ishiguro constructed his mechanical "doppelganger", the android robot Geminoid HI-1, using powerful electronics, silicone rubber and pneumatic actuators [204]. This robot looks very similar to the original and can be used to mimic Ishiguro, who controls this robot remotely. Ishiguro uses a microphone to capture his voice and a camera to track his face and head movements. In a live-setting study, the researchers examined the response of participants who interacted with the Geminoid, while it was tele-operated by Ishiguro. Interestingly, only 37.5% of the interviewed visitors reported an uncanny feeling with 29% even enjoying the conversation [69]. To investigate the effect of uncanny valley on the neuronal level, a recent study has used

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[5] During the games the subjects were lying in the MRT scanner and could not see the agents against which they play. However, they have seen the agents before the experiment started.

fMRI and a repetition suppression[6] paradigm. Presenting the participants with videos of human, humanoid robot and an android robot (robot with human appearance) has shown that the uncanny valley effect should not be ignored [253]. In this study, the participants viewed video clips of different transitive and intransitive hand actions of a human agent, an android agent and a humanoid robot demonstrating that activation in the IPL or IFG was not selective for appearance or motion of different agents per se [253]. Instead, the increased activation in the IPL appeared as a result of mismatch between appearance and motion in case of the android robot with human appearance but robotic motion. These findings could be explained by presence of prediction errors, since the MNS predicts biological movement in case of biological appearance and therefore has to negotiate an agent that does not move biologically. Therefore, when designing the humanoid robots it is important to remember that the high degree of realism is not always the best solution and the robot's exterior should correspond to its purpose.

Although the infant studies point to the importance of human-like appearance for goal attribution, the question of how the MNS processes motor actions of artificial agents has lead to contradictory answers. Some studies claim that the MNS does not respond or responds weakly if the perceived actor is an artificial agent [64,66,276], whereas other more recent ones provide evidence that observing robotic actions leads to similar or even stronger activations in the MNS than human actions [76,112,206,253]. In the following, we will present the controversial studies in more detail.

Oberman and colleagues have shown that the mu-rhythm, which is considered to be the EEG-marker of the mirror neuron activity, is reduced both when participants view human and robotic actions, suggesting a similar level of MNS-activation during observation of both agents [206]. Further, Gazzola and colleagues have shown that despite differences in shape and kinematics between the human and robot arms, the parieto-frontal mirror circuit was activated during observation or human and robotic actions [112]. Also, Peeters et and colleagues has demonstrated that observation of both human and robotic hand actions leads to bilateral activation of a mirror network formed by the intraparietal and ventral premotor cortex [217]. Finally, a number of behavioral studies supported the idea of attenuated motor priming for movements performed by an artificial agent [182,227,228].

In contrast to these findings, Chaminade et al. (2010) using fMRI have shown that in brain areas important for processing emotional stimuli, activity was reduced in response to robot expressions compared with human expressions [66]. Further, Tai et al. (2004) scanned volunteers using Positron Emission Tomography and showed that the MNS was activated only by observation of human, but not robotic hand closing and opening actions [276]. Finally, on the behavioural level, it has been demonstrated, that the Simon effect[7] is

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[6] Repetition of a stimulus often results in a reduction in blood oxygen level-dependent (BOLD) signal in brain areas that encode that stimulus, as measured by fMRI

[7] Simon effect is the phenomenon that reaction times are usually faster and more accurate when the stimulus occurs in the same task-irrelevant relative location as the response.

biologically tuned and occurs only when participants interact with conspecifics, but not with a non-biological agent (e. g. wooden hand) [286].

Due to these contradictory findings, it is still not clear how the MNS processes observation of actions performed by artificial agents. Further, it is unclear how the MNS activity is modulated by goals of actions which are performed by artificial agents.

1.6.2 **Action and actor familiarity**

Familiar actions have been shown to evoke higher MNS activity than unfamiliar actions and observer's prior motor experience in observed actions seems to correlate with the signal increase in the MNS areas [2,47,74,75]. Given that we have more motor expertise with human actions than with robotic actions, one might predict stronger MNS-activation when observing human actions. Consistent with this assumption, a number of studies investigating the plasticity of the MNS showed a stronger MNS-response when the observed actions were performed by human compared to (i) robotic agents [66,195,261,276], (ii) other non human agents [71,91], (iii) animals [31] and (iv) same-race than different-race individuals [184]. Also behavioral work investigating how observed actions influence simultaneously performed actions has reported greater interference effects when participants watched a human actor moving with human kinematics compared to constant velocity [165], and when watching a robotic agent moving in a human-like manner compared to an artificial manner [212]. Further, [32] proposed that only actions belonging to the motor repertoire of the observer (e.g., biting and speech reading) are mapped into the motor system of the observer whereas actions that do not belong to the natural repertoire of a human being (e.g., barking) are recognized based on their visual properties.

There is experimental evidence that in healthy individuals, also familiarity with the observed actor modulates the activity in regions of cortex thought to contain mirror neurons [47,48]. Regions of inferior frontal gyrus (IFG) and inferior parietal lobule (IPL) also show preferential activity to faces of self as compared to familiar other faces [289]. Therefore, the MNS and thus the capability to attribute intentions may be sensitive to the familiarity of both the kinematics of movement as well as the actor's appearance. Knowledge about this issue is important for the design of humanoid robots for interaction with humans.

1.6.3 **Biological motion**

Biological motion is a motion of a biological agent engaged in a recognizable activity, such as walking or performing sports. Besides being non-rigid, biological motion is characterized by a number of constraints caused by the articulated structure of the animal body [265]. The information about the type of motion can be recovered even from sparse input, like point-light displays (moving images created by placing lights on the major joints of a walking person and filming them in the dark) [155]. The ability to perceive biological motion arises early in life. Already at four months of age infants look at human point-light motion sequences for longer durations than at the same number of point-light dots undergoing random motions [14].

On the neuronal level, it seems that biological motion triggers a stronger activation of the human MNS than non-biological motion [125,254,291]. The importance of biological movement for triggering motor resonance has been supported by investigations performed by [165,212]. The authors tested how observed actions influence simultaneously performed actions. They reported greater interference effects when participants watched a human actor moving with human kinematics compared to constant velocity profile [165] and when watching a robotic agent (see Figure 6c) moving in a human like manner compared to a non-biological manner [212]. Additionally, TMS studies show that the detailed temporal characteristics of an observed human movement are reflected in the motor system of the observer [21], indicating that the MNS is very sensitive to how a movement is performed. However, accurate biological movement velocity in a robot is only possible by implementing human prerecordings into robot’s motion. In my study, we would like to test when also an approximation of biological movement (minimum jerk, see section 3.1) might be sufficient for perception of a robot as an interaction partner.

1.6.4 **Movement variability and self-propulsion**

A number of studies suggest that another factor, which might be of crucial imprtance in perceiving someone's action as being goal-directed, is the variability of movement (typical for biological but not artificial agents). Thus, significant activations of the MNS during observation of videos of a robotic hand were shown in [112], but only if the hand performed 5 different actions within a block and not when the exact same action was repeated for 5 times in a row. Similarly, in an earlier study, infants might have been unable to attribute goals to a moving box because it repeated exactly the same movements in consecutive trials [226]. Thus, in a different study using the same setup but a variable box trajectory in every trial, 6.5-month-old infants were capable of attributing goals to the box [79]. Therefore, movement variability might be important feature for designing robots for the human-robot interaction. This is also an issue which I would like to test in my study.

Another agent characteristic which seems to play a role in intention attribution is the capability of self-propulsion. In a recent study, five-month-olds attributed goals to a self-moving three-dimensional block after seeing it repeatedly move back and forth across the stage [185]. However, they did not attribute goals if the block had a handle extending past the stage, so that it was not clear whether it moved itself or has been pulled by the experimenter. Thus, one cue for characterizing an entity as an intentional agent might be the capability of abruptly changing the speed and the direction of movement, undergoing non-rigid transformation, or generally being capable of independent and irregular movements [226].

1.6.5 **Top-down effects**

It seems that during observation of a non-biological agent, already an imagined suggestion about its nature might have an effect on the behaviour of the observer. Liepelt & Brass (2010) tested the effect of a belief manipulation about the animacy of an observed action in a motor priming task by using an animation of a moving leather hand [182]. Before the experiment, the participants were presented with either a human model or a wooden hand wearing a leather glove. Although a basic motor priming effect was present regardless of whether participants believed that the movement was executed by a biological or a nonbiological agent, the priming effects were larger when participants believed to interact with a human hand rather than with a wooden hand. In [287], the participants performed the complementary social Simon task under the implemented belief of interaction with either an unseen human or a computer program. Despite the fact that all response sequences from either “partner’’ were generated by computer, results indicated that the strength of Simon effect was higher in the “human” condition, indicating that believe about agent nature might influence how we perceive our interaction partners.

Further, similar effects were also found in a different study [270]. The authors compared the interference effect during observation of a moving person with observation of either biological or non-biological moving dot stimuli. Interestingly, MI was only observed for both biological and nonbiological velocity profiles when the participants were informed that they were observing pre-recorded human movement and not when the dot motion was described as computer generated. Thus, it seems that the relevant processing of the dot motion might involve the participant imagining the (unobserved) arm movement that caused the observed dot motion, leading to activation of premotor neurons and hence the interference effect.

These findings suggest that the belief regarding the biological origin of an agent might play a critical role in the triggering of the interference effect. In support of this, it has been shown that in human–humanoid interaction, the perception of an agent as a “social entity”, for example, due to the observer’s beliefs, is critical for eliciting MI rather than any individual appearance or motion kinematics [257]. Therefore, it seems that not only the appearance of the agents matters but also the belief about their nature. Even if they are not visible, the fact that they are non-biological may impair the simulation procedure. Notably, previous studies which reported similar MNS activations for observation of human and robotic actions used stimuli depicting only the hand of the artificial agent [112,206]. It is therefore not implausible that subjects entertained the possibility that the hand might have been controlled by a human being. In my study, we do not use body parts or abstract stimuli for the presentation of robot movements. Instead, we show whole-body movements minimizing the possibility that the subjects imagine that the movements of the robot are controlled by a human.

It seems that personal attitudes to the observed actions matter [261]. The authors used fMRI to investigate the effect of personal attitudes on perceptions on dance which was performed by a human agent and a humanoid robot in either an artificial (rigid, robotic) or a natural manner. The perception of motion smoothness was characterized by a large intersubject variability which resulted from differences in personal backgrounds and attitudes toward expressive body actions. The results of this study indicate that action processing is influenced by personal attitudes to the art of dancing during observations of expressive body actions.

1.7 **Possible implications of present findings**

In the future, humanoid robots might be used for the variety of tasks, for example, personal assistance duties [305], teleoperation or even cooperative work in the open air [18]. Robots might have a potential use in education and therapy of children with autism spectrum disorder[8], elderly care (e.g. nursing homes) and neurorehabilitation[9]. Due to an increase of life expectancy and a reduction of child birth rate in many industrialized countries, the amount of people who require assistance in everyday activities will grow in the future. A decent proportion of these people will spend much time in nursing homes. At the moment, it is unclear who will take care of all of these old people. Therefore, one prospect is to use robots with appearance based on the human body to perform human tasks such as providing personal assistance or cognitive therapy.

1.7.1 Role of anthropomorphism in acceptance of robots

Human-like robots like ASIMO [190], HPR-2 [300], Armar III [4], or Toyota partner robots [176] may prove to be the ideal agents to interact with people because they have human-like bodies. Many researchers argue that using robots with a humanoid form will make the interactions with them more intuitive and pleasant because people will be able to use their experience from social interaction with other humans when interacting with robots [26,27]. Thus, the effort on the part of the user dealing with the requirement to learn a new technical vocabulary will be minimized. Further, human-like bodies will allow the humanoids to integrate into environments already designed for human morphology. Thus, it is traditionally assumed that the obvious strategy for integrating robots successfully into human environments and increasing their acceptance for the majority of non-technical users is building them with a certain degree of anthropomorphism [88]. The tendency to anthropomorphize increases with the number of human attributes displayed by an artificial agent [86], A human-looking shape and fluent, predictable movements are supposed to enable even untrained people to apply social models acquired with human partners to naturally and intuitively explain, understand, and predict what a robot is about to do.

Some researchers have tested how people perceive robots of varying degrees of human-likeness. Goetz and colleagues showed that people prefer more humanlike robots for jobs requiring more sociability [118] and also Krach and colleagues showed a linear relationship between the degree of anthropomorphism of a machine (computer, functional robot, humanoid robot, human) and cortical activation in brain areas related to ascribing mental states to agents [170]. Further, Hinds and colleagues demonstrated that, in a joint task, mechanical-looking robots are treated less politely than robots with a more human-like appearance [141]. Further, this study showed that humans treated mechanical-looking robots in less socially interactive way compared to more human-looking robots. Thus, our expectations are higher with regard to abilities and reliability for humanoid robots in contrast to mechanical-looking robots. This reduces the uncertainty and facilitates collaboration.

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[8] Autism is a complex developmental disability that causes problems with social interaction and communication.

[9] Neurorehabilitation facilitates the recovery of functional skills lost after neurological diseases or accidents.

1.7.2 Applications of humanoid robots in the medical sector

Robots for assisting everyday duties offer a significant advantage in addressing the need of the elderly to ameliorate the motor deficits caused by major age-associated neurological syndromes such as stroke. In the medical sector, humanoid robots can provide assistance to the patients with mental or motor skill impairments by giving them physical therapy, instructing them on task goals, coaching them, monitoring their performance. In the home setting, robots might support independent living (e.g. eating, bathing, toileting, getting dressed, providing household maintenance). Examples of assistive robots are 'nursebot' Pearl [220] , or the German Care-o-bot [121] . A healthcare robot can perform tasks which might not be possible or practical for humans: e.g., lifting a bariatric patient or monitoring medication levels in a patient's system. Recent studies demonstrated the success of using assistive robots in elderly care [277], social learning in children with autism spectrum disorder [95] and stroke rehabilitation [191].

Apart from assistive living, an important sector in which humanoid artificial agents will be used in the future is neurorehabilitation. While human caregiving cannot and will not be replaced, assistive artificial agents can extend substantially the capacities of therapists who work with patients suffering from motor impairments after stroke. Many patients who suffered stroke go on to live with motor disabilities like some level of paralysis, with one side being more affected than the other. Those affected may have difficulties performing everyday activities such as eating, dressing, using the bathroom and grasping objects. The patients often compensate for upper extremity deficits by using the less–affected (non–paretic) arm, and voluntarily suppressing the use of the more–affected (paretic) arm. Therapeutic interventions for stroke typically consist of intense one–on–one practice with a trained clinician. They aim at encouraging the use (and recovery) of the paretic arm and restoring the capacity to manage the activities of daily living. Over the last decades, promising strategies have been introduced based on action observation therapy [101]. Action observation produces an increase in the excitability of the corticospinal path and therefore facilitates subsequent movement execution (for review see [33] by directly matching the observed action onto the internal simulation of that action. It has been shown that action observation has a positive impact on recovery of motor functions after stroke [92] and there is evidence that action observation may also induce cortical plasticity [271]. The authors showed that when participants simultaneously performed and observed congruent movements, the learning of these movements was potentiated with respect to learning through motor training alone. This indicated that the coupling of observation and execution strongly facilitates the formation of motor memories. Since the action-observation training should optimally be repeated during the therapy course many times, humanoid robots might serve as models for training and relearning tasks by imitation in patients who suffer from hemiparesis after stroke. With the help of robots, individuals will use the affected limb in the types of meaningful, unconstrained, functional tasks that are encountered in daily life, and can also practice in the home setting.

Another field where humanoid robots are currently applied in the clinical setting is the therapy of Autistic Spectrum Disorders (ASD). Recent studies suggest that interaction with robots can trigger imitative behaviour in children with ASD because in these children the neural mechanism underlying the coding of observed actions might be tailored to process socially simpler stimuli and be not able to process the highly complex and potentially unpredictable behaviour exhibited by humans [244]. Also, the robot is not limited by the emotional responses (like getting stressed and inpatient) which human therapists may have during treatment. Thus, the use of humanoid robots allows for a simplified, safe, predictable and reliable environment where the complexity of interaction can be controlled and gradually increased. The robots may serve as therapeutic and educational aides to teach children with ASD basic social skills. These skills will help them to communicate and interact with others.

Among the robots designed for communication there are not only assistive robots used for service such as the support of independent but also pet-like companionship robots the function of which is to enhance health and psychological well-being of elderly users by providing companionship. Examples are the Japanese seal-shaped robot Paro [297], the Huggable [273] both specifically developed for experiments in eldercare. Another example of interactive robot, a creature-like robot, Keepon, has a potential to be used in the remedial practice for children with autism [169]. Social functions implemented in companion robots are primarily aimed at increasing health and psychological well-being such as increasing positive mood in elderly living in nursery homes. Some robot platforms, like for example “CB” [68] can also be used to study the underlying processing of the human brain and the results of this research can later be used in the treatment of social impairments.

2 Aims and Hypotheses

In this thesis, I investigate behavioral and neural correlates of goal understanding in humans and non-human primates. To test how different characteristics of agent's appearance contribute to the ability of attributing goals on the behavioural and the neuronal level I use artificial agents. The advantage of using artificial agents in contrast to humans is that their appearance and action kinematics can be manipulated in a more simple way than the complex aspects of human morphology and behavior. The suggestion that using humanoid robots in the neuroscience research will lead to a better understanding of mechanisms involved in social interactions has already been proposed by a number of previous studies [61,64,68].

My first aim was to find out whether, during observation of movements directed to different goals, the goals of the action will be covertly simulated by the observers' MNS independently of the agent nature (human vs. artificial). The second aim of the thesis was to investigate what morphological and kinematic features an agent has to exhibit so that observation of his action will lead to motor resonance on the part of the observer. This motor resonance will in turn produce motor interference in the movements of the observer if the observed action is incongruent to the performed action. Finally, I wanted to investigate whether the goal attribution capacity is an evolutionary heritage and whether goal understanding is a precondition for simple forms of social learning.

Clarifying these questions will lead to better understanding of processes that are required for successful and intuitive intention understanding. In the future, my results might contribute to a better understanding, diagnosis and therapy of medical conditions involving the impairments of social cognition such as autism spectrum disorder, schizophrenia, psychopathy or social phobia. Further, the findings will be of importance for the design of humanoid robots for social interaction with humans in the area of medical therapy. In the future, human-like artificial agents could help patients with hemiparesis to train their paretic arm and relearn daily activities. They can also be used as assistants for the elderly in nursing homes and in therapy for children with autism spectrum disorders.

In the following, I will explain what aspects of intention understanding and motor resonance have been accessed in individual studies performed in this thesis.

2.1 Agent's features which facilitate motor interference in dyadic interaction[10]

As stated in the introduction, to date it is not clear whether motor resonance and thus motor interference need a tight match between one's own and the observed agent's physical features

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[10] Parts of the text used in this chapter have been published as "Kupferberg A, Huber M, Helfer B, Lenz C, Knoll A, Glasauer S. (2012) Moving Just Like You: Motor Interference Depends on Similar Motility of Agent and Observer. PLoS ONE 7(6): e39637. doi:10.1371/journal.pone.0039637"

to emerge during action observation. These features could be, for example, presence of certain morphological features (a body, head, face, and extremities), ability to move determined by joint configuration (motility) or movement kinematics (trajectory, velocity and variability).

In the original study, which tested the influence of movement observation on the movement of the observer [166], motor interference (MI) appeared in case of human movement but not in case of artificial movement produced by an industrial robot (see Figure 6b). Interestingly, two later studies have demonstrated MI when subjects watched a humanoid robot performing movements based on implemented prerecordings of motion in a human experimenter (see Figure 6c) [62,212]. Interestingly, this MI disappeared when the same robot moved with a constant-velocity profile. However, it is still unclear which aspect of human motion, absent in robotic movements, was responsible for evoking MI while observing movements based on human prerecordings. Thus, the interference effect in [62,212] might have been triggered by either non-constant velocity (acceleration and deceleration), or variability of movement amplitude and trajectory (e.g. due to fatigue or constraints caused by anatomy of the human arm) during repeatedly presented movements. Further, previous studies which indicated the importance of biological velocity [62,212] were not able to disentangle whether biological motion is the only requirement for MI or whether other morphological similarities between agent and observer have to be present. Finally, previous studies have compared only biological vs. constant velocity profiles but have not investigated whether an artificial approximation of the biological velocity might be sufficient.

Thus, in the absence of top-down cues, the question remains which basic features of the observed agent and the observer have to match for MI to occur. In this study we investigated what aspects in the appearance (for example, head and body), motility (ability to move resulting from the joint configuration) and movement kinematics (variability, velocity) of the observed agent are responsible for triggering MI during observation of incongruent movements (see Table 2). With motility, we mean the ability to move. Thus, with “similar motility” we refer to the capacity of an agent to move in a similar way as another agent. As an example, although a dolphin and a shark have a similar body shape, they swim using different styles: due to the different configuration of their body, sharks swim in a side to side motion and dolphins swim in an up and down motion. In my study, when using the robots, we manipulated the configuration of the robot arm “JAHIR” relative to the observer.

If artificial motility and appearance were sufficient, we expected to see an effect of MI on movement production while viewing videos of incongruent movements performed by an industrial robot arm JAHIR. Alternatively, absence of MI during observation of artificial motion of an industrial robot arm might be caused by either its artificial motility, which results from the joint configuration that does not match the one of the human arm, or its artificial appearance. To test for the role of biological motility, we presented subjects with the rotated video of the industrial robot arm (JAHIR 90°), which in respect to joint configuration now resembled more a human arm (see Figure 8). In the comparison between the two videos of the industrial robot arm, the kinematics of the end effector (the gripper) of the robot arm did not change relative to the observer, but the kinematics of the joints relative to the observer did, since the video was turned by 90°. To test for the importance of human-like body shape, we presented the subjects with a humanoid robot which had the same industrial arm mounted in a human-like configuration, but additionally had a torso and a head. In case that the biological motility but not the appearance is required for MI, we expected to see MI both for JAHIR 90° and JAST. In case that only human-like appearance is required for eliciting MI, we expected to see MI only in case of humanoid robot and human, but not when observing an industrial robot.

In case that movement variability is not important for triggering MI, we expect the interference effect to be present during observation of incongruent movements of at least the humanoid robot which had human-like appearance and motility. Otherwise, if movement variability is important, the MI would be present only for the observation of the human agent.

	Movement kinematics (biological velocity and movement variability)	Human-like appearance	Human-like motility
Human (MH)	+	+	+
Humanoid robot (JAST)	-	+	+
Industrial robot arm, human-like configuration (JAHIR 90°)	-	-	+
Industrial robot arm, artificial configuration (JAHIR)	-	-	-

Table 2: Summary of agent characteristics in the MI study.

2.2 Neural correlates of goal attribution during action observation– an fMRI study

If the MNS is involved in intention understanding through simulation, its activation makes the goal attribution possible. But how does it react if the observed agent is not animate and does not move with a biological movement velocity? The studies which have shown similar MNS-activity in response to observation of robots and humans [76,112,206,253] have only compared a repertoire of simple motor actions (as a whole) performed by humans with those performed by robotic actors. No study investigated whether there is differential MNS-activity between the actions of an artificial agent targeted at different goals. In the past, only one study investigated the coding of different intentions in artificial agents, failing to show MNS activations perhaps because using animated computer-generated agents instead of video recordings [56]. However, similar activations when observing motor acts performed by humans and artificial agents (as shown by [76,112,206,253]) do not necessarily imply that the same networks are involved in understanding the goals of actions of the artificial agent. Indeed, during action understanding we not only recognize motor acts such as grasping or pointing to an object based on the movement pattern (motor intention such as grasping or pointing), but also the “higher” goal in which these acts are embedded (cognitive intention). Thus, every single intentional motor act is often involved in a further action chain leading to a predefined outcome. For example, grasping (motor intention) directed at a certain goal (e.g. piece of bread) is an intentional action, which, in a hierarchical system of action understanding stands above the elemental action of grasping (which can be recognized by movement pattern), but below complex action chains such as making a sandwich (cognitive intention, see Figure 7). Thus, the question, whether MNS differentiates actions directed to different goals performed by a robot is not trivial. Understanding action goals and attributing intentions requires understanding the actor's motivation in reaching for a certain object. It is a step toward recognizing the actor as an intentional agent despite the knowledge that it cannot have mental states. For the human observer it might be therefore difficult to attribute the intention of, e.g., repairing something when he/she sees a robot grasp a tool, and even more difficult to think about eating, when food is grasped by the robot. Consequently, even if the grasping action of a robot activates the observer's MNS, object-specific coding of the intention associated with the observed action is expected only if the observer interprets the grasping action with respect to a potential future goal. Alternatively, it is possible that actions of the robot might be recognized solely on their visual properties, without being simulated. Thus, in a previous study it has been shown that actions which do not belong to the motor repertoire of the observer, like monkey's lip-smacking or dog's barking, cannot be mapped in the on the observer's motor system and instead are recognized based on their visual properties [32].

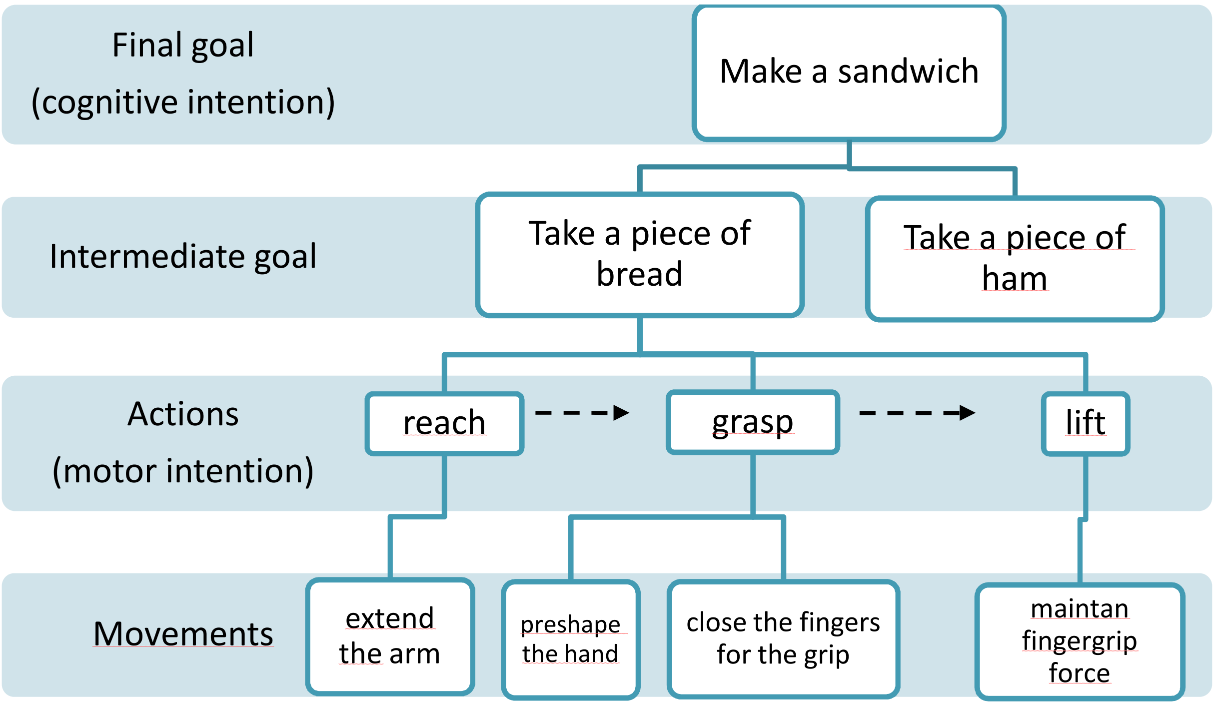

Figure 7: Hierarchical organization of movements, actions, goals and intentions. A final goal may involve several immediate goals, each of which requires a sequence of basic actions, and each action is composed of several movements.

In the present study, we used fMRI to investigate the flexibility of the MNS during observation of hand actions of an inanimate agent focusing on MNS-involvement in recognizing different action types (e.g. grasping vs. pointing) and processing their goals. To this end, we compared brain activation while watching videos of grasping and pointing actions aimed at different object categories (tools and food items). The different object categories suggest different motor intentions in the action chain (e.g. eating something vs. repairing something). If the MNS is sensitive to different action types performed by the robot, we expected to see a stronger activation in the IPL for grasping vs. pointing actions based on previous human studies contrasting observation [122,219] and execution [102] of grasping and pointing actions. In case that, similar to a human agent, the MNS is involved in processing goals of inanimate agents, the robot's actions will be considered goal-directed, we expected to see a differential activation in the IFG and IPL and premotor cortex (PMC) when comparing actions directed to different goals. The activation of these regions has previously been observed in studies investigating intention attribution by contrasting MNS activity triggered by observation of similar or same action types aiming at different goals [130,131,148,177] and comparing goal-directed actions to non goal-directed actions [168]. To make sure that the possible difference in MNS activation for different object categories is not a result of superficial object features resulting from hand-object interaction (position of fingers, grip type), we used multiple objects with different shape and size in every category. Using pointing as a contrast to grasping is motivated by the fact that apart from the difference in kinematics, the first one, being a communicative gesture [281], can either indicate the actor's desire to later interact with the object (e.g. grasp it), or be used for directing someone's attention to the object to fix a common frame of reference. Communicative actions have been shown to trigger no priming effects when performed by an artificial agent [183] and, in contrast to a human partner, a sudden social request from a robotic agent had no influence on the kinematics of a pre-planned action [251]. Therefore, observation of pointing performed by the robot might lead to a different activation pattern in the MNS than if the actions are performed by a human.

2.3 Is goal understanding innate? – a preferential looking times study

It is most likely that the neural circuitry thought to support social cognition consists of mechanisms that are relatively old in evolutionary terms. In the past decade, fMRI and EEG and behavioral studies have been conducted to investigate how we think about others' minds, how we understand actions, how we feel about morality and how we perceive emotion. However, much of this work has focused mostly on humans. Few studies have examined brain mechanisms of social cognition in non-human primates. As stated in section 1.3.1, there are two different accounts considering the origin of the intention attribution capacity. The first group of researchers claims that it is innate and triggered by certain biological features [99,51,157,180,224,226]. The second group of researchers argues that goal attribution is first learned by collecting experience with human agents and later gradually extended to agents which are less human-like [194,197,282,304], such as dolls. However, it is difficult to test whether intention attribution to dolls is innate because infants are familiar with using them as intentional agents in play situations with other infants or their parents and thus may be eager to attribute goals to them. Thus, the findings available so far are not able to distinguish whether the very young infants' understanding of goal-attribution is based on associative learning or triggered by innate cues because in both cases later fine tuning could be possible [52]. Similarly, using human agents as models for testing goal-understanding in monkeys [40] using the Woodward paradigm [304] (see section 3.3.1) might have a limitation that captive marmosets are exposed to humans on a daily basis. Thus, it is not possible to distinguish whether this flexibility is simply based on associative learning processes or whether there is a more general goal-attribution mechanism, which responds to a broader array of potential intentional agents. Using previously never encountered agents, like monkey-like robots, where no associations could be formed before the experiment, may help to clarify whether intention understanding is innate. Common marmoset is a small New World monkey and a well-suited species for answering these questions, since this primate is renowned for its well developed social skills (reviewed in [38]).

	Experience	Monkey-likeness (legs, head, quadruped, tail)	Biological motion
Conspecific	+	+	+
Robot	-	+	-
Box	-	-	-

Table 3: Summary of agent characteristics in the preferential looking-times study

By manipulating the appearance and the motion of the used model agents we might help to answer the question regarding which cues (e.g. presence of a body with a head, biological motion, monkey shape and size) an unfamiliar entity must exhibit in order to be perceived by these monkeys as an intentional agent (see Table 3). To pinpoint the role of familiarity, biological motion kinematics and monkey-like features for intention understanding, we performed three different experiments. In the first experiment, we presented the marmoset monkeys with videos depicting goal-directed actions of a conspecific agent. In the second experiment, we presented the monkeys with actions of a monkey-sized quadruped robot with head and tail and in the third experiment, the same robot disguised as a box. In contrast to the experiment with a human agent as the model [40], the robot’s size and shape were similar to those of a conspecific. However, the robot could not move with a biological velocity, giving us an opportunity to test for the influence of movement velocity on goal attribution. Finally, covering the robot with a black box allowed us to test for the role of body shape for goal attribution. Importantly, in contrast to a human agent and a conspecific, the marmoset monkeys have never observed the robot or the box being engaged in goal directed actions so that goal attribution to these agents might indicate an innate capacity to do so.

Since a number of studies demonstrated a link between intentional understanding and social learning in humans infants, (e.g. [267]), the second aim of the study was to investigated whether the link between the goal-attribution capacity and social learning is a human development or whether it is already present in non-human primates. The type of learning we investigate in the present experiment is called stimulus enhancement. It is a form of social non-imitational learning which occurs when the observation of a conspecific performing an action on an object facilitates the probability of interaction with that object, even in the absence of the demonstrator and at a later time point [139,140]. Stimulus enhancement is a common proximate mechanism fostering safe incorporation of novel foods into the diet of naive individuals from more knowledgeable individuals.

We expected that stimulus enhancement, like imitation [178,280,282], might be linked to goal attribution. To test this hypothesis, after the last test trial of each experiment, each monkey was allowed to enter the testing compartment and make the choice between the two objects seen in the videos. In contrast to [34,296], we do not use food reward but the natural curiosity of monkeys towards new objects. If the monkey's first choice and the time which it spent exploring the object were influenced by the agent’s choice only if they perceived it as an intentional agent who behaves in a goal-directed way, this would suggest that (i) the function of the perception of goal-directedness goes beyond action understanding and drives the own behavioural choice of the observer and (ii) the social learning mechanism at work goes beyond a reinforcement of interest towards the object approached by a second entity.

3 Experimental procedures and data analysis

3.1 Agent’s features which facilitate motor interference in dyadic interaction [11]

We[12] used the MI paradigm described in [212], but replaced live presentations with video clips depicting horizontal and vertical movements of either the humanoid robot JAST or a human agent. The use of video presentations allowed us to control for the between-subject variability in the movements of the human agent, which might lead to variability in the subjects' movements. Further, by implementing the so called *"minimum-jerk"* velocity profile [97] into the movements of the robots, we achieved a quasi-biological acceleration and deceleration without movement variability. Similar to a biological non-constant velocity movement, the implemented minimum-jerk movement starts slowly, accelerates smoothly to a peak velocity near the midpoint and then decelerates slowly [179]. This results in a smooth, bell-shaped velocity profile, in which mathematically the derivative of acceleration (jerk) is minimized over the movement. Thus, by preventing abrupt changes in movement velocity, in contrast to the constant velocity profile, minimum-jerk movements look smoother and more natural [144].

3.1.1 **Subjects**

Eleven female and fourteen male graduate students from the local Department of Neurology participated in the first experiment. Twelve female and ten male right-handed graduate students from the local Department of Neurology (age range: 20-25 years) participated in the second experiment. The experiments were approved by the ethics committee of the medical faculty of the LMU and conducted in accordance with the Declaration of Helsinki. All participants gave their written informed consent.

3.1.2 **Stimuli**

In the first experiment, the videos of both the robot "JAST" (see Figure 8b) and the human (see Figure 8a) agent were rear-projected in a pseudo-randomized order on a white semitransparent screen (120cm×160cm) located ca. 1.5m in front of the participant. The use of video presentations allowed us to control for the between-trial variability in the movements of the human agent, which otherwise might have been an additional factor causing increased variability in the subjects' movements. JAST had an “animal” head, and a torso with two industrial arms covered with a plastic “shirt”. The robot was capable of producing movements

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[11] Parts of the text used in this chapter were published as “Kupferberg A, Huber M, Helfer B, Lenz C, Knoll A, Glasauer S. (2012) Moving Just Like You: Motor Interference Depends on Similar Motility of Agent and Observer. PLoS ONE 7(6): e39637. doi:10.1371/journal.pone.0039637”

[12] I will use “we” throughout the methods and results sections, not as pluralismaiestatis, but as pluralismodestiae. This work has been conceived with the help of many people, so I will use “we” to speak for all of them.

with human-like minimum-jerk velocity profiles directed by the shoulder joint (Huber et al., 2008). The human agent shown in the videos was always the same male person.

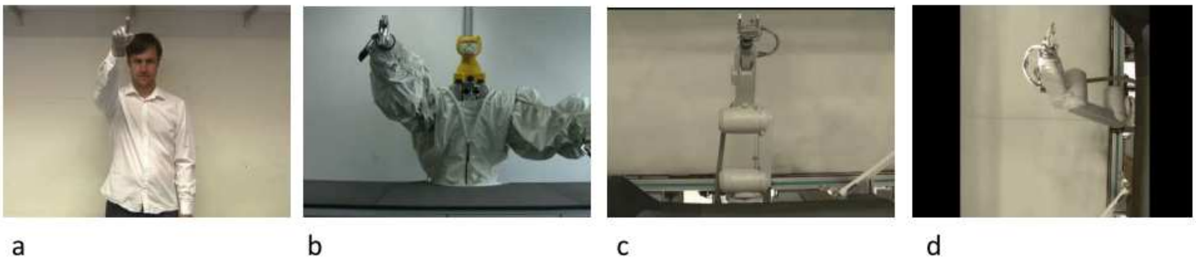

Figure 8: Screenshots from the videos used in the MI-study. The participants were instructed to perform horizontal or vertical movements while viewing the videos and fixating on the right hand of a) a human agent (MH), b) the humanoid robot JAST, c) the industrial robot arm JAHIR and d) JAHIR rotated. The agents performed congruent or incongruent movements. Figure was adopted from [175] with permission from the publisher.

In the second experiment, the videos of the human agent and the industrial robot arm JAHIR (Mitsubishi, RV-6SL; Figure 9; see [179]) were rear-projected on the screen in a pseudo-randomized order (see Figure 8c). In contrast to the humanoid robot JAST, which had an “animal” head and the robot arm, JAHIR consisted of one of the arms of JAST and has been left uncovered. Thus, both robots had arms with six degrees of freedom and were capable of producing movements with a minimum-jerk (quasi-biological) velocity profile [97]. The forearm ended in a metallic gripper connected by a wrist joint (see Figure 8c, d).

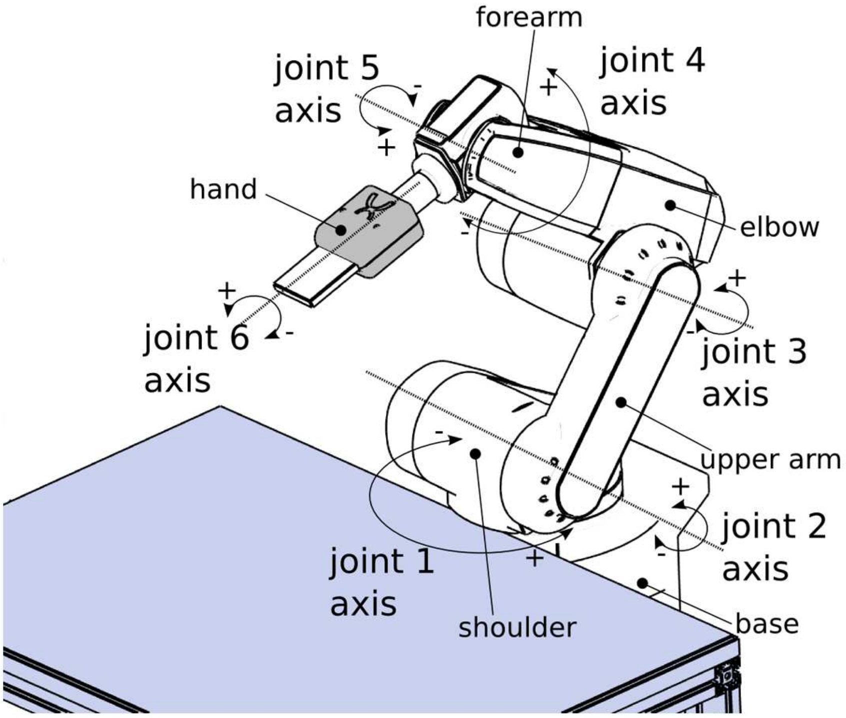

Figure 9: Drawing of the robot arm JAHIR. JAHIR consisted of a base, upper arm and forearm connected though joints. Figure was adopted with permission from [175].

JAHIR consisted of a base, an upper arm and a forearm which are connected through a shoulder joint and an elbow joint (shown by circle arrows in the Figure 9) and was mounted on a working bench (see Figure 8c). To make the joint configuration resemble the joint configuration of the human arm for additional testing, for the second test condition, the video of JAHIR was rotated 90° to the left (see Figure 8d). Thus, the configuration corresponded to that of JAST.

During the vertical condition, JAHIR performed an up-and-down movement with an amplitude of 50 cm using its shoulder joint (J2 axis) and the elbow joint (J3 axis) (see Figure 9). During the horizontal condition the movement was performed by the shoulder (J1 axis and J2 axis), the elbow (J3 axis), and the wrist joint (J5 axis).

3.1.3 **Procedure**

The human experimenter depicted in the video clip performed horizontal and vertical movements with the amplitude of 50 cm. To make the robot gripper and the human hand look more similar, his hand had been painted in a silver color (see Figure 8a).

In an additional baseline control condition, the subjects were instructed to produce horizontal and vertical movements without looking at their arm.

In the first experiment, the observed agent (H, human or R, robotic) performed either spatially congruent (C, same direction) or incongruent (I, perpendicular) movements (frequency: 0.5 Hz) with the right arm (see Figure 10a, b). Like in the second experiment, this resulted in a 2×2×2 experiment design with eight experimental conditions and three factors: (1) *movement plane (*Horizontal/Vertical), (2) *congruency* (Congruent/Incongruent), and (3) observed *agent* (Human/Robot) plus 2 baselines.

In an additional experiment 10 participants who participated in the second experiment were retested while viewing horizontal and vertical, congruent and incongruent videos of the robot JAHIR. For this experiment, the videos of JAHIR were rotated 90 degrees to the right and scaled in a way that the movements of the robot arm had the same horizontal and vertical amplitude in both directions as in the original video. For an overview of all conditions see Figure 10.

In both experiment, one trial (duration: ca. 30s) was performed for each of the eight conditions. At the start of each new condition, the participants were informed (by an instruction appearing on the screen) of the plane in which to move their arm and instructed to keep in phase with the experimenter's and robot's movements. The kinematics of the endpoint of their right index finger was recorded at 240 Hz using the magnet-field based motion tracking system Polhemus Liberty (a small 1×1 cm sensor was fixed to the tip of the participant’s index finger).

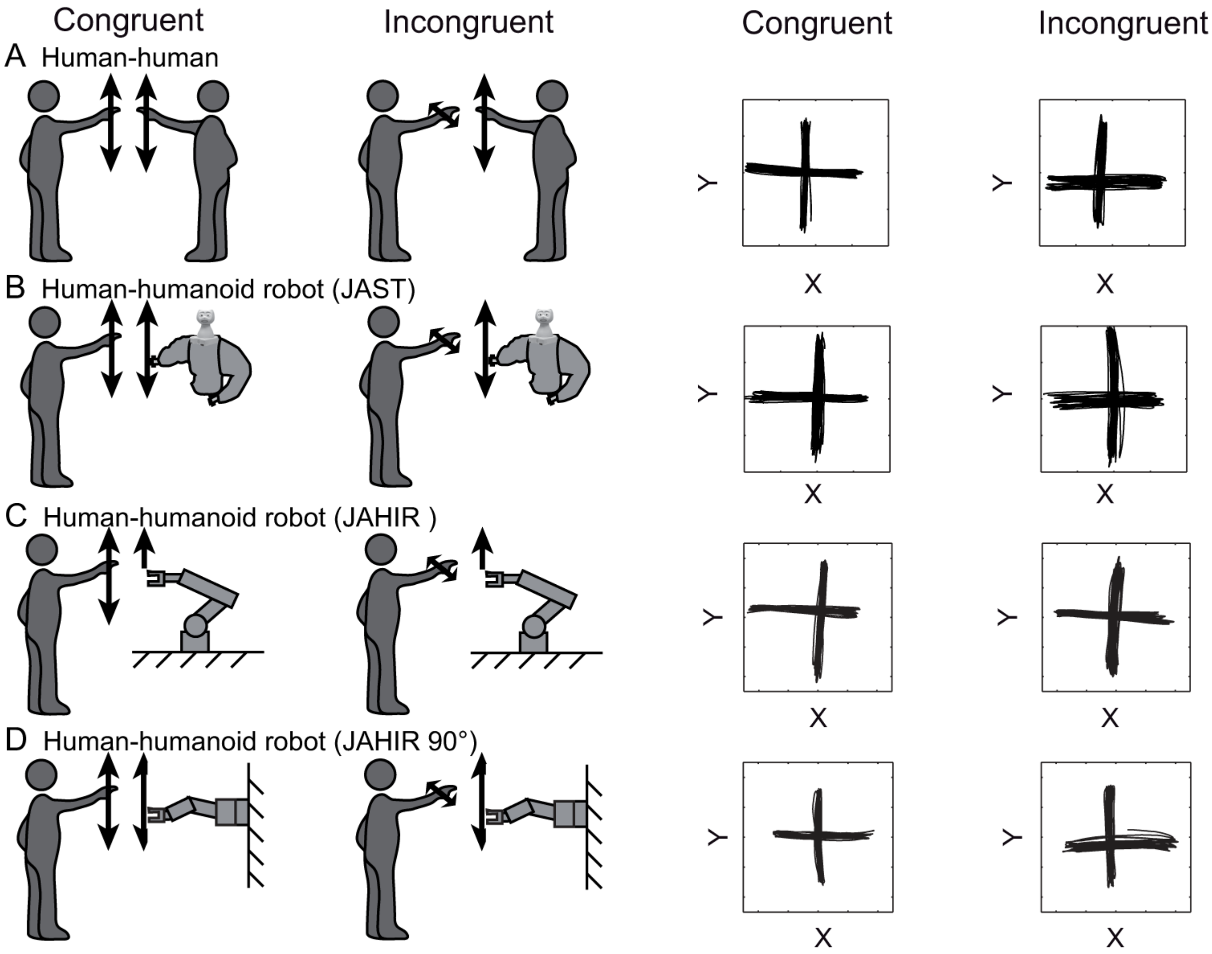

Figure 10: Overview of all experimental conditions in the MI-experiments. Left: experimental conditions (only vertical agent movement is shown). Right: examples of movement trajectories performed by the observing subjects. Figure was adopted with permission from [175].

3.1.4 Data analysis

After data acquisition, fingertip positions of subjects were filtered with a 20Hz second order Butterworth filter and the data from each trial was split into single movement segments (from right to left and from top to the bottom and vice versa). This split was done by finding data points at which the x-values (in case of horizontal movement) and z-values (in case of vertical movement) reached their maxima and minima (for a sample of horizontal movement, see Figure 11). The standard deviation of fingertip position within the plane orthogonal to the plane of movement (see Figure 11c) was used to quantify the interference. The mean of the deviations of all single movements within one trial was calculated for each subject and then across all the participants.

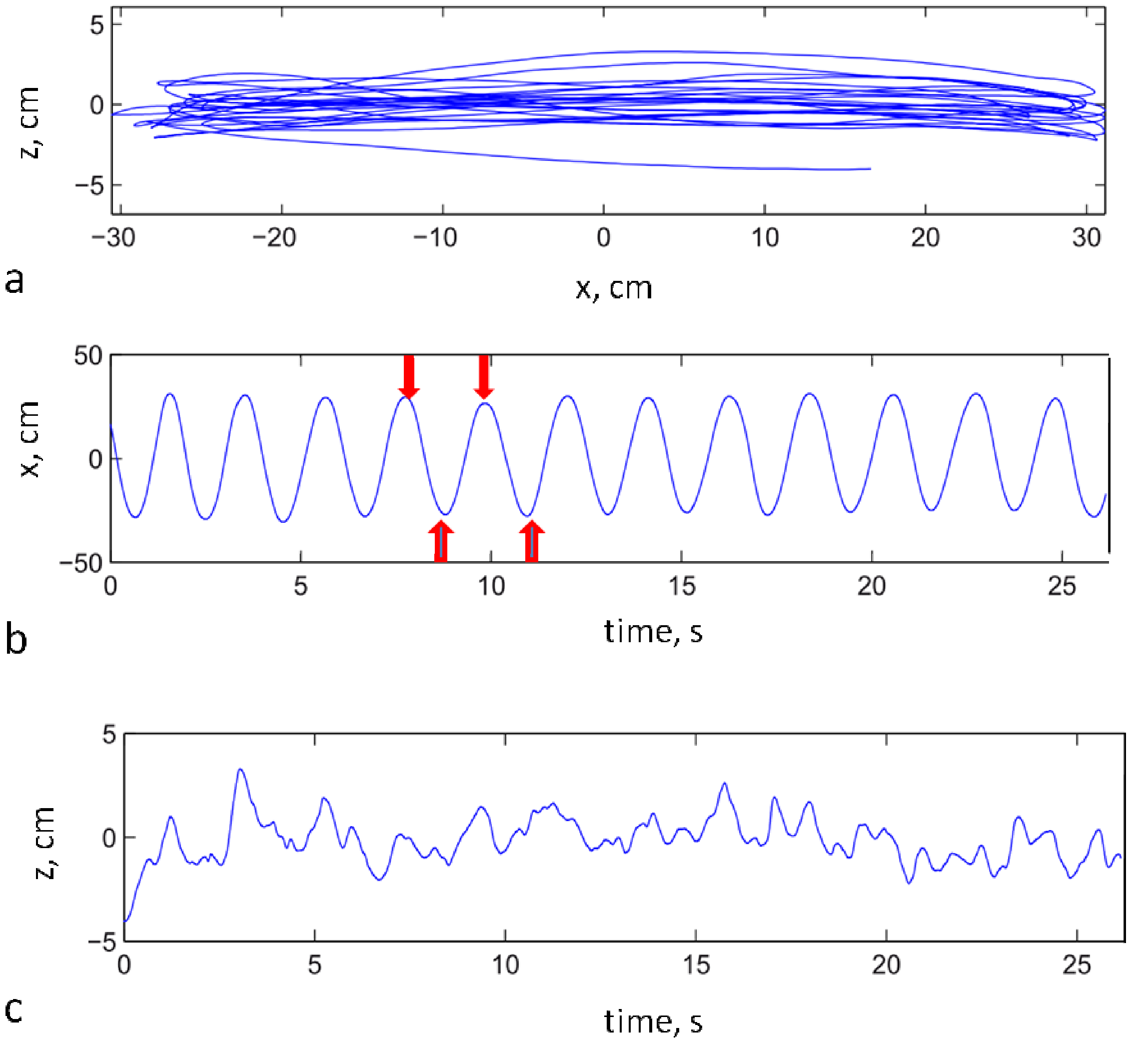

Figure 11: Sample of movement trajectory variance in the z- and x-plane during the instructed horizontal movement. The blue line represents the trajectory of movement. The red arrows represent the points in the data where the movement trajectory in the instructed movement plane has reached its minima and maxima.

As a standard measure of MI, most previous studies used variance or standard deviation (SD) of fingertip position of the observer from the *instructed* axis of movement [5,22,49,120,166,270] (for an exception see [63,212]). This standard measure of fingertip SD relies on a spatial frame of reference, i.e., the instructed horizontal or vertical direction of movement, but is composed of several components contributing to the overall variability and thus to the quantification of MI: (i) tilt away from the instructed direction, (ii) variability of movement direction within a single trial, and (iii) curvature of the individual movements. Evidently, reliance on a spatial reference frame to measure MI might induce higher SD if the movement of the observed agent deviates from the instructed direction and thus make comparisons between experiments more difficult. However, so far, no study has examined the contribution of each component to MI. Therefore, we also investigated the components contributing to the quantification of MI.

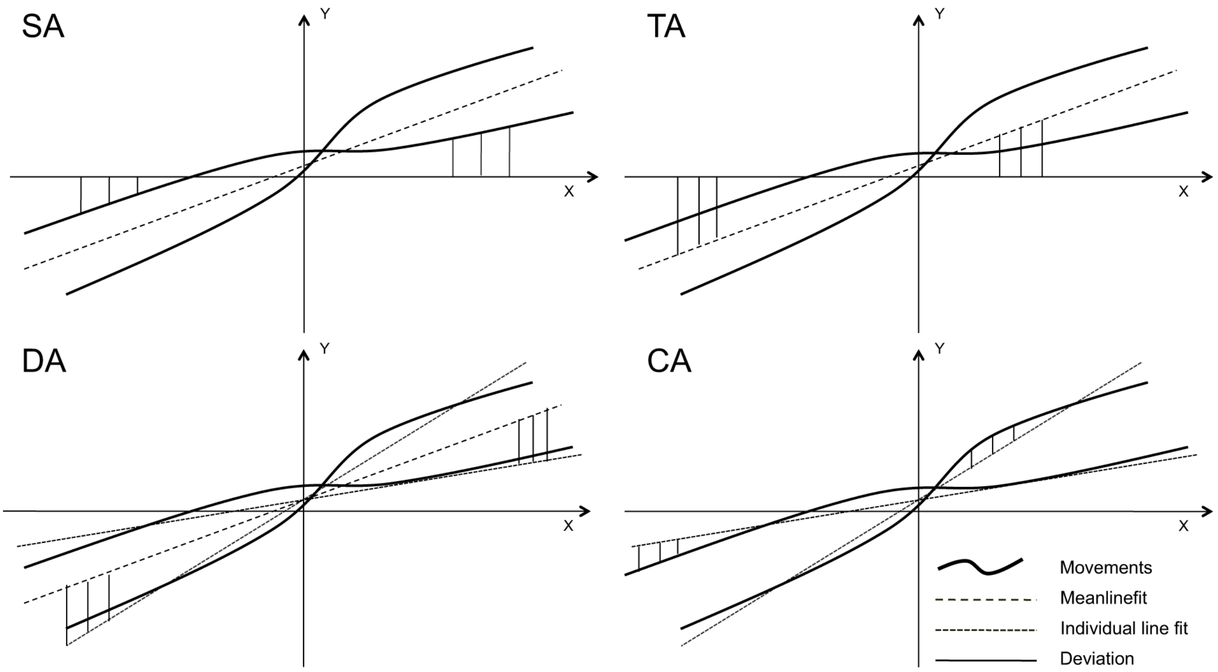

Figure 12: Illustration of the types of analysis which were performed in the MI-study. These analysis types were standard analysis (SA), tilt analysis (TA), deviation analysis (DA), curvature analysis (CA). In the SA, we calculated the deviations of the individual movement from the horizontal or vertical axis. In the TA, we calculated the tilt (or shift) of the overall line fit from the horizontal or vertical axis. In the DA, the deviations of line fits for individual movements from the overall line fit have been calculated. Finally, in CA, we calculated the deviations of every single movement from the straight line fitting this movement. Figure was adopted with permission from [175].

The standard deviation of fingertip position from the y-axis in case of instructed vertical movement and x-axis in case of instructed horizontal movement was calculated for each subject and movement (see Figure 12, SA). The average standard deviation for each condition and subject was used for statistical analysis. This analysis will further be referred to as *standard analysis (SA).*

To investigate the different types of contributions to SA we applied 3 additional types of analyses to the data. To determine the amount of curvature of each individual movement in a 30s trial, a least-squares individual line fit was determined for each movement and the standard deviation (see Figure 12, dotted lines in CA) of the actual movement from this line was calculated. The average of SD across all single movements was calculated for each trial to estimate the curvature. This kind of analysis will further be referred as *curvature analysis (CA).* A similar analysis has been used in two previous studies investigating MI [62,212].

In the second analysis method we determined the best line fit to all individual movements in a 30s trial and then calculated the standard deviation of each *individual line fit* from this *overall line fit* (see Figure 12, DA). This overall line fit, which represents the average direction of movement, does not necessarily need to correspond to the instructed movement along the horizontal or vertical axis (as assumed in the *standard analysis*) but might be tilted or shifted with respect to it. Thus, the deviations in this type of analysis (*deviation analysis, DA*) are composed of the shift (or tilt) of every single movement with respect to the overall plane of movement.

In the final analysis, we determined the deviation of the average direction of movement (overall line fit) from the x-axis (see Figure 12, TA) in case of horizontal movement and the y-axis in case of vertical movement. This type of analysis will be referred to as *tilt analysis (TA).*

To test if there is a correlation between these different contributing factors and the standard analysis (SA) we investigated the observation of a human agent, since the database for these cases was the largest. First, we excluded outliers from the SA data of each condition until none of the values fell out of the 95% interval. Due to this outlier rejection, 19 data points (4.6%) were excluded from the analysis. For the complete statistical analysis (all factors), this procedure resulted in excluding 5 subjects from the first and 7 subjects from the second experiment. For the standard analysis, pooling across movement direction (see Results for justification) after outlier removal allowed us to use data from all but two subjects (one from each experiment). For two other subjects from the present experiment, due to technical difficulties, data could be obtained only for observation of the robot but not observation of the human agent.

The correlation analysis was performed across values obtained by different types of analysis (SA, CA, DA, TA) for the four conditions of human agent observation: horizontal congruent (HC), horizontal incongruent (HI), vertical congruent (VC) and vertical incongruent (VI). We detected a correlation (from moderate to strong) between each of the contributing factors CA, DA, TA and SA in most of tested conditions: HC, HI, VC and VI. Therefore, to show that values from the DA, CA and TA are contributors of the SA, we performed a multiple linear regression with these factors as independent variables and SA values as dependent variables in the following conditions: HC, HI, VC and VI.

3.2 Neural correlates of goal attribution during action observation– an fMRI study[13]

3.2.1 The principles of functional magnetic resonance imaging

Ogawa et al. [207] discovered that the oxygenation level of the haemoglobin acts as a contrast when put into an external magnetic field. Combined with the growing computational power, this finding formed the basis for a new technique: functional Magnetic Resonance Imaging (fMRI). The contrast in fMRI images is generated by the Blood Oxygenating Level Dependent (BOLD) effect. The fundamental signal for BOLD fMRI comes from hydrogen atoms, which are abundant in the blood molecules of the brain.

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[13] Parts of the text from this chapter have been used in the study submitted for publication to Neuroimage as "Kupferberg A, Iacoboni M, Flanagin V, Huber M, Kasparbauer A, Schmidt F, Borst C, Glasauer S Action- and goal-specific fronto-parietal activation during observation of actions performed by artificial agents and humans."

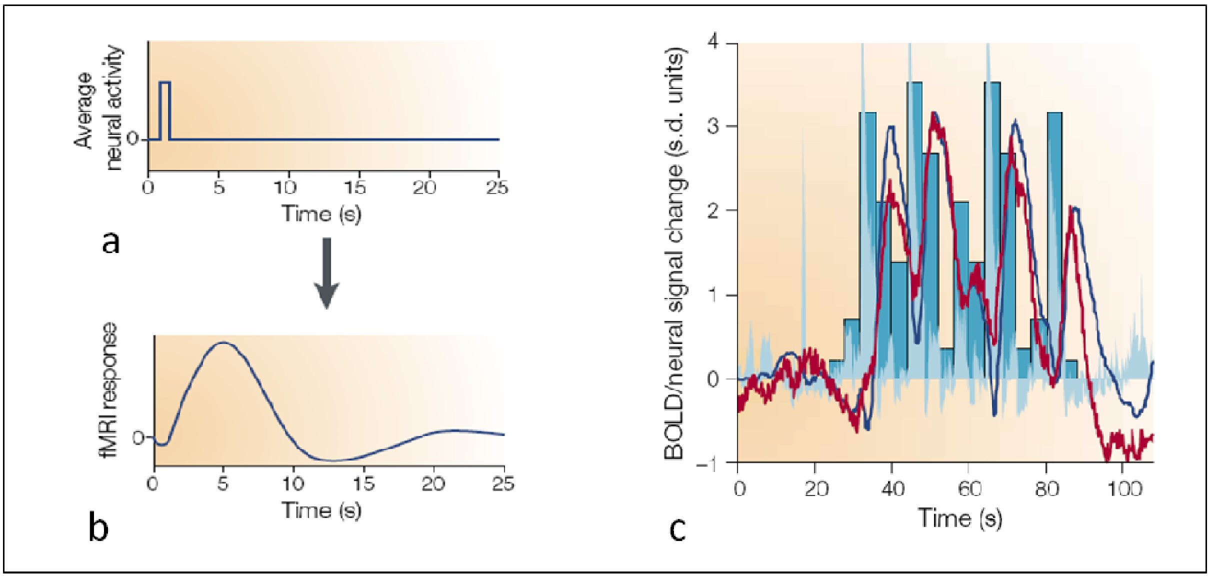

Figure 13: Neural activity and BOLD signal. a) Hypothetical plot of a brief pulse of neuronal activity. b) This pulse leads to an increase in the local blood flow after a delay of approximately 1-5s and rises to a peak over 4-5s before falling back to baseline. This leads to local changes in the relative concentration of oxyhemoglobin and deoxyhemoglobin. The increase is described by a hypothetical haemodynamic response function (HRF) corresponding to the fMRI response in the lower panel. c) Comparison of the measured functional magnetic resonance imaging (fMRI) response with that predicted from the local field potential (recording of neuronal activity with a microelectrode). Light turquoise: measured neuronal activity. Red curve: measured fMRI response. Blue curve: predicted fMRI response. Both figures were adopted from [137].

The indicator of increased brain activity is the blood flow and blood oxygen concentration in the active brain area. Signal processing is used to reveal these active regions on functional MRI scans. For better understanding, the physiology of the local blood flow changes in active brain areas is described in detail in the following. Neuronal activity requires energy in the form of adenosine triphosphat (ATP). Since the brain does not store energy, it must create ATP through the oxidation of glucose. During neuronal activity, the active neurons must be continuously provided with new oxygen bound on haemoglobin through increase in blood flow. Haemoglobin exists in an oxygenated and deoxygenated state. When haemoglobin has no oxygen bound, each haem-group of a haemoglobin molecule has a net magnetic moment because of iron’s four unpaired electrons. In the oxygenated state, oxygen binds to iron (constituent of the haem component of haemoglobin) and causes the net magnetic moment to disappear. Molecules of deoxyhaemoglobin are paramagnetic, e.g. they have magnetic field gradients that alter the spins of nearby diffusing hydrogen nuclei and introduce an inhomogeneity into the nearby magnetic field. In contrast to diamagnetic oxyhaemoglobin, which has no influence on the MR signal intensity, the presence of deoxyhaemoglobin reduces the MR signal intensity. During neural activity, the increase in blood flow leads to a higher concentration of oxygenated haemoglobin in comparison to deoxyhemoglobin. This increases the local MR signal. This increase is described in the haemodynamic response function (HRF) which is assumed to be the response of the neurovascular system to a brief period of neural activity and thus increased metabolic requirements for the neurons (see Figure 13a, b) [137].

It is assumed that fMRI signal is approximately proportional to a measure of local neural activity, averaged over a spatial extent of several millimeters and over a time period of several seconds. In fact, a good agreement between the amplitudes of fMRI-signal and microelectrode recordings of neural activity has been demonstrated (see Figure 13c) (see [137] for review). Thus, in the active brain area the intensity of a voxel in the fMRI image is increased due to the increase of oxyhaemoglobin and this effect is used as the bases of the BOLD signal.

3.2.2 **Subjects**

Twenty healthy right-handed individuals with normal or corrected-to-normal vision participated in this study (age range: 21 to 39 years; mean=26.6 years; SD=4.2; 10 females). All participants were recruited from the university and local populations, gave a written informed consent and were monetarily compensated for their time. The study was performed in accordance with the Declaration of Helsinki and approved by the ethics committee of the medical faculty of the Ludwig-Maximilians-University Munich.

3.2.3 **Action execution experiment**

The experiment has been conducted in two sessions: (i) action execution experiment as localizer for motor regions and (ii) action observation experiment. These experiments were performed on two separate days with an interval of several months. The action execution experiment has been performed a few months later since we wanted to minimize the influence of self-experience on action observation. The purpose of action execution was to allow localizing voxels[14] that show activity during both action execution and action observation (the characteristic feature of the mirror neurons) and thus determine the regions of interest that possess execution and observation properties.

3.2.3.1 ***Experiment design***

The experiment consisted of three test conditions and one control condition. In the test conditions the subjects had to grasp objects from different categories: food, tool and a geometric shape (block) and in the control condition, the subjects had to solely observe the objects. The experiment was segmented in 3 runs and each run lasted 4.5 min. Each run was structured in 6 test blocks (grasping objects, 30s), which were separated by 6 control blocks (looking at the objects without moving the arm, 18s). Each test block consisted of 3 trials (10s/trial) in which the subject was instructed to grasp a certain object with their right hand, lift it and then put it back (see below in description of apparatus to understand why a single

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[14] Each voxel typically represents the activity of a particular coordinate in three dimensional space. The size of a voxel typically represent a volume of 27 mm^3 (a cube with 3mm length sides).

trial required 10 seconds). There were two blocks for grasping an object from every object category in each run which resulted in 6 blocks per run.

The whole experiment consisted of 54 test trials (3 runs × 2 blocks × 3 object categories × 3 trials) and 18 (3 runs × 6 blocks × 1 trial) control trials. To reduce the cognitive demands caused by frequent task changes, we employed a design in which the subjects had to grasp an object belonging to the same category of object (tool, food, or block) during each block repeatedly (e.g., TTTCFFFCBBBC) and the order of the blocks was randomized in every run.

3.2.3.2 *Apparatus, stimuli and procedure*

Prior to the scanning session, subjects were extensively trained outside the scanner to grasp tool and food items without moving their arm too much. During the experiments, the subjects lay supine within the magnet and wore headphones to reduce the noise from the scanner. Through a system of mirrors they could view the stimuli and their hand without moving the head (see Figure 14b). As illustrated in Figs. 1a, the apparatus consisted of a table, which was placed at the level of the subjects' hips. Thin wooden boards (30×20 cm) with objects were attached to it by means of Velcro straps. Different objects pairs were attached to the boards. The apparatus was placed approximately 10 cm above the subject's pelvis in order to place the objects at a comfortable and natural grasping distance. The middle part of the apparatus (on which the wooden boards were fixed) could be rotated by means of a plastic knob at the side of the table. At the beginning of each new trial, the experimenter (standing at the side of the subject) rotated the apparatus and thus presented the subject with a new pair of objects. The experimenter received auditory instructions when to start a new trial by earphones connected to the computer in the control room. While the subjects grasped the objects, the experimenter removed the old board and attached a new board with new objects to the back side of the table.

Between the trials, the subjects held their right hand at the level of their navel and put their right index finger on a response button. The extended left arm was oriented parallel to the trunk in a relaxed position. In order to minimize head movements, the subject's upper body and head were fixed to the scanner bed by a wide fabric belt and a narrow fabric strap respectively. The right arm of the subjects was also supported by appropriate supports and restrained by the belt to minimize movements of the arm and hand during force production. This arm belt allowed full motion of the wrist (in order to grasp and reach any object comfortably), but limited motion at the elbow and the shoulder (however, enough to move the lower arm from the resting position toward the stimuli). The subjects were instructed to start the first grasping action as soon as the experimenter turned the board with objects toward them.

During the experiment, subjects were presented with different pairs of objects attached to the board and composed of a tool and a food item on either side and a cylindrical block in the middle (see Figure 14a). Six mock tools, six food items, and a building block were used as stimuli respectively. The object to be grasped in each trial was indicated by the letter "W"

(Werkzeug), “E” (Essen), or “K” (Kreis) written on the plastic block. If the letter was “W”, the subjects grasped the tool, if the letter was “E”, the subjects grasped the food item, and if the letter was “K”, the subjects grasped the block. If a fixation cross was depicted on the block, the subjects were to perform the control task in which they were instructed to attend to the objects from the previous trial while fixating the block.

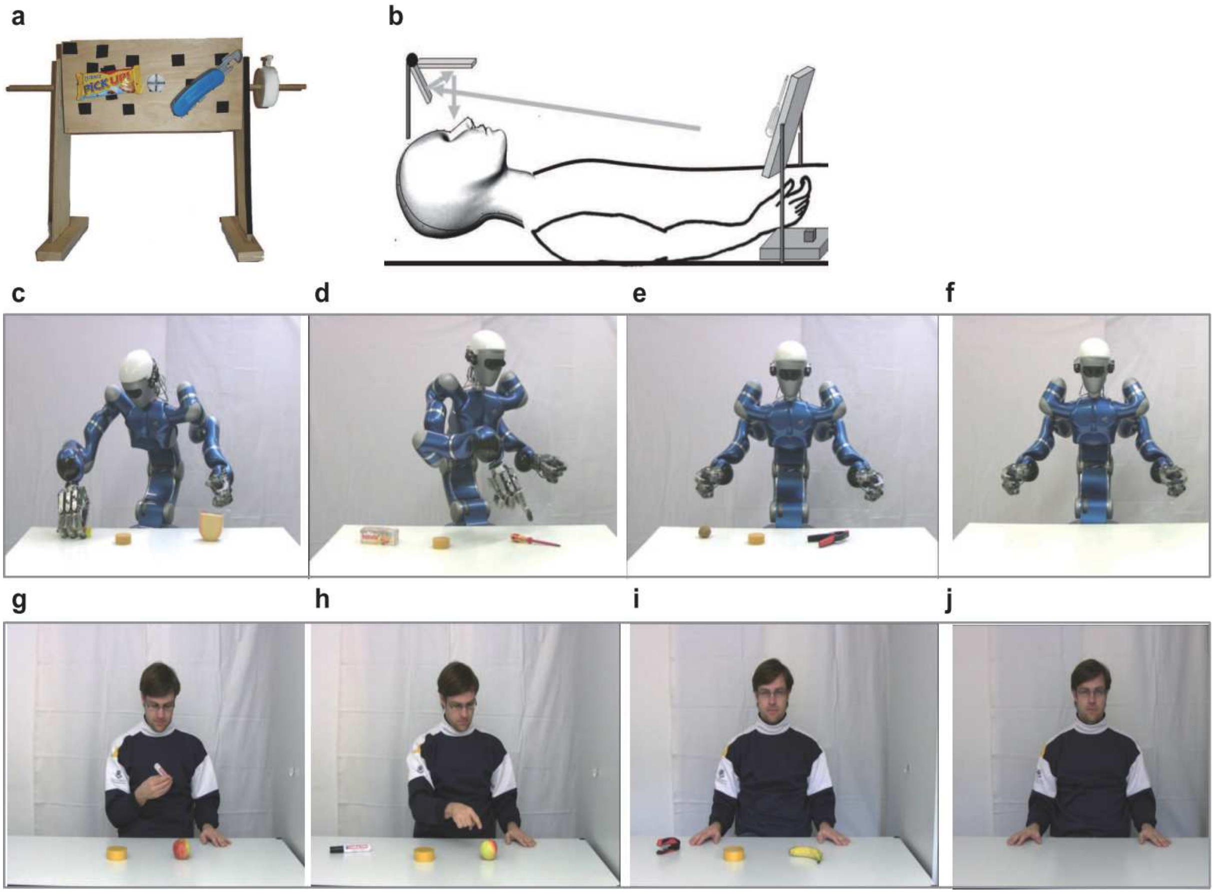

Figure 14: Setup and stimuli in the fMRI study. In the action execution experiment, subjects lying in the scanner could observe the objects fixed to the apparatus (b) through a system of mirrors (a). The apparatus could be rotated by the means of a knob on one side of it. The figures c-j depict screenshots from movies presented to the subjects in the action observation experiment: c,g) Robot and human grasping d,h) robot and human pointing e,i) baseline with objects, f,j) baseline without objects.

During grasping, the subjects moved their right arm to the target location and grasped the object, lifted it, and put it back while thinking about the object’s function. We did this for the following reason. The execution of these grasping actions directed at different object categories in the artificial lab environment may make them devoid of the meaning they get in real life. Thinking about the object’s function while executing the grasping action should activate the representation of the intention typically associated with grasping action. After returning the object to its place, the subjects placed the hand to the starting position and waited for the next trial to start. Prior to the grasping action and after it as well as during the control trial, subjects were instructed to press a button on the device located under their hand (see Figure 14b) to indicate start and end of the action. After the experiment, the subjects were asked whether they had difficulties thinking about the function of the object.

3.2.4 Action observation experiment

3.2.4.1 Stimuli, design, task and procedure

While being scanned, subjects were asked to carefully observe series of video sequences presenting grasping and pointing actions performed by either a human or a robot. In addition the subjects were presented with videos of motionless human and robot agents (static baseline). Video sequences were rear-projected onto a screen positioned in the scanner while the subjects saw the images through a mirror located above their head. The experiment consisted of 14 conditions with a 2 (human/robot) × 2 (grasping/pointing) × 3 (tool items, food items, and block) design and additional static control conditions: 2 (human/robot) × 2 (baseline with objects/baseline without objects) (see Figure 14c-j; for video stimuli, see supplementary material). Similar to the action execution experiment, in the present experiment tools, food items, and a plastic block served as stimuli (14 different pieces in each category). In case of pointing, however, only food and tool items were used as targets. Indeed, our main contrasts of interests involve grasping vs. pointing crossed with humans vs. artificial agents.

None of the subjects were familiar with the block and therefore were given a number of examples of how the block might be used (stopper for a door or a window, building a tower, paperweight). During the grasping action, the actor in the video lifted his right hand from the starting position on the table, transported it to one of the objects, grasped it, lifted the object, transported it to the middle of the body, and looked at it for 2 seconds after which the trial ended. During the pointing condition, the actor pointed to the object with the index finger and returned the hand to the starting position on the table. The side of the table at which the objects were positioned as well as the category of the objects (tool and food items) was randomized; the block was always located in the middle between two other objects. The objects belonging to different categories used in the experiment had similar size but different shapes so that the configurations of the grip were randomized over the whole experiment.

The experiment consisted of 4 runs. Each run lasted 7 min and consisted of 5 blocks presenting human grasping and pointing actions, 5 blocks of motionless video of the human, and 10 corresponding blocks for the robot. During each block, 4 actions of the same agent were targeted at different objects in randomized order. The blocks were separated from each other by baseline blocks in which each agent was depicted either with or without objects lying in front of him (baseline with objects, baseline without objects). Each action lasted 5s and was separated from the following action by a 1s-lasting grey screen so that each experimental block lasted 24s. Baseline blocks (with and without objects present, see Figure 14i, j) consisted of 3 motionless sequences (lasting 5s) of robot or human separated by 1s grey screen so that the baseline block lasted 18s. For each agent, there were 15 grasping actions aimed at food items, 15 grasping actions aimed at tool items and the same amount of pointing actions. Additionally, there were 15 grasping actions directed at the block. The order of different actions (pointing and grasping), the agent to be observed, the object type, and the baselines were counterbalanced over every run. After each trial a grey screen was shown and the participants were instructed to press one of the two buttons. After the pointing and grasping actions, if the participants attributed an intention to the observed action, they pressed the left button. If they had difficulties to associate the observed action with a certain intention, they pushed the right button. In case of baseline (static video), the subjects had to press either button.

After the experiment, participants were debriefed on intention attribution to every single action shown in the experiment for both agents. They were presented with a picture of every single object shown in the experiment and asked to write down their opinion about “what the respective agent was planning to do with the object” when they observed the human or the robot grasping or pointing to the objects. Further, the subjects were asked about the ease of intention attribution to the robotic in comparison to human agent: “Did you find it equally difficult to guess a possible outcome of actions in case of human and the robotic agent (yes/no)?” In case of a negative response the subjects had to comment on their answer by naming the agent whose intentions were more difficult to understand. Further, the subjects were asked about the naturalness of the robot movement: “Did you find the movement of the robot natural? (yes/no)”. Finally, we asked the participants about the ease of intention attribution to pointing in comparison to grasping actions: “Did you find it equally easy to think of a future action outcome in case of pointing and grasping?” Again in case of a negative response the subjects had to comment on their answer by naming the action in which the intention attribution seemed more difficult.

3.2.4.2 Trajectory and velocity of the robot arm movement

The upper body of the robot holds a total of 43 controllable degrees of freedom (2x7 in arms, 5 in the torso, 2x12 in hands). The trajectory of the robot movement can be described as a polynomial of the third order $y(x)=a_3 \cdot x^3+a_2 \cdot x^2+a_1 \cdot x+a_0$, in other words, a cubic interpolation between initial and final configuration of the joints. The velocity of the movement was chosen with a low acceleration so that the movements were less jerky and looked sufficiently smooth. The initial robot videos have been accelerated applying 300% velocity using the Adobe Premiere Pro 2.0 package so that the duration of the movement corresponded to the duration of the human movement.

3.2.5 fMRI data acquisition

All BOLD-sensitive (blood-oxygen-level-dependent) fMRI images were acquired on a 3T whole-body scanner (GE Signa HDx) using a standard echo-planar imaging (EPI) sequence and an 8-channel radiofrequency (RF) head coil for signal reception. The sequence had an echo time (TE) of 60 ms, matrix: 96×96; field of view (FOV): 220 mm, and a voxel size of

2.3 x 2.3 x 3.5 with no gap. All slices were oriented parallel to the anterior-posterior commissure. The action execution session used 37 interleaved slices with a repetition time (TR) of 2.25 and the action observation session used 39 interleaved slices with a TR of 2.34. During each experimental session, a T1-weighted anatomic reference volume was acquired using a 3D acquisition sequence.

3.2.6 **fMRI data analysis**

First level analysis

Image analysis was performed using MATLAB (Mathworks Inc., Natick, MA) and SPM5 (Wellcome Department of Cognitive Neurology, University College London). Images of each condition were corrected for head movements by alignment to the mean image. The data for each subject were normalized using coregistration to the individual anatomical image and segmented into MNI standard coordinate space. The data were also smoothed by a Gaussian filter (8mm FWHM).

At the single-subject level, we applied a high-pass filter (453 s) to remove baseline drifts. The regressors of interest for the all conditions (see below) were entered into a general linear model (GLM) as boxcar functions convolved with the hemodynamic response function. In the action execution experiment, the baseline condition was not explicitly modelled. In the action observation experiment, all control conditions were modelled since we had 2 control conditions for every agent (see Figure 14e, f, i, j). In both experiments, head motion parameters were included in the analysis as regressors of no interest. For the action observation experiment, images of parameter estimates for the contrasts of interest were created for each subject. These contrasts were: grasping tool, grasping food, grasping block, pointing to tool, pointing to food, baseline with objects, and baseline without objects for robot and for human respectively.

Conjunction between action execution and action observation

The SPM conjunction null method [203] was used to assess activation common to two experiments for the conditions “*execution of grasping food&tool minus baseline*” and “*observation of a human agent grasping food&tool minus baseline with objects*.” To restrict the activations only to areas with both motor and visual properties, we defined the ROIs as voxels in the conjunction analysis which overlap with the anatomical regions of interest from the Wake Forest University Pick Atlas [188]: the left/right IPL, left pIFG[15], and the bilateral premotor cortex. These regions have been reported to be associated with the MNS in most studies (see Figure 3) [210]. The so created “ROI mask” was used to mask the activations presented in the results section. In the random effects analysis, voxels exceeding a statistical threshold of $p < 0.05$ (FDR-corrected for multiple comparisons) are presented. In the figures, significant voxels are overlaid on a single subject MNI template. The nomenclature of

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[15] There was no activation in the right IFG in the conjunction analysis.

anatomical structures lying outside the ROIs follows the Harvard–Oxford structural atlas and the Jülich histological atlas [90].

SPM ANOVAS

The second-stage (random effects) group analysis was used to create images for displaying the activations of the MNS areas depending on the observed action type, the goal of the action and the agent (for overview see

Table 4). To this end, the individual contrast images (created in the first-level analysis) were entered into 3 different ANOVAs. The first ANOVA (*action ANOVA I*) was performed on the factors action type (grasping/pointing), agent (human/robot) and goal (grasping tool, food) and aimed at investigating how the activity in the MNS areas is modulated depending on the type of action, but also the nature of the agent, and the goal. Since grasping, but not pointing was additionally targeted to the geometric shape (block) the second ANOVA (*goal ANOVA I*) with factors goal (grasping tool, food, block) and agent (human/robot) was used to test for the differences in activation between grasping specific everyday objects (tool and food) and an abstract shape (block). To investigate whether the difference in the activity when comparing different agents might be based on the superficial difference in their appearance, a third ANOVA with factors baseline type (with objects/without objects) and agent (human/robot) was also performed (*agent ANOVA I*) .

ANOVAS EFFECTS	**Action**	**Goal**			**Agent**
	Grasping (G)>Pointing(P)	***Tool(T)>Food(F)***	***Tool (T) >Block(B)***	***Food(F)>Block(B)***	***Robot(R)>Human(H)***
SPM ACTIVATIONS					
action ANOVA I *action type×goal×agent*	for H and R in rIPL, lIPL, PMC				
goal ANOVA I *goal×agent*		for H and R in rIPL, lIPL, PCM	rIPL, lIPL, PCM, pIFG	for H and R in rIPL, lIPL, PCM, pIFG	rIPL, lIPL, PCM
agent ANOVA I *baseline type×agent*					no difference for static pictures of R and H
PERCENT SIGNAL CHANGE					
action ANOVA II *region×action*					
post hoc action ANOVA II *action type×goal×agent*	for H and R in rIPL, lIPL, PMC				for G but not P in rIPL, lIPL, PMC
goal ANOVA II *region×goal×agent*					
post hoc goal ANOVA I *goal×agent*		for H and R in rIPL, lIPL, PCM	for H and R in rIPL, lIPL, PCM, pIFG	for H and R in rIPL, lIPL, PCM, pIFG	rIPL, lIPL, PMC
agent ANOVAII *region×agent×state*					
post hoc agent ANOVAII *agent×state*					for G but not for static in rIPL, lIPL, PMC

Table 4: Main ANOVAS and their results. The depicted ANOVAS were used to investigate the influence of observed action-type, goal of action and agent on the MNS activity. Post-hoc ANOVAS were performed to clarify the nature of interactions described in the text.

Percent signal change ANOVAS

To investigate the effect of *goal*, *action type* and *agent* depending on the brain *region*, we calculated the mean percent signal change in every ROI (right IPL, left IPL, PMC, left IFG) for each condition and subject. To this end we used the mean intensity (beta values of the voxels) in that region in comparison to the mean intensity over all brain voxels. Individual mean percentage signal change values for each ROI in each condition were averaged across subjects and entered in three different repeated-measures ANOVAs. The purpose of percent signal change ANOVAs was to determine *whether in each ROI* there were significant differences in mean signal strength as function of *action type* (grasping/pointing), *agent* (robot/human), *goal* (tool, food, block). Similar to the ANOVA design for the contrast images (see above), but with the additional differentiation between the different ROIs, the first ANOVA was performed on the factors *region* (right IPL, left IPL, PMC, left IFG), *agent* (human/robot), *action type* (grasping/pointing) and *goal* (tool, food) (*action ANOVA II*). To see the goal-dependent activations for tool and food items vs. geometric shape, the second ANOVA was performed only for the grasping action and contained all three types of objects (*goal ANOVA II*). It was performed on factors *region* (right IPL, left IPL, PMC, left IFG), *goal* (grasping tool, food, block) and *agent* (human/robot). The third ANOVA was aimed at investigating whether solely the difference in the agents' appearance may lead to differential activations in the ROIs (*agent ANOVA II*). In this ANOVA we therefore included both static conditions and grasping conditions (we call this factor *state*) for both agents resulting in an ANOVA with the factors *region* (right IPL, left IPL, PMC, left IFG), *state* (grasping/static), and *agent* (human/robot). When these three main ANOVAs showed significant main effects or interaction effects, post-hoc ANOVAs and t-tests were performed to determine whether and how a given condition significantly differed from other conditions.

3.3 Is goal understanding innate? – a preferential looking times study[16]

3.3.1 Preferential looking paradigm

The preferential looking time procedure, also known as the *dishabituation paradigm*, [269] has been used extensively by developmental psychologists to assess cognitive abilities in prelinguistic human infants [245,268,304], and recently has been employed with nonhuman primates to explore comparable skills [250,290]. Dishabituation experiments are thought to help us understand what kinds of predictions infants and primates make about their world and how they see the world. The power of the technique is that it provides a tool to investigate cognitive abilities across species in the absence of training by reinforcement or punishment.

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[16] Parts of the text used in this chapter were used in the study "Kupferberg A, Glasauer S, Burkart JM Do robots have goals? How agent cues influence action understanding in non-human primates." submitted for publication.

The methodology is simple; an infant is repeatedly shown a stimulus, and as soon as it becomes habituated to the stimulus, it becomes disinterested and observes the stimulus for a shorter period of time. At this point, a new stimulus is shown. If the infant sees the new stimulus as different from the target stimulus, , the infant will look longer at the new stimulus. Otherwise, if the stimulus is repeated, the infant's looking times will decrease further. Woodward [304], for example, showed that even in the first half-year of life infants encode goal-directedness over spatiotemporal properties of the human reaching gesture. In this experiment, infants were familiarized with an agent grasping one of two target objects located on different sides. For the test trials, the location of the target objects was switched. Goal attribution was inferred when the infants' attention recovered when the target of the action changed (incongruent event) but not when the trajectory of the grasp changed (congruent event). The assumption was that looking times in case of change of goal and not trajectory indicate that the subjects represented the previously shown action not in terms of its superficial features, like location in space, but in terms of its goal.

One might assume that longer looking at the incongruent test event is driven by perceptual properties of the test stimuli like preference for repeated grasping of the same object. However, the fact that intention understanding as shown by the looking-time paradigm can have an influence on later action production speaks against the low-level explanation. Thus, 8- and 10-months olds' understanding of the ultimate goal of an action presented by the experimenter as tested by the Woodward-paradigm correlates with the frequency with which infants later produce well-planned solutions in this action task [267].

As in human child experiments conducted by [304], monkeys were familiarized with an agent grasping one of two target objects located on the left and right side of them (Experiment 1) or approaching it (Experiment 2 and 3). After switching the location of the target objects, goal attribution was inferred if the monkey's attention recovered when the target of the grasp changed (incongruent event) but not if the trajectory of the grasp changed (congruent event). Like in Woodward-paradigm described above, we assumed that if subjects interpreted the actions of agents as being goal-directed, they should look longer at the incongruent event. If the monkeys simply preferred perceptual novelty (e.g. a different path trajectory), they were expected to look longer at the congruent test event.

3.3.2 **Subjects**

The participants in Experiment 1 were three male and seven female marmoset monkeys ranging between 4.1 and 7.5 years (see Figure 15). They were kept in two groups (4 and 6 individuals) in different cages separated by a wire grid. In Experiment 2, nine adult marmosets (five males and four females) were tested. The monkeys were kept in two family groups (two breeding pairs and their offspring) and their age ranged from 1 to 11 years (mean age 3.5 years). In the third experiment, 10 adult marmosets living in two groups (age range 2 to 8 years, mean age 4.2 years) were tested.

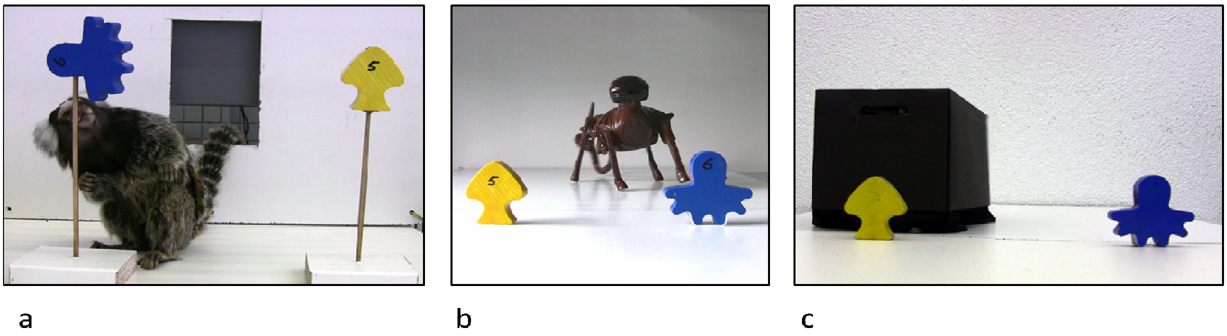

Figure 15: Models used in the preferential looking-times study. The models were a conspecific (a), a robot (b) and a box (c).

3.3.3 Object attractiveness test

In order to guarantee that subjects equally preferred the two objects of each pair used in the experiment, we tested the reaction of eight groups of marmosets, who did not participate in the main experiments, to eight different objects. For this purpose, we presented each group with four objects, different in color and shape, in a randomized order, and recorded two dependent variables, indicating the degree of attractiveness of the object. The first variable was the latency (time span starting at object presentation until the first group member approached the object), and the second variable was the interaction time (tactile manipulation of the object by this individual). The values of these variables for each object were averaged across all groups (represented by one individual of each group who first approached the object) and used as a measure of attractiveness of an object. Based on the results of paired samples t-test performed on these variables, two pairs of "equally attractive" objects were composed. To confirm this composition of pairs, in the second test, both objects of one pair were presented to the eight marmoset groups. The experimenter recorded which one of the two objects was approached first (and thus would be more attractive) by the marmosets for every group separately.

3.3.4 Housing and experimental setup

The marmosets participating in the experiments were housed in indoor home cages which consisted of one or multiple units (1.0×0.75 m and 1.7 m height) depending on the group size. These cages contained ropes, branches and a heated sleeping place. In summer, the animals had free access to outdoor cages, either every day (in case of bigger groups) or every second day (in case of smaller groups). The floor of the cage was covered with a substrate of biological soil. The marmosets were fed three times a day: early in the morning (with gum, mealworms, and pap supplemented with vitamins and minerals), at 11 o'clock (fresh fruits, vegetables and mushrooms), and in the afternoon (cheese, boiled eggs, fish or nuts). Water was always available.

The testing cage consisted of three compartments: screen compartment, experimental compartment and preparatory compartment (see Figure 16). The first compartment containing an LCD-monitor was separated from the experimental compartment by a Plexiglas divider. The monitor was connected to a laptop located outside the cage. While watching the videos, the marmosets stayed in the experimental compartment and between the trials they entered the preparatory compartment through a guillotine door. During the testing of each animal, the rest of the group stayed in the waiting cage which was visually isolated from other compartments (see Figure 16). The ceiling and the lower part of the grid of the experimental compartment were lined with Plexiglas, so that the marmosets would stay on the floor during the test.

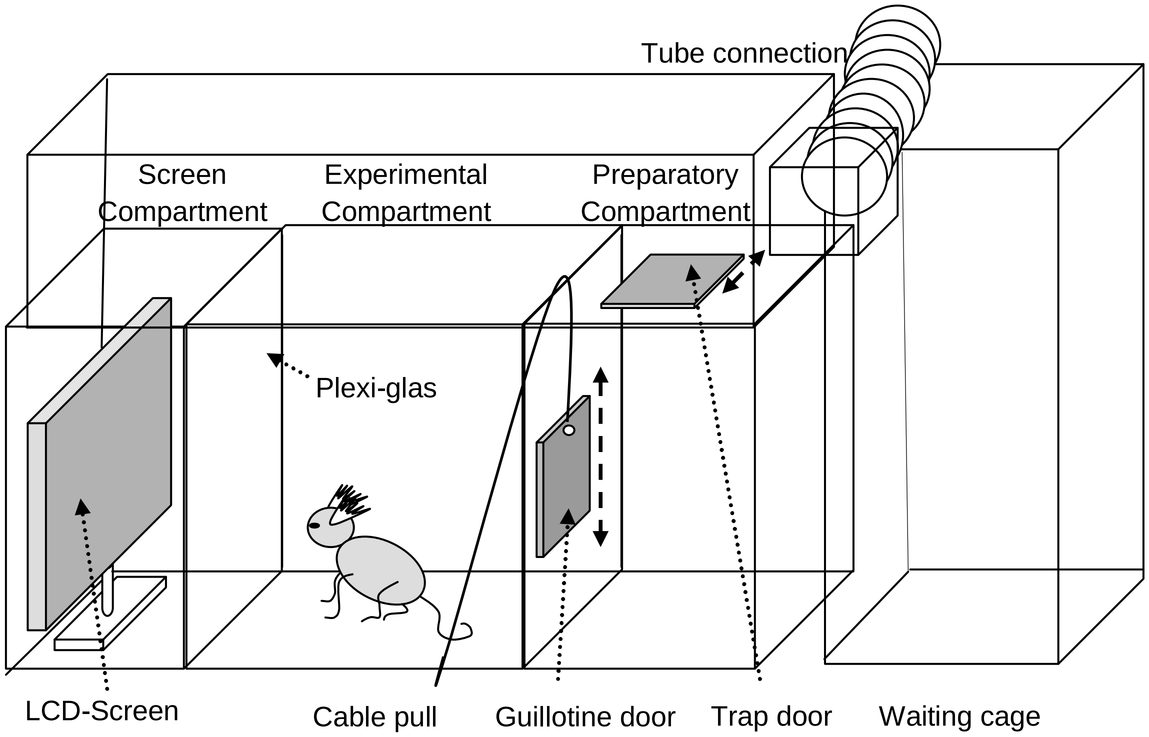

Figure 16: Experimental setup in the preferential looking-times study. The monkeys entered the testing cage via tube connections and could switch between experimental and preparation compartment through a guillotine door. Figure adopted with permission from (Burkart et al., 2011).

The testing of the participants in the experiments took place either in the morning or in the afternoon, before the subjects obtained their snacks. Therefore, during the testing, the animals were neither food nor water deprived. The experiments were approved by the Veterinary Office of the Canton of Zurich (*license number105/2004*). During the experiments, the monkeys were free to join or leave at any time: their participation was voluntary, and their feeding habits were not modified to encourage participation. Most subjects have previously been tested in other experiments and thus often had contact with humans during experimentation, but were never handled.

Between the trials the marmosets stayed in the preparation compartment, which was connected to the experimental compartment by a guillotine door (see Figure 16). For the entire duration of the test, the marmosets were filmed with a digital video camera (HV20, Canon) from a distance of ca. 50 cm. The video image depicted the whole testing cage including the image on the LCD screen.

3.3.5 Familiarization with the experimenter and the setup

To permit the monkeys to get used to the experimenter, testing cage and testing procedure, one month before testing, some of the daily meals were distributed by the experimenter and every second day the monkeys were allowed to go inside the test cage as a whole group and explore it for ca. 30 minutes. Once the monkeys were comfortable with staying in the testing cage together with other individuals, they were trained to stay there on their own, while the remaining group members were in the waiting compartment of the test cage. Every monkey stayed separated from the other group members for increasing durations of time, until it was comfortable being alone in the testing cage for at least five minutes without showing signs of distress (e.g. piloerection, escaping attempts).

3.3.6 Video stimuli and paradigm

Instead of life presentations as used in [40], we presented the monkeys with video stimuli. This enabled us to control the timing and the details of the presentation when repeatedly presenting the same video clips to different subjects.

In the first experiment, we used an adult family member (female breeder) as agent (see Figure 15 a). The videos depicted the monkey who entered the experimental compartment through the guillotine door and approached one of two different objects positioned on the left and right hand side of the door respectively (see Figure 17). To additionally collect test data from the female breeder, we recorded analogous videos with the male breeder as model and presented them to the female. The two objects used in the video clips had different shape and colour (yellow/blue). For each of these objects, five different video clip types (each lasting 10s) were recorded: three for the habituation trials, one for the incongruent test event and the last one for the congruent test event. In the three habituation trials, the subject observed one and the same object being contacted (touching and sniffing) by the model monkey. In the last two video clips, the positions of the objects were reversed and the monkey now approached either a new object (incongruent object) along the old pathway (incongruent test event) or an old object (congruent object) along a new pathway (congruent test event, see Figure 17).

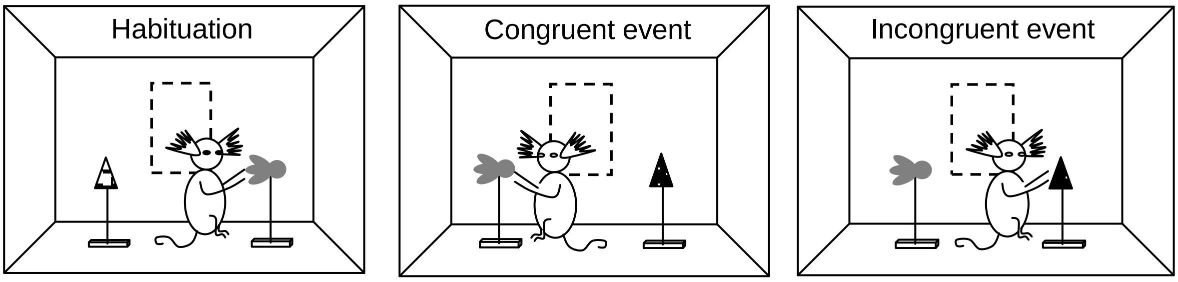

Figure 17: Video stimuli used in the looking-times study. Three habituations trials and two test trials presented to the subjects in the first experiment. Modified figure adopted with permission from (Burkart et al., 2011).

The habituation videos used in the second experiment depicted a monkey-sized brown quadruped robot with very simple front legs without any joints (see Figure 15b). This robot was a modified version of ROBOPET by WowWee Robotics, Hong Kong. It could walk forward and sit down and its movements were based on the principle of dog locomotion. In the videos, it approached one of the objects, stopped in front of it, waggled and sat down.

In the third experiment, the robot was covered with a paper-made black box (see Figure 15c), so that the dynamics of the agent’s movement remained identical as in the second experiment, since the box was moved by the robot itself. Thus, the behavior of the robot and the black box were identical with regard to approach trajectories and kinematics, as well as the waggling movement. An additional black cloth along the bottom of the box ensured that the legs of the robot were not visible.

3.3.7 **Procedure**

On the testing day, five trials were presented to the marmosets, three habituation and two test trials, a congruent and an incongruent one. The order of test trial types (incongruent, congruent) and the type of the object (blue/yellow) was counterbalanced between subjects. The experimenter started the video as soon as the marmoset entered the experimental compartment and looked at the video screen. After the video was over, the experimenter lured the monkey back to the preparation compartment by offering it a mealworm. The inter-trial interval was determined by the time which the marmoset needed to eat the mealworm and re-enter the experimental compartment.

3.3.8 **Familiarization with video-stimuli**

Our experiments were based on the looking-time methodology, which provides a way to assess spontaneously available cognitive tendencies of animals. Instead of life presentations we used video stimuli, since live presentations with conspecifics would have required extensive training of the model subjects. There are a number of studies demonstrating that video playback is perceived as an adequate stimulus by monkeys [6,50,299], including common marmosets [39].

To provide the marmosets with sufficient exposure to the stimuli and the video screen, all marmosets were presented with “familiarization” trials on the day before the actual experiment was performed. In these trials, the monkeys watched the same habituation videos which were used for testing on the next day. Since the marmosets have a short attention span [232], the purpose of this familiarization was to assure that the monkeys had seen all relevant aspects of the video. Thus, if during one trial the marmosets looked at the screen for less than 30% percent of the duration of the video (10s), the trial was repeated a few minutes later, until at least three trials were attained in which the marmoset's looking duration reached the criterion of 30% of the video duration. The videos from the pre-testing were analysed in the evening of the same day. In case that it was not possible to obtain three such trials on one day, the procedure was repeated on the next day until three trials were collected.

3.3.9 **Object preference test**

In order to find out whether the subjects would copy the object choice of the model individual, the test ended with a free choice trial. After the last test trial, the monkeys were allowed to enter the testing compartment and make the choice between the two objects themselves by approaching them and possibly exploring them.

3.3.10 **Data coding and analysis**

Since all experiments were videotaped, looking time data were analyzed by the experimenter in a frame-by-frame fashion (25frames/s) using the software INTERACT, version 8.0 (Mangold international GmbH, Arnstorf, Germany). The monkey was considered to be looking at the screen if it oriented its head towards the screen and did not focus on anything else. Since the monkeys often approached the entities which they focused on, the place of focus could often be verified by the subsequent behavior. The coding of the position of the monkey's head was easy since they have conspicuous white tufts around their ears. The other entities where the monkeys looked at were normally the experimenter, the mealworms lying on the floor or the location on the floor where the monkeys would put their paws for the next step.

To assess inter-rater reliability, the entire data from the three habituation trials and two test trials has been analyzed by a second observer who recorded looking times in a frame-by-frame fashion from videos, just like the first experimenter. The second observer was blind to the type of the test events. His judgments were compared with the looking times recorded by the experimenter. In the first experiment, the interrater-agreement was between 94% und 98%. The other three experiments were additionally analyzed by a third rater, who coded all test trials, but not habituation trials. She was also blind with regard to the experimental condition. The percentage frames for which the observers' judgments agreed was 96%. We used the data recorded by the experimenter for the analysis.

We used Kolmogorov-Smirnov statistics to test whether the data sets deviated from a normal distribution. Since all data was normally distributed, we used parametric statistical analyses (repeated measures ANOVAs and paired samples t-tests).We first tested whether the looking times significantly differed in the congruent and incongruent test events depending on the agent. To this end we used repeated measures ANOVA performed on the factors *test trial order* (congruent first/incongruent first) as between-subject factor and *congruency* (looking time duration in the congruent vs. incongruent test event) as well as *agent* (conspecifics/robot/box) as within-subject factors. Further, we also performed repeated measures ANOVA to test for the effect of the habituation (decrease of the looking times) in the course of three habituation trials.

4 Results

4.1 Agent’s features which facilitate motor interference in dyadic interaction

4.1.1 Results from standard analysis

To compare the MI effect elicited by action observation of the human, the humanoid robot (JAST), and the industrial robot (JAHIR, artificial joint configuration; present experiment) we used the standard analysis. We combined all data to yield a repeated-measures ANOVA design with three within-subjects factors and one between-subjects factor. We used *movement plane* (horizontal/vertical), *congruency* (congruent/incongruent), and *agent* (human/robot) as within-subjects factors and *robot* (humanoid JAST/industrial JAHIR) as between-subjects factor resulting in a mixed 2×2×2 within-subject design with 2 between-subjects conditions. The combined analysis (33 subjects; conditions a, b, and c in Figure 8) revealed a significant main effect for *congruency* [F(1,31)=10.5; p<0.0028] that confirmed motor interference. The strength of motor interference depended on whether the agent was a human or a robot and the type of the robot as shown by a significant three-way interaction *agent*×*congruency*×*robot* [F(1,31)=4.38; p=0.044] (see Figure 18).

Since the factor *movement plane* became neither significant as main effect nor as interaction, we pooled data across this factor. This allowed us to include data from subjects who previously were excluded due to an outlier (see section 3.3.4). The pooled analysis (43 subjects) with *congruency* (congruent/incongruent), and *agent* (human/robot) as within-subject factors and ROBOT (humanoid JAST/industrial JAHIR) as between-subjects factor resulted in a main effect for *congruency* [F(1,41)=20.2; p<0.0001] and a significant three-way interaction *agent*×*congruency*×*robot* [F(1,41)=4.53; p=0.039], confirming the results above.

To further investigate how subjects reacted to the observation of human, humanoid robot, industrial robot and rotated industrial robot (industrial 90°) movement, we performed separate post hoc analyses (repeated measures ANOVA) with *congruency* (congruent/incongruent) as within-subject factor. This analysis revealed an effect of congruency for the human agent [F(1,42)=18.5; p<0.0001], humanoid robot JAST [F(1,23)=5.54; p=0.027], rotated industrial robot arm JAHIR 90° [F(1,9)=6.77; p=0.029], but not JAHIR [F(1,18)=1.34; p=0.26; n.s.] (see Figure 18). In both direct comparisons human-JAST and human-JAHIR 90°, the interaction *agent* ×*congruency* was not significant (both p>0.54), showing that there was no difference in MI between the human agent and these robots. In contrast, the comparison human-JAHIR yielded a significant interaction *agent*×*congruency* [F(1,18)=7.11; p=0.016], confirming that MI was not present for JAHIR. Since the industrial robot was the same in both presentations – mounted on the table in JAHIR and rotated in JAHIR 90° – this result implies that a human-like joint configuration (with respect to the observer) is a crucial factor for triggering MI.

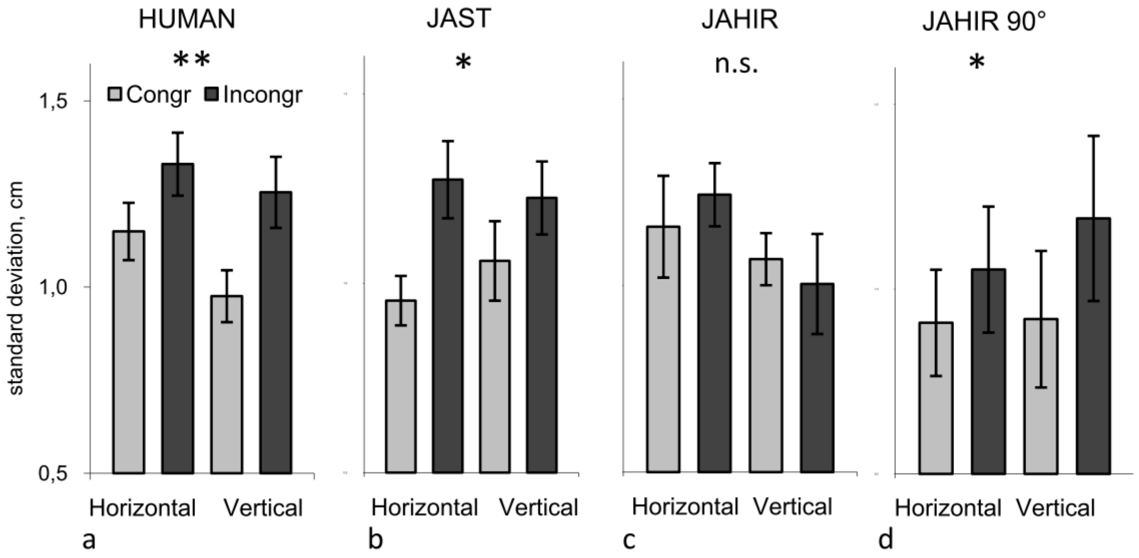

Figure 18: Results of the MI study using the standard analysis. The bars represent standard deviation (SD) of movement from the instructed movement plane during observation of incongruent and congruent movements of the human agent (a), humanoid robot JAST (b), industrial robot JAHIR (c) and rotated industrial robot JAHIR90° (d). Data from all subjects, i.e., each graph represents a different number of subjects (see text). Error bars represent standard error of the mean. Stars denote significance (** p<0.01; * p<0.05). Figure adopted with permission from [175].

Finally, to test for the presence of facilitation effects on one's own movement during observation of congruent movements of a different person, which would manifest in a more accurate movement in comparison to the baseline where no other person is present, we used a repeated measures ANOVA with factors *agent presence* (agent/baseline) and *direction* (vertical/horizontal) for data obtained while watching incongruent and congruent movements of a human agent and baseline data. The effect of *agent presence* could be shown only in the incongruent condition [F(1,24)=5.6 p<0.026] with a higher variance in one's own movement during observation of incongruent movements than during the baseline. However, no additional accuracy in case of congruent movement observation could be shown [F(1,24)=0.37; p>0.54].

4.1.2 Other measures of motor interference

Most previous studies used a measure for MI that is dependent on a space-fixed coordinate system, i.e., the deviation of subjects' movement trajectory from the instructed movement plane (SA) (see Figure 12). However, such an analysis depends on accurate alignment of movement directions between the subject and the observed agent, and might have led to different results if this alignment was absent. In contrast to it, we tested which components of the movement contribute to MI.

To investigate whether the deviations from the movement plane (DA), tilt of the movement plane with respect to the coordinate system (TA) and the curvature of the movement (CA) are differentially influenced by observation of congruent and incongruent movements, we performed separate analyses (repeated measures ANOVA) of our data while observing a human with *movement plane* (horizontal/vertical) and *congruency* (congruent/incongruent) as within-subject factors. This analysis revealed an effect of congruency for DA [F(1,32)=27.7; p<0.001] (see Figure 19a) and for TA [F(1,32)=9.6; p<0.005] (see Figure 19b) but not for CA [F(1,32)=0.376; p<0.8] (see Figure 19c). For DA there was an additional effect of direction [F(1,32)=7.2; p<0.011] due to higher deviation in the horizontal plane than in the vertical plane and an interaction between direction and congruency [F(1,32)=8.0; p<0.008] due to a stronger effect of incongruence in the horizontal than in vertical plane.

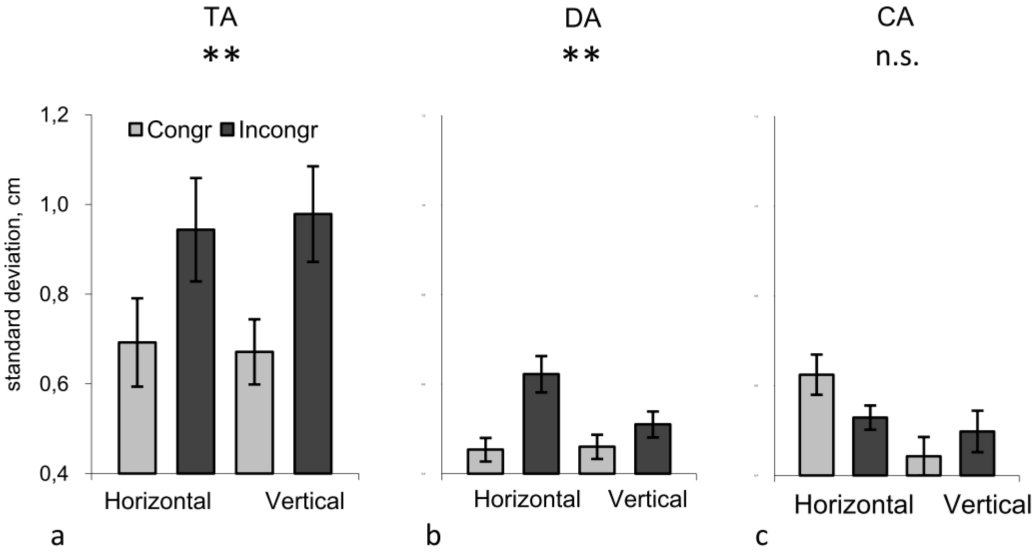

Figure 19: Results from different analyses for observation of human agent in the MI-study. a) Actual plane tilt of movement (mean line fit) with respect to the horizontal and vertical directions (TA). b) Standard deviation of individual line fit from the mean line fit (actual plane of movement) (DA). c) Curvature of single movements with respect to a straight line (individual line fit) (CA). Error bars represent standard error of the mean. Stars denote significance (** p<0.01). Figure adopted with permission from [175].

Correlation analysis (corrected p-level p=0.004 for 12 tests) of the different factors contributing to MI has shown a significant positive correlation between SA and TA in four conditions (all n=33 subjects): HC [r=0.681, p<0.001]; HI [r=0.786, p<0.001]; VC [r=0.484, p<0.004]; and VI [r=0.760, p<0.001]. SA and DA also correlated in all conditions (HC [r=0.409, p=0.018]; HI [r=0.386, p=0.026]; VC [r=0.592, p<0.001]; and VI [r=0.460, p=0.007]), even though only VC was significant due to the Bonferroni correction. Similarly, SA and CA significantly correlated only in the vertical conditions: HC [r=0.488, n=33, p=0.037]; HI [r=0.120, n=33, p=0.5060]; VC [r=0.769, n=33, p<0.001]; and VI [r=0.540, n=33, p=0.001].

Finally, a multiple regression analysis was used to test if the factors curvature, movement variability, and plane tilt significantly predicted the SD of the movement with respect to the horizontal and vertical axis during observation of congruent horizontal human movements.

The results of the regression indicated that the three predictors explained more than 88% of the variance of the standard analysis in each condition with TA and DA contributing most.

4.2 Neural correlates of goal attribution during action observation– an fMRI study[17]

4.2.1 Behavioral results

The debriefing of subjects at the end of the action observation experiment has shown that all subjects were able to attribute an intention to the actions of both human actor (in 95% percent of all trials) and robotic actor (in 94% percent of all trials) (see Figure 20a). However, 50% of the subjects reported that it was more difficult to attribute an intention to grasping and pointing actions of the robot in comparison to the human agent (see Figure 20b). Finally, 40% of subjects reported that the grasping movements of the robot seemed unnatural in contrast to human movements (see Figure 20d).

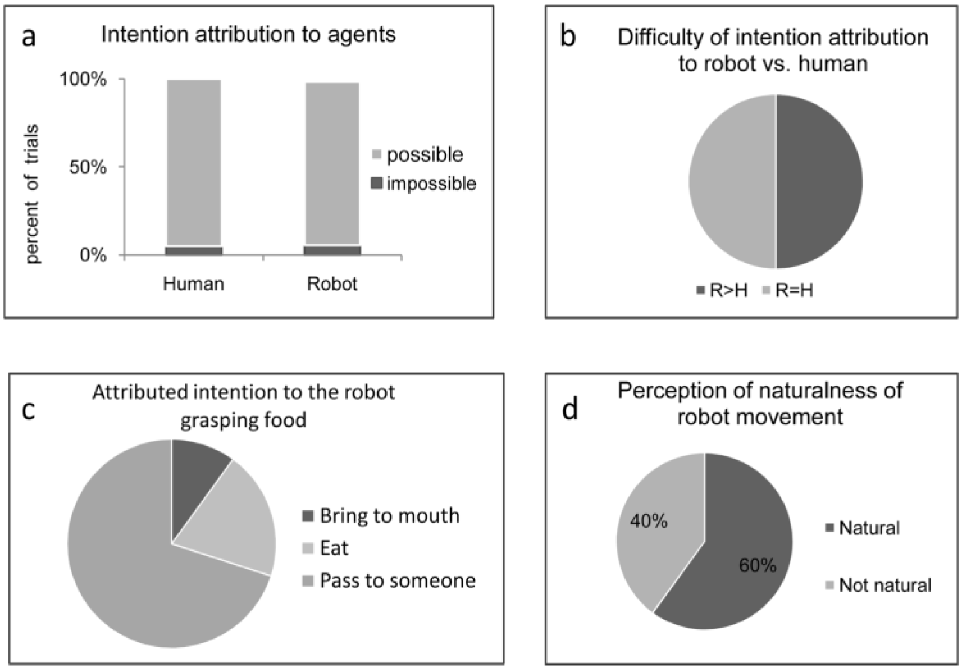

Figure 20: Behavioral results in the fMRI study. a) Subjective ability to attribute a certain intention to human and robot during observation of grasping and pointing. b) Difficulty in attributing intention to human vs. robotic agent. c) Intention attributed to robotic agent for grasping food d) Subjective perception of the naturalness of robot movement.

The subjective reports indicated that the intention attributed to the robot and the human during tool and block grasping was identical for both human and robotic agents in every subject. In case of the tool items, this intention was to use the tools appropriately to its function (e.g. fixing something, repairing something, measuring something, gluing parts together). For the

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[17] Parts of the text from these chapter have been used in the study submitted for publication to Neuroimage as “Kupferberg A, Iacoboni M, Flanagin V, Huber M, Kasparbauer A, Schmidt F, Borst C, Glasauer S Action- and goal-specific fronto-parietal activation during observation of actions performed by artificial agents and humans.”

block, the attributed intention was either to use it as a stopper for a door or for a window (47%) or to use it as a building block (53%). In case of observing a human agent grasping food item, the attributed intention was "eating" for all subjects. For the observation of the robot, the attributed intention in case of food grasping was either "eating" (10% of all subjects) or "bringing the object to the mouth (20% of all subjects) or "giving/offering the food item to another agent" (70%) (see Figure 20c). To investigate the difference between these two types of subjects who either attributed the intention of "giving away the food item" or the intention of "eating"/"bringing to the mouth" to the robot, we performed a t-test between these two subject groups using contrast images for "pointing to food items". However, this t-test revealed no difference in activation depending on the attributed intention in any of the brain regions.

In case of pointing, 50% of all subjects regarded the pointing gesture as the desire of the agent to grasp the object himself and the remaining subjects understood the gesture as a request to the observer to grasp the object. We again performed a t-test on the contrast images of "pointing to tool & pointing to food items" for subjects who regarded the pointing action as the agent's desire to direct the subject's attention to the object vs. those who interpreted pointing as the agent's desire to grasp the object himself. However, a t-test performed on these two groups of subjects did not reveal any differential activity in any of the brain regions.

4.2.2 **Conjunction analysis of action observation & execution**

The MNS-related brain areas activated by the execution of grasping were located in bilateral PMC, pIFG , anterior IPL and left primary motor cortex, whereas observation of grasping activated the posterior IPL (angular gyrus) and the posterior IFG on the left side. The conjunction analysis of action observation and action execution activated the bilateral superior frontal gyrus, premotor cortex (PMC), inferior parietal lobe (IPL) including the anterior intraparietal sulcus (aIPS), middle temporal gyrus, inferior temporal gyrus, lateral occipital gyrus, lingual gyrus, primary somatosensory cortex, secondary somatosensory cortex, temporo-occipital fusiform gyrus and parahippocampus. Further activations on the right side were located in superior temporal gyrus and parahippocampus and on the left side in the frontal lobe, the supramarginal gyrus, pIFG (pars opercularis), angular gyrus, insula, the middle frontal gyrus, paracingulate, and cingulate gyri (see Figure 21a).

The regions of interest were defined as voxels located in the overlap of the activations obtained in the conjunction analysis with the anatomical regions of interest: bilateral IPL, left pIFG, and the premotor cortex from the WFU Pick atlas (Figure 21b). The so created "ROI mask" was used to mask the activation in all displayed contrasts.

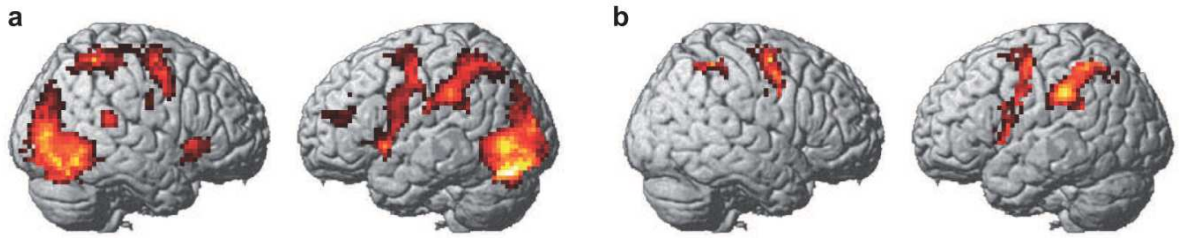

Figure 21: Functional activations in the fMRI-study. a) Brain regions active in the conjunction analysis of execution and observation of grasping actions of a human agent (directed at tool and food items). Before the images for action observation and execution were entered in the conjunction analysis, we subtracted the baselines in each experiment (baseline with objects and object observation respectively) from them. b) ROI mask: overlap of activations of the conjunction analysis with the ROIs from the WFU Pick atlas (left and right IPL, bilateral PMC, left pIFG).

4.2.3 Action type-dependent MNS-activations for human and robotic agents

The comparison between grasping and pointing actions (*action type ANOVA I*) after masking revealed increased symmetrical activations in the bilateral premotor cortex (PMC), in the left and right IPL and the left IFG (see Figure 22a). No brain areas were activated stronger for pointing than for grasping.

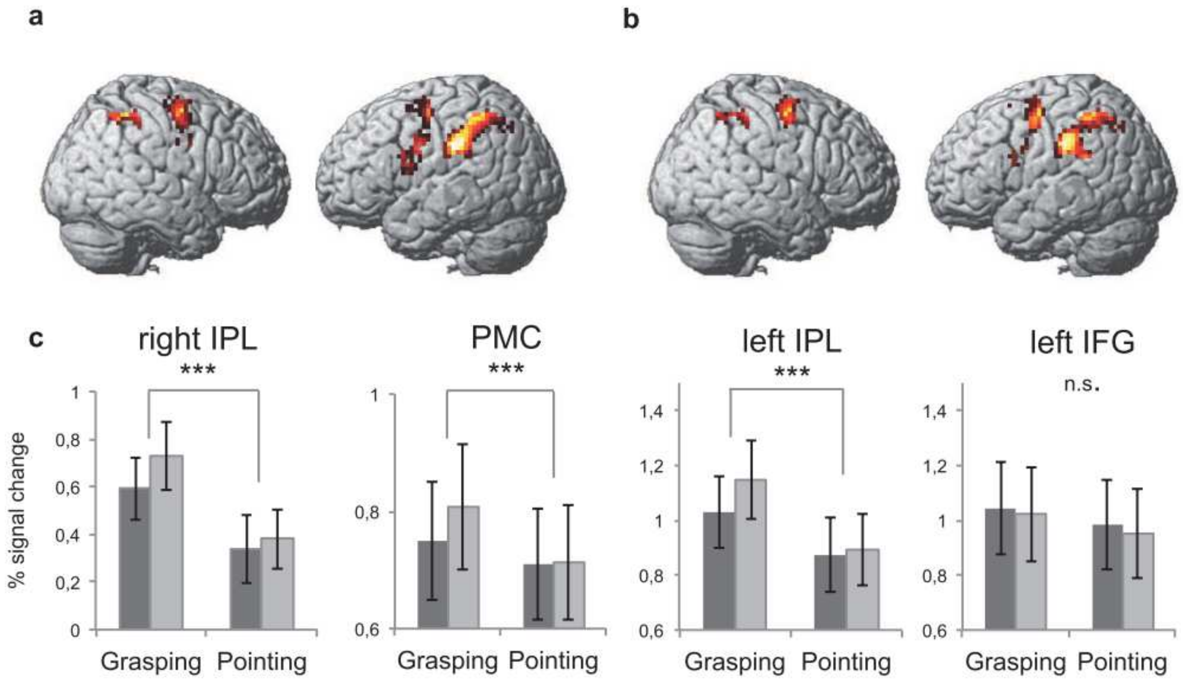

Figure 22: Modulation of MNS-activity by observation of action type and agent. Activation for observation of “grasping minus pointing” (a) and “robot minus human” (b) were stronger in the bilateral IPL and PMC. All displayed activations are masked by the ROI mask. c) Mean percent signal change (averaged over 20 subjects) during observation of grasping and pointing actions of robot (light grey) and human (dark grey) directed at both tools and food items in the right IPL, PMC, left IPL and left IFG. Error bars represent standard error of the mean.

The *action ANOVA II* performed on the percent signal change of the ROIs revealed significant main effects of *region* [F(3,57)=7.8 p=0.001], *action type* [F(1,19)=59.4 p=0.001], and *goal* [F(1,19)=9.1 p=0.007]. Significant two-way interactions were found for *region×agent* [F(3,57)=7.7 p=0.001] and *region×action type* [F(3,57)=26.78 p=0.001]. A significant three-way interaction again showed region-specific activations [*region×agent×action*, F(3,57)=3.1 p=0.033] indicating the necessity of performing separate post-hoc ANOVAs for each ROI. The *post-hoc action ANOVA II* (*action type×goal×agent*) performed for each ROI separately revealed significant effects of *action type* with an increased activation for grasping in comparison to pointing in the left IPL [F(1,19)=42.8 p=0.001], right IPL [F(1,19)=84.13 p=0.001] and PMC [F(1,19)=13.9 p=0001], but not in the pIFG (see Figure 22c). Additionally, significant effects of agent and goal and a significant interaction *action type×agent* were found for the IPL bilaterally (see below, and Figure 22c). This nature of this interaction will be investigated more closely in the section 4.2.5.

4.2.4 **Goal-dependent MNS activations for human and robotic agents**

The *goal ANOVA I* aimed at displaying the effect of *goal* (tool, food, block) on MNS activations during grasping, showed increased activity for tools vs. food in the bilateral PMC and IPL and tools vs. block/food vs. block in the same regions but additionally in the left IFG (see Figure 23a, b, c). The *goal ANOVA II,* used to investigate the effect of goal in each region separately, revealed significant main effects of *region* [F(3,57)=5.0 p=0.004], *agent* [F(1,19)=14.6 p=0.001], and *goal* [F(2,38)=29.03 p=0.001]. Two-way interactions were significant for a *region×agent* [F(3,57)=10.6 p=0.001] and *region×goal* [F(6,114)=9.7 p=0.001], but not for *agent×goal* suggesting that the processing of the action goal was similar in both agents. To clarify the difference between the ROIs, we performed the *post-hoc goal ANOVA II* (*action goal×agent*) for each region separately. This ANOVA revealed a main effect of *goal* in all four regions [left IPL F(2, 38)=25.2 p=0.001, right IPL F(2, 38)=15.8 p=0.001, left posterior IFG F(1, 38)=9.4 p=0.001 and bilateral PMC F(2, 38)=14.6 p=0.001] (see Figure 23d), but again no interaction of *agent×goal*.

Although the effect of *goal* has been revealed in all ROIs, it is still unclear whether this effect originates only from the differential activity triggered by tool&food items vs. block or tool vs. food items, or both. To clarify this, we performed third-level post-hoc ANOVAs including only two object categories (tools vs. food items; tools vs. block, food vs. block) as factor *goal* and two agents (human, robot) as factor *agent*. The increase in BOLD response for observation of grasping tool vs. food items could be shown in the left [F(1,19)=13.96 p=0.001] and right IPL [F(1,19)=27 p=0.001] and the bilateral PMC [F(1,19)=6.9 p=0.017] (see Figure 23a). A higher activation for grasping tools vs. block could be shown in all regions [left IPL F(1,19)=31.4 p=0.001; right IPL F(1,19)=18.4 p=0.001; left IFG [F(1,19)=13.9 p=0.001]; PMC F(1,19)=22.8 p=0.001] (see Figure 23b). Observation of grasping of food items vs. block revealed increased activations in the left IPL [F(1,19)=20.55 p=0.001], left IFG [F(1,19)=10.2 p=0.004] and bilateral PMC [F(1,19)=9.83 p=0.005] (see Figure 23c). There was no interaction of *agent×goal* in any of the post-hoc ANOVAS.

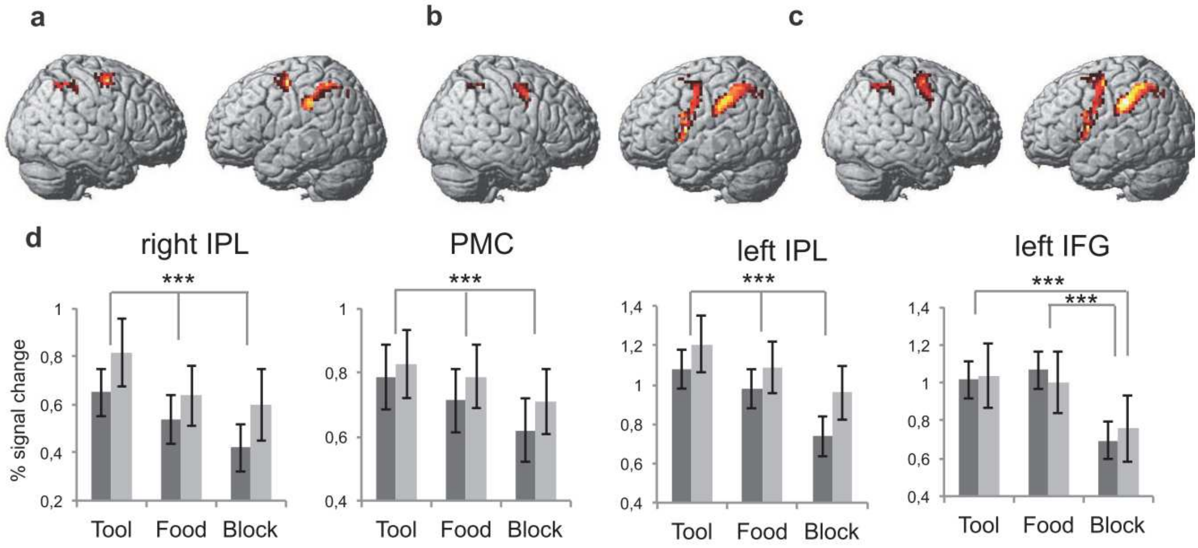

Figure 23: Functional activations for observation of grasping. a) “tool minus food”, b) “tool minus block” and c) “food minus block”. Activations for the observation of “grasping tool minus food items” were stronger in the bilateral IPL and PMC. Activations for observing “grasping tool and food items vs. block were found also in bilateral PMC and IPL but additionally located in the left IFG. All activations are masked by the ROI mask. c) Mean percent signal change in the right IPL, PMC, left IPL and left IFG (averaged over 20 subjects) during observation of grasping actions of human (dark grey) and robotic agent (light grey) directed at tools, food items and block.

To test whether also during pointing the MNS areas differentiated between different goals, we looked at the results of the *action ANOVA II* performed on factors *agent*, *goal* and *action type.* This ANOVA showed the effect of *goal* in the left IPL [F(1,19)=8.4 p=0.009], right IPL [F(1,19)=41.7 p=0.001] and the bilateral PMC [F(1,19)=10.9 p=0.004], but no interaction *goal*×*action type* suggesting that also during pointing, the MNS differentiated between different goals.

4.2.5 Agent-dependent MNS activation

The *agent ANOVA I* revealed that there is no effect of agent if we compare the baseline conditions depicting the static pictures of the two agents. To investigate whether agent-related and region-related activity changes are caused by the difference in appearance of the two agents or their movement kinematics (biological vs. artificial) we performed the *agent ANOVA II* on the percent signal change values of the ROIs using the factors *region*, *agent* and *state*. In this ANOVA, for the factor *state* we used the contrast images for *baseline with objects* and *grasping block* (since the increase of activation for the robot was found irrespectively of the goal of grasping). The ANOVA revealed significant main effects of *region* [F(3,57)=5.2 p=0.003], *agent* [F(1,19)=4.5 p=0.047] and *state* [F(1,19)=24.02 p=0.000]. Further, we found significant two-way interactions *region*×*agent* [F(3,57)=3.9 p=0.013], *region*×*state* [F(3,57)=5.3 p=0.003], *agent*×*state* [F(1,19)=5 p=0.038] and a three-way interaction *region*×*agent*×*state* [F(3,57)=2.9 p=0.040]. To investigate the nature of this three-way interaction, we performed the *post-hoc agent ANOVA II* in each ROIs for *agent×state*. In the posterior IFG, no effect became significant. The main effect of *agent* became significant in the left IPL [F(1,19)=6.8 p=0.017] and right IPL [F(1,19)=6.8 p=0.017]. A main effect of *state* was found in bilateral IPL and PMC [left IPL F(1,19)=16.1 p=0.001, right IPL F(1,19)=18.7 p=0.000, PMC F(1,19)=19 p=0.000]. Similarly, the interaction *agent×state* was significant in these regions [left IPL F(1,19)=8.4 p=0.009, right IPL F(1,19)=6.4 p=0.02, PMCF(1,19)=19 p=0.008]. To clarify the nature of the interaction of *agent×state* in IPL and PMC, we performed paired t-tests for factor *agent* during the static condition (baseline with objects) and movement (grasping block) condition. In all ROIs, the factor *agent* was significant during grasping, but not during the static baseline [left IPL: t(19)=3.7 p=002; right IPL: t(19)=3.2 p=004; PMC: t(19)=2.2 p=0.04]. The absent of the effect *agent* when observing the static pictures indicates that the mere appearance of the robot did not lead to differential modulation of the MNS.

As can be seen from the Figure 22c, an increased activation of the bilateral IPL (and perhaps PMC) for observing the robot as compared to the human was found only during grasping but not pointing. Since the *action ANOVA II* revealed a three-way interaction *region×agent×action type*, the *post-hoc action ANOVA II* was performed to investigate the nature of this interaction for each ROI separately. This ANOVA revealed an interaction of *agent×action type* in the left IPL [F(1, 19)=5.8 p=0.025] and the right IPL [F(1,19)=8.4 p=0.009], but not in the PMC and IFG. To investigate the nature of this interaction we repeated the ANOVA with the factors *agent* and *goal* for different action types (grasping and pointing) separately. In line with the activations shown on the Figure 22c, we found the main effect of the factor *agent* in left IPL [F(1,19)=12.7 p=0.002] and right IPL [F(1,19)=14.9 p=0.001] for grasping but not for pointing. This indicates that the increase activity associated with robot was specific only for grasping actions.

4.3 Is goal understanding innate? – a preferential looking times study[18]

4.3.1 Object attractiveness test

To compose object pairs in which both objects were equally attractive for the marmoset monkeys, we compared the variables latency and interaction time for all four objects. Based on similar values of these variables, we composed two pairs of objects: Object1/Object2 and Object3/Object4. The latency was 11.9 s in case of the first object; 15.5 s in case of the second object; 22.5 s in case of the third object and 23.6 s for the forth object. The interaction time with the objects was 27.7 s; 30.7 s; 14.1 s and 11.7 s respectively. The paired samples t-test of the latency and object interaction time performed on the first pair revealed no significant differences between the two objects (t(6) =-0.90 p<0.856 for the interaction time and t(7)= -1.095 p<0.31for the latency). The t-test of the latency and interaction time

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[18] Parts of the text used in this chapter were used in the study “Kupferberg A, Glasauer S, Burkart JM Do robots have goals? How agent cues influence action understanding in non-human primates.” submitted for publication.

performed on the second pair revealed no significance either ($t(6)=0.505$ $p<0.631$ for the interaction time and $t(7)=0.115$ $p<0.912$ for the latency). These pairs were presented to the marmosets in an object-choice task. In case of the pair Object1/Object2, both objects were approached four times. In case of the pair Object3/Object4, Object3 was approached five times and Object4 three times. The chi-square test performed on the number of approaches of both objects in each pair showed that the marmosets approached both objects randomly without having preference for any of them in both pair one [$X^2(1, N=8)=0$, $p=1$)] and pair two [$X^2(1, N=8)= 0.5$, $p<0.48$)].

4.3.2 General results

To test whether the looking-times of monkeys decreased during the habituation trials in all experiments, we performed an ANOVA on the factors *dishabituation* (habituation 1, habituation 2 and habituation 3) and *agent* (conspecific, robot, box). This ANOVA has shown an effect of *dishabituation* [$F(2,60)=37$; $p=0.000$]. The absence of interaction effect *habituation×agent*, indicated that during habituation, looking times decreased in all three experiments. Thus, repeated observation of an action directed toward the same goal resulted in habituation to the stimulus as reflected in the decrease of the looking times (see Figure 24).

An overall analysis of variance performed on factor *congruency* (incongruent/congruent test event) as within-subjects factor and *test-trial order* (congruent event first, incongruent event first) and *agent* (conspecific, robot, box) as between-subjects factor has revealed the main effect of *congruency* [$F(1,27)=7.37$, $p=0.011$] and an interaction of *congruency×agent* [$F(2,27)=10.1$, $p=0.001$]. There was no interaction of *congruency×test trial order*, suggesting that the average reaction times for the test events were not significantly different across the three experiments.

To test for the nature of the interaction effect *congruency×agent,* we repeated the ANOVA with the factors *congruency* and *test trial order* for each agent separately.

4.3.3 Goal attribution to a conspecific

An overall analysis of variance (ANOVA) was used to examine the duration of looking on the screen during the first three habituation trials. The looking times at the monkey’s action showed a significant effect of the trial number, demonstrating a significant decrease of looking times in the last versus the first habituation trial [$F(2,16)=18.5$; $p<0.000$] (see Figure 24a). Thus, repeated observation of an action directed toward the same goal resulted in habituation to the stimulus.

The second ANOVA examined the effects of *test trial order* (congruent event first, incongruent event first) and congruency (incongruent or congruent test events) on the duration of looking times. There was no main effect of *test trial order* [$F(1,7)=3.1$; $p<0.121$]. However, there was a main effect of *congruency*: the monkeys looked significantly longer at the incongruent action event than at the congruent test event [$F(1,7)=24.6$; $p<0.002$] (see

Figure 24a). There were no significant interactions between any factors. At the individual level, all nine monkeys looked longer at the incongruent test event.

4.3.4 Goal attribution to a robot

The repeated analysis of variance examined the effect of test *trial order* on the duration of looking during the three habituation trials. Similar to the first experiment, it revealed a main effect of *dishabituation*, that is, the subjects looked significantly longer at the first habituation trial than at the second and the third habituation trials [F(2,18)=10.5; p<0.001] (see Figure 24b).

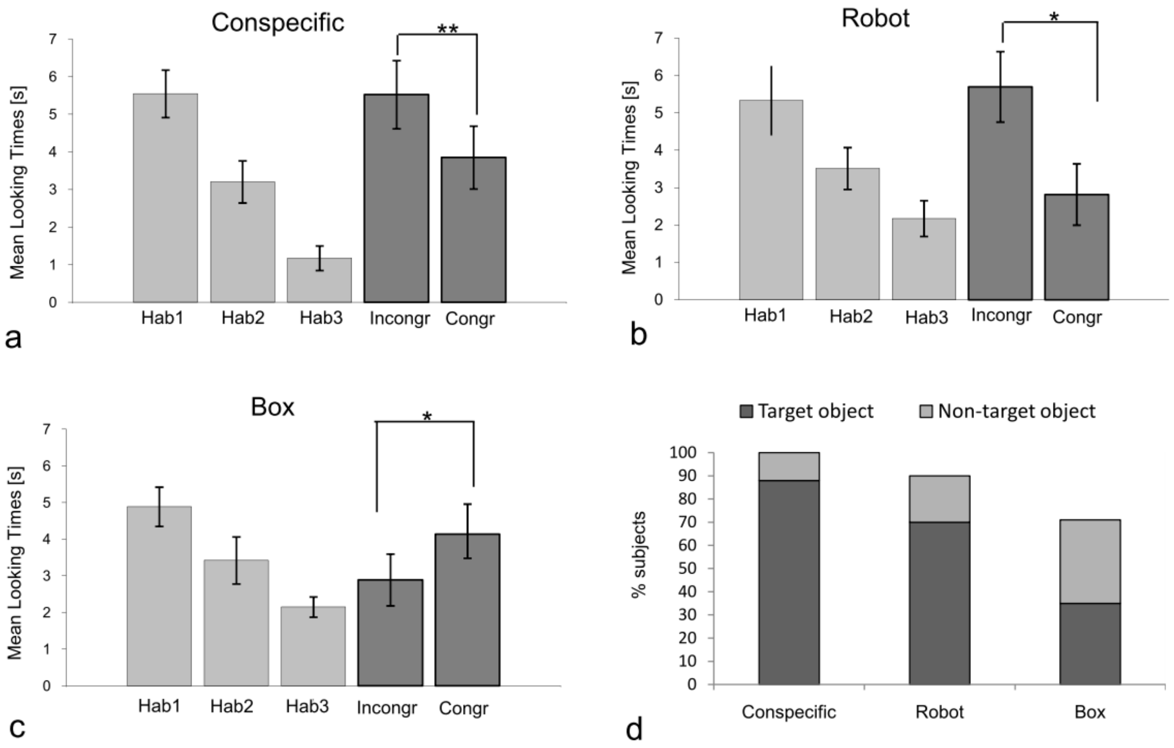

Figure 24: Averaged looking times in the preferential looking-times study. The bars represent average looking times (in seconds) for the three habituation events (light grey) and the two test events (dark grey) in the first experiment (a), second experiment (b), third experiment (c). The vertical bars indicate SEM (standard error of the mean). Figure c depicts the percentage of monkeys who approached at least one of the objects in the final test (light grey) and the percentage of monkeys who approached the congruent object first (dark grey).

The second repeated measures ANOVA has shown that the monkeys looked for a longer time duration if the agent approached a different goal than if it used a different trajectory [F(1,8)=6.9 p<0.03] (see Figure 24b). At the individual level, eight monkeys looked longer at the incongruent test event and two monkeys looked longer at the congruent test event. ANOVA revealed no effect of test event order [F(1,8) = 2.37; p <1.62)] on the looking times in the test conditions.

4.3.5 **Goal attribution to a box**

The repeated measures ANOVA performed on the looking times obtained in the habituation trials revealed a main effect of *dishabituation*, that is, the subjects looked significantly longer at the first habituation trial than at the second or the third habituation trial [F(2,28)=10.27; p<0.001] (see Figure 24c).

The second ANOVA revealed a significant effect of *congruency* [F(1,12)=6.1; p<0.029]. In contrast to the Experiments 1 and 2, the monkeys looked significantly longer at the congruent event (see Figure 24c). At the individual level, 3 out of 14 monkeys looked longer at the incongruent event, 10 looked longer at the congruent event and 1 monkey looked equally long at both events. There was no effect of test trial order [F(1,12)=1.3; p<0.277].

4.3.6 **Social learning test**

In the final object preference test performed after the first experiment, all monkeys but one have chosen the object which has been previously approached by the conspecifics (see Figure 24d). The paired sample t-test showed that after approaching the object, all monkeys interacted longer with the object which was previously preferred by the model monkey compared to the other object [t(8)=3.49; p=0.008)] (see Figure 25). The chi-square test revealed that object choice in the final test was not random but directed at the object which the model has preferred [X^2(1, N=9)= 5.44, p<0.01)]. Additionally, all monkeys approached at least one of the objects.

After the second experiment, 7 out of 10 monkeys have chosen the congruent object and one monkey did not approach any of the objects (see Figure 24d). From these seven monkeys, five have looked longer at the incongruent event. Although chi-square test revealed no preference of monkeys for the congruent object [X^2(1, N=8)=2.77; p<0.095)], the paired sample t-test has shown that all monkeys spent a significantly longer amount of time interacting with the object approached by the robot during the habituation [t(8) =4.08; p<0.003)] (see Figure 25).

After the third experiment, 5 of the 14 monkeys have first preferred the object which has previously been approached by the box during habituation, 5 monkeys have chosen the object previously ignored by the demonstrator and another 4 monkeys have not chosen any of the objects (see Figure 24d). The chi-square test has shown that the monkeys have chosen the object randomly X^2(1, N=10)=0; p=1). Additionally, paired sample t-test showed no difference in the object exploration time t(13) = -0.155.107; p<0.879) (see Figure 25). Thus, it seems that the monkeys had no preference for any of the objects if the model approaching the object was a box.

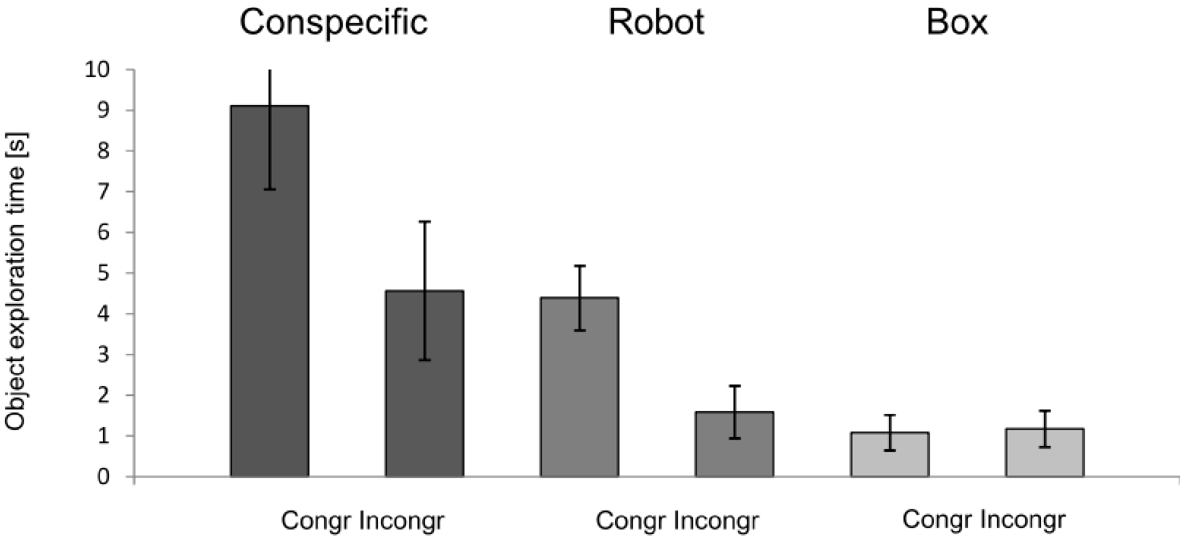

Figure 25: Duration of object exploration in the looking-times experiment. Bars represent the amount of time (in seconds) which the monkeys spent exploring the congruent and the incongruent object after approaching it in each experiment.

4.4 Summary of results

4.4.1 Evaluation of human-robot interaction by motor interference[19]

In two experiments we investigated how different aspects of appearance, motility (ability to move resulting from the joint configuration) and movement kinematics (movement velocity, movement variability) of the observed agent influence motor interference (MI). Participants performed arm movements in horizontal and vertical directions while observing videos of a human, a humanoid robot, or an industrial robot arm. The latter was presented to the subjects in either artificial (industrial) or human-like joint configuration (see Figure 10c, d).

Results from the first and second experiment

The results of the first experiment have shown that a humanoid robot with a limited human-likeness in its appearance may trigger the same type of implicit perceptual processes as revealed by MI as a human agent, given that it moves with a quasi-biological velocity. Further, we showed that movement variability is not crucial for eliciting MI. Finally, we demonstrated that MI can be elicited by using an approximation of biological velocity (quasi-biological velocity) in the robot’s movements.

The second MI experiment demonstrated that the same industrial robot arm performing exactly the same movements induced MI when it had human-like motility, i.e. when it was presented in a joint configuration similar to the human arm (tilted by 90°) (see Figure 10d), but not when it was shown in the standard industrial configuration (see Figure 10c). Note that

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[19] Parts of the text used in this chapter have been published as “Kupferberg A, Huber M, Helfer B, Lenz C, Knoll A, Glasauer S. (2012) Moving Just Like You: Motor Interference Depends on Similar Motility of Agent and Observer. PLoS ONE 7(6): e39637. doi:10.1371/journal.pone.0039637”

the kinematics of the end effector (the gripper) of the robot arm did not change relative to the observer in the two configurations; only the robot arm in the tilted, human-like joint configuration moved in a way which resembled a human arm movement (human-like motility).

Together both experiments indicate that movement variability and accurate biological velocity as well as human-like morphology (like head, torso and 2 arms) of an inanimate entity are not required for triggering MI during action observation. However, at least quasi-biological movement velocity and human-like motility (capability to move like a human arm resulting from the joint configuration) of an agent are necessary for eliciting MI in the movement of the observers. To my knowledge, this is a novel finding, since previous studies could not distinguish the role of agent's appearance and its movement velocity for engaging MI in the observer.

Results from different analyses of MI

The analysis of the three contributing factors indicated that SA correlated with the movement curvature (CA), tilt (or shift) of the overall movement plane in respect to the vertical or horizontal plane (TA) and deviations of individual movements from the overall movement plane (DA). As expected, the regression analysis showed that the combination of the three factors DA, CA and TA explained approx. 90% of the movement trajectory deviations from the instructed movement plane. However, the curvature of the individual movements (CA) contributed only negligibly to the overall effect (see Figure 19c), The DA analysis revealed a significantly higher SD in the horizontal than in the vertical plane (see Figure 19b), which might be due to a difference in the biomechanical properties of forearm movements in horizontal and vertical planes or due to the fact that the deviations during horizontal movement might have been facilitated by gravity. Since the overall tilt from the instructed movement direction (TA) plays such an important role in MI (see Figure 19a), future investigations need to assure careful calibration of the spatial coordinates of both the movements of the observed agent and of the test subjects.

4.4.2 Do robots have goals? – an fMRI study[20]

The aim of the second study was to assess whether MNS activity during action observation is modulated by action type (motor intention) and action goal (cognitive intention) not only when observing humans, but also artificial agents. To this end, we recorded the brain activity of subjects observing videos of human and robotic grasping and pointing actions aimed at different object categories (tools and food items). These object categories suggested different intentions in the following chain of motor actions (e.g. eating or repairing something respectively). Apart from action observation, the subjects performed grasping actions directed to these different object categories themselves. This enabled us to localize the regions active

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[20] Parts of the text from this chapter have been used in the study submitted for publication to Neuroimage as "Kupferberg A, Iacoboni M, Flanagin V, Huber M, Kasparbauer A, Schmidt F, Borst C, Glasauer S Action- and goal-specific fronto-parietal activation during observation of actions performed by artificial agents and humans."

during action observation and execution by conducting a conjunction analysis between those two conditions. The overlap of the conjunction analysis with the four predefined regions of interest (based on [210]) revealed activations in the bilateral premotor cortex and left and right inferior parietal gyrus. Additionally, activity was found in the pars opercularis of the left inferior frontal gyrus (see Figure 21b). We used the mask composed from these regions to mask the results in all contrasts of interest.

For observation of grasping vs. pointing performed by both agents, our functional results have shown a clear signal increase in bilateral IPL and PMC in case of grasping (see Figure 22a). This indicates that MNS-activity was modulated by observation of different action types performed by both human and robotic agents (see Figure 22c). To my knowledge, no previous study was able to assess this.

We further investigated goal attribution to observed actions, which we define as differentiating between the same action type (either grasping or pointing) directed at different goals. The bilateral IPL, PMC, and left pIFG showed sensitivity to the goal of the action, again during observation of both agents. Although the activity in the bilateral IPL and PMC was increased for the robotic agent, no interaction between agent and goal was present in any of the ROIs, suggesting that movements of both agents were processed as being goal-directed. Observation of grasping tool items vs. food items (both object categories suggesting a specific intention) revealed increased activity for tools in the bilateral IPL and PMC (see Figure 23). Observation of grasping a block (geometric shape) caused smaller activation than for tool or food in IPL and PMC, but also in the left pIFG, which did not differentiate between tool and food (see Figure 23).

The modulation of the MNS activity by goal is a new finding since all previous studies only compared levels of MNS activation during action observation across agents (humans vs. robots) and did not test whether the activations are present if contrasting actions of inanimate agents directed to different goals. Differential MNS activity was consistent with the data obtained by button presses and the debriefing after the experiment. The analysis of the button presses indicated successful intention attribution to both agents in over 95% percent of trials (although 50% of subjects reported that it was more difficult to attribute intentions to robot than to the human agent, see Figure 20a). Consistent with that, in case of grasping tools, all subjects indicated that they anticipated the human and the robot to use the tool appropriately to its expected “well-known” function independently of agent nature. However, when observing the robot’s grasping action directed at food items, approximately 1/3 of subjects attributed the intention of “eating” or “bringing to the “mouth” (like for the human) and 2/3 of the subjects attributed the intention of giving/offering the food to someone else.

When observing grasping actions performed by the robot in comparison to the human agent, activation was stronger in the bilateral IPL (see Figure 22b, c). Interestingly, this difference was absent when comparing the static baselines of the two agents to each other as well as comparing pointing actions performed by both agents (see Figure 22c). This suggests that the increased activation for observing the robot grasping objects was triggered neither by its artificial appearance nor by its non-biological movement. Likely, the signal increase was attentional, since the grasping action of the robot was executed from above, a rather unusual type of grasp.

4.4.3 Is goal understanding capacity innate? – a preferential looking times study[21]

To clarify whether the capability to attribute goals is innate or learned by experience, we examined the marmoset monkey's goal attribution to two previously unencountered agents displaying different degrees of monkey-likeness. We supposed that if the marmosets could attribute goals to an inanimate monkey-like agent, this would indicate the innateness of the goal-attribution capacity.

In the first experiment we have shown that common marmosets attribute goals to actions of their conspecifics, even if these are presented in video clips. This finding indicates that the monkeys, like 6-months old human infants [304] habituated not to the physical properties of the action (motion path), but to its goal (a certain object). It seems that the monkeys tried to predict the actions of their conspecifics on the basis of the goal-directedness of the event observed during the habituation trials and thus expected that the subsequent action of the agent would be directed towards the object that has previously been approached. This pattern of results was obtained in spite of the fact that the congruent event was visually more dissimilar to the habituation event than was the incongruent event (which, in fact, displayed the very same action). In the second experiment, we demonstrated that the goal attribution mechanism still works if the agent presented in video clips is a monkey-sized quadruped robot which the monkeys had never before observed to behave in a goal-directed way previous to the experiments. However, when a moving geometric box with no monkey-like features was used as agent, the monkeys were no longer able to attribute goals to its actions (third experiment). Thus, although monkeys attribute intentions to their conspecifics and can extend this capacity to infer goals of inanimate, conspecific-like agents, they are not to be able to do so in case of objects with only a small degree of morphological similarity. Therefore, since the monkeys attributed goals to previously unencountered agents, the capability of goal understanding seems to be innate.

The second purpose of this study was to investigate whether the capability of marmosets to recognize goals of an entity has an effect on their readiness to accept such an entity as a model in a social learning context. In the final object preference test, we have shown that monkeys were more likely to learn from a conspecific and from the robotic model than from the box. Since the monkeys also attributed goals to conspecific and robotic agents but not to the box, we argue that capability of social learning is linked to goal attribution. This is a novel finding since our results indicate that stimulus enhancement, which is a more simple form of social learning is a subject to goal attribution.

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[21] Parts of the text used in this chapter were used in the study "Kupferberg A, Glasauer S, Burkart JM Do robots have goals? How agent cues influence action understanding in non-human primates." submitted for publication.

5 Discussion

5.1 Agent and action characteristics which facilitate motor interference, MNS activity and intention attribution

5.1.1 Role of agent appearance and motor system (motility)

The results of the MI study suggest that the requirement for MI during observation of incongruent movements is not the biological nature of the observed agent, its human-like appearance (like possessing a head and torso), or its biological velocity, but rather its human-like motility. Of course, human motility implies at least some similarity in the agent’s appearance such as human-like general morphology of the observed body part. In contrast to Albert et al. (2010), who suggested that human shape is a crucial factor in triggering MI [5], and Chaminade & Cheng who claimed that MI can be triggered only when the whole body is visible [61], my study shows that a robot which has an arm displaying a human-like joint configuration and moves with smooth movement velocity is able to elicit MI. Thus, the presence of the shoulder joint with lower and upper arm might have facilitated the subjects’ association of JAHIR 90° with the human arm. The importance of similar motility of the observing and executing agent is in line with previous studies mentioned in the introduction which indicated that in infants simulation can take place only when the observed action can be transformed to the own body of the agent. Therefore, it is conceivable that in the original study by Kilner et al. (2003) MI was absent during observation of robotic arm movement not only because the robot moved with artificial velocity, but also because the robot's artificial joint configuration did not allow observers to map its movements to the human body [166]. My findings imply that if robots will be used as models for people with disabilities for training of a certain body part, it will be sufficient if the movement of only this body part can me mapped into the subject’s body.

In contrast to the MI experiment, since the robot presented to the monkeys had only shoulder joints (but no knee joints), I cannot argue that the mechanism involved in monkey goal attribution and thus motor resonance requires exactly the same motility of the observed agent. However, similar motility in case of monkeys might not necessarily mean the presence of the same joint configuration but simply the presence of four limbs and quadruped motion. This assumption could explain the absence of goal attribution to a box, which had no limbs. Accordingly, a study showed that cotton-top tamarins, which, like common marmosets, belong to the family Callitrichidae, attribute the capacity to change location only to living animals (like mice and frogs) but not to inanimate limbless agents such as a moving ball or a moving clay face [136]. Previous studies which show that capuchin monkeys do not attribute goals to rods [218] are in line with this finding. Nevertheless, I argue that the presence of morphological features (body, head, and extremities) is an important cue for the monkeys in order to perceive an entity as an intentional agent.

The finding, that observation of a robot may trigger the same degree of MI as a human agent is in line with the findings of my fMRI experiment, which has demonstrated that MNS resonates as a response to movement observation of a humanoid robot with artificial appearance. The neural simulation of different action types performed by the robot is indicated by the fact that grasping activates the bilateral IPL and PMC stronger than pointing. Further, my data show that not only the type of the action, but the goal of the action might be simulated when observing robotic grasping and pointing actions (see Figure 23). Supporting this interpretation, the debriefing after the experiment has shown that the participants were able to attribute an intention to almost every robotic action (see Figure 20). This is not self-evident because previous infant studies claimed that agents must first be categorized as animate before their behavior can be interpreted in terms of goals [194,304]. Attribution of a different intention depending on the goal of an action and presence of this differential activation during observation of both agents indicated that similar cortical networks are contributing to goal attribution when observing both humans and artificial agents despite artificial movement velocity and appearance. Thus, it seems that the component of MNS that codes goals represents intentional motor actions independently from the nature of the performing agent and its movement velocity (biological vs. non-biological).

Consistent with finding that MNS in humans is activated by actions of inanimate agents, an fMRI study in monkeys showed that at least the most anterior sector of the ventral premotor cortex (area F5a) responds to robotic movements [201]. This finding is in line with my result revealing that monkeys can extend the goal attribution capacity to unfamiliar inanimate, conspecific-like agents, like the robot which has been used in the monkey experiment (see Figure 15b). However, the monkeys seem not to be able to extend goal attribution to objects which do not have the shape of a human or of an animal, like a box (see Figure 15c). The necessity of at least some morphological similarity for goal attribution to unfamiliar agents might be explained by the simulation theory which has been described in the introduction [107,119]. The simulation procedure reduces the possible range of actors, whose intentions the observer might be able to simulate, since for simulation, the observed actor should have the same motor constraints as the observer. Thus, we can project our own internal experiences onto other agents only if these agents are similar to us (the "like me" hypothesis) [194].

The combination of the results from the present monkey experiment with the previous experiments showing that marmoset monkeys [40] and macaque monkeys [245] attribute goals to a human experimenter, indicates that in order to be seen as an intentional agent by a monkey, the agent either has to exhibit a monkey-like morphology (like in case of monkey-like robot) or be familiar to it (like in case of human). However, it is also possible that difference in shape of the body (like in case of humans) does not impair goal understanding as long as the entity has certain features characterizing biological agents such as a body with head and extremities. Together with previous studies on infants [77,116,157,158,159,224] my findings support the assumption that understanding goal-directedness is not limited to actions of conspecifics and that prior experience with a certain agent is not required for this ability.

5.1.2 Role of biological motion

Taken together, the results from the MI and functional experiments indicate that, in comparison to observation of human actions, the motor resonance is not reduced during observation of actions performed by artificial human-like agents even if they do not move with biological movement velocity.

	Agents	Conditions	Movement plane	Result	Conclusion
Kilner et al., 2003	1) Human 2) Industrial robot	a) Human: biological movement b) Robot: constant velocity	Vertical/ horizontal	MI only in a)	MI typical only for biological agents
Oztop et al., 2005	1) Human 2) Humanoid robot DB	a) Human: biological. motion; b) Robot: human prerecordings	Diagonal	MI in a) and b)	MI depends on the biol. movement profile and humanoid shape
Chanminade et al., 2005	see Oztop et al., 2005	a) Human: biological motion b) Robot: artificial movement c) Robot: human prerecordings	Vertical/ horizontal	MI in a) and c)	MI requires biological motion kinematics
Shen et al., 2009	Humanoid robot	Robot: constant velocity	Vertical/ horizontal	MI: absent	MI cannot be triggered by constant movement velocity
Shen et al., 2011	1)Humanoid robot 2) Pendulum 3) Moving dot	a) Robot: constant velocity b) Pendulum:constant velocity c) Dot: constant velocity	Vertical/horizontal	MI: trend towards significance	See Shen et al. 2009
Hardwick et al., 2012	Human	Human: biological movement	Horizontal/ Vertical	MI present	MI present for human movement

Table 5: Overview of studies which investigated MI in live settings. The table was adopted with permission from [174].

In addition to findings presented in [62,120,165,166,212] showing that biological movement was crucial for triggering MI (see Table 5), I now demonstrated that quasi-biological movement velocity is sufficient to elicit this effect. Therefore, motor resonance can already be triggered using an agent which moves with an approximation of biological velocity profile. Interestingly, two studies have demonstrated that in case of a moving geometrical shape, the MI can also be triggered by constant velocity [22,270] (and Table 6). However, in these studies, abstract moving dots instead of embodied robots were used. As an explanation for the presence of MI despite non-biological appearance and velocity, Bouquet et al. suggested that in case of the dot, a single moving point-light dot might have led to a greater accessibility of motion information than the robotic arm used by [166]. This suggestion is supported by the fact that individuals show a natural tendency to focus upon movement of the hand during observation of arm movements [192]. Thus, the moving dot might have activated the movement of the participant's hand towards it, irrespective of the type of movement.

However, it seems that when it comes to human-like agents, the constant velocity will impair motor interference. A recent study investigating the effect of agent shape [256] indicates that even a human-like joint configuration cannot compensate for jerky movements produced with constant velocity [256]. Thus, although [256] used the robot KASPAR2, the appearance of which is very similar to a human (it has 6 degrees of freedom in its arms and hands and a skin-like silicon-rubber mask on its face), in the original MI paradigm [166] no MI could be demonstrated when using it as the model, which according to my studies has been caused by constant movement velocity of the robot.

	Agents	**Conditions**	**Movement plane**	**Live/ Video**	**Result**	**Conclusion**
Kilner et al., 2007	1) Human 2) White disk	a) Human: biological motion b) Human: constant velocity c) Disc: minimum-jerk motion d) Disc: constant velocity	Vertical horizontal	Video	MI in a), c), d) but not in b)	MI depends on biological movement and not on humanoid shape
Stainley et al., 2007	1) Human 2) White dot	a) Human: biological motion b) Dot: human prerecordings c) Dot:constant velocity profile	Vertical horizontal	Dot: video Human: live	MI in a), b), c)	MI does not require biological velocity
Jackson et al, 2006	1) Human 2) Point light figure	a) Human: biological motion b) Point-light figure: human prerecordings	Forth/back up/down	Video	MI neither in a) nor in b)	MI not in case of goal free-movements
Bouquet et al., 2007	1) Human 2) Dot	a) Human biological motion b) Dot: human prerecordings c) Dot: artificial motion	Vertical/ Horizontal	Video	MI in a), b), c)	MI does not require human shape and biological velocity
Albert et al., 2010	1) Human 2) Dot	a) Human: biogical motion b) Dot: human prerecordings	Vertical/ Horizontal	Video	MI in a) stronger than in b)	MI is significantly stronger for human than for abstract shape
Gowen et al., 2008	1) Human 2) White dot	a) Human: biological movement b) Dot: human prerecordings c) Dot: constant velocity	Horizontal Vertical	Video	MI in a) and b)	MI depends on biological movement profile

Table 6: Overview of studies which investigated MI by using videos of point-lights or dots. The table was adopted with permission from [174].

The demonstration of MI and therefore motor resonance, when observing a robot moving with a minimum-jerk velocity profile is supported by results of my fMRI study, which showed the MNS-based neuronal simulation of robotic movements produced with an approximation of biological movement velocity. My results from the looking times experiment also indicate that marmoset monkeys are able to attribute goals to individuals with conspecific features who are incapable of producing biological motion. Therefore, in contrast to [14], biological motion is not a necessary cue for goal attribution in monkeys. However, based on the number of previous studies investigating the importance of biological velocity [62,120,165,166,212] I argue that in humans, at least a quasi-biological velocity is required for triggering motor resonance when observing non-goal-directed movements. This assumption is also supported by a recent study, showing that in human-robot interaction, a "minimum jerk" velocity profile, which is closer to a biological one, facilitates motor interaction in a handover task in contrast to trapezoidal (more jerky) velocity profile [144].

The ability to distinguish biological from non-biological motion is useful for recognizing the movements of other animate beings and for prediction of their future actions and making an appropriate response. Some studies have suggested that perception of biological motion plays a role in social cognition more broadly [81] including the discrimination of living from non-living entities [156,284] or gender [283] or individuals from one another [150].

5.1.3 **Role of agent and action familiarity**

Conflicting results of previous studies

In the introduction, I mentioned that previous studies have led to conflicting results concerning the question whether the MNS can be activated by processing action of inanimate agents and whether biological velocity and human-like appearance are required for motor resonance. Researchers supporting the familiarity account claim that during action observation, familiarity and presence of the observer's prior motor experience in the observed action positively correlate with the signal increase in his MNS areas [2,47,74,75]. Researchers supporting the "*agent-independent*" goal-coding account suggest a similar MNS-activation for the processing of unfamiliar (artificial) and familiar (human) actions [112,206].

Supporting the first account, a stronger MNS-response was demonstrated when the observed actions [195,276] or facial expressions [66] were performed by a human compared to a robot. Further, observation of movements performed by objects [71,91] or animals [31] led to a weaker MNS activation when compared to those performed by human agents. Also behavioral studies investigating how the observed actions influence simultaneously performed actions has demonstrated greater interference effects when participants watched a human actor moving with natural kinematics vs. constant velocity [165]. The same outcome was present when watching a robotic agent moving in a human-like compared to a non-biological manner [212].

In support of the second account, [56] demonstrated no difference in the IFG- and IPL-activity when comparing brain response elicited by the observation of object manipulation by four agents with different degree of human-likeness (a human, a humanoid robot, stacked boxes and a mechanical claw[22]). Additional evidence indicating that the MNS is sensitive to non-biological nature and motion kinematics of the observed agent comes from recent studies demonstrating activity in the MNS-areas during observation of humanly impossible movements [71,246] or animated geometric shapes which manipulate simple objects [231].

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[22] However, this finding might also be a result of passive viewing task or usage of computer-generated/televised stimuli instead of videotaped ones [127,189,259].

Further, using EEG, [87] have shown that the P1[23] wave was enhanced in response to happy compared to neutral facial expressions for robotic as well as for human stimuli, suggesting that emotional expressions of robots are encoded as early as those of humans. Additionally, two recent studies indicated the same degree of activation in the MNS when observing hand actions performed by humans and robots [112,253]. Finally, [206] found equal mu suppression[24] effects during the observation of human and humanoid robot's opening and closing hand movements, and [117] showed similar premotor activation when observing human and humanoid emotional facial expressions (in fact, there was a larger response for humanoid actions at some coordinates). Also behavioral studies showed motor facilitation [227] and interference effects on the movement of the observer [175,212] when observing robotic actions.

How my results help to clarify the nature of conflicting findings

We found increased activity in the MNS areas responding to action observation for the robot in case of grasping actions but no difference between human and robot neither for the static pictures nor for pointing actions. I suggest that these findings might be explained by the fact that robotic movements were performed with an unusual hand trajectory which looked unnatural to the subjects (in fact, 40% of the subjects perceived robot's movements as being not natural, see Figure 20d). As stated in the methodological section, the robot's joint configuration required heightening of the hand right before lowering it for the grasp – thus, in contrast to the human who grasped the objects from the side, the robot grasped them from above. The interpretation that the trajectory of the robot and not the artificial movement velocity and appearance is responsible for the stronger activation in case of the robot is supported by the fact that during pointing, as well as during static conditions, there was no difference in the BOLD signal in the regions of interest between observing human and robotic agents.

Based on the *predictive coding framework* [151,200,234], I argue that the signal increase in PMC and IPL during observation of robotic grasping might be due to the higher prediction error when watching movement performed with an unusual trajectory [103]. This framework claims that when observing agents, we generate expectations about how they might move based on our own motor system, the form of the agent's body [31], the goal of action [107] or/and environmental context [183]. We then compare these expectations to the observed motion and get a stronger activation for the larger prediction error. Consistent with my findings, a number of studies showed increased activity in the IPL and PMC when observing robot-like human [76] and robotic motion [112] when compared to natural human motion. Further, a higher activation in the left IPL and SPL when observing robotic faces has been shown in [217] and [117].

Our results therefore contradict the suggestion that MNS responds most robustly only when watching familiar compared to less familiar movements. Instead, I argue that studies which

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[23] P1 is an early ERP component which is positive and is related to processing of visual stimuli

[24] Mu suppression is an indirect measure of mirror neuron activity and is recorded over the sensorimotor cortex with electroencephalography

found a stronger MNS-activation when observing familiar vs. less familiar actions [47,48] have used stimuli with different characteristics than the studies which were described in the paragraph above [76,117]. On the one hand, as in the present experiment, the observation of unfamiliar actions might have lead to increased prediction error and greater BOLD signal compared to observation of ‘generally familiar’ human actions [76]. On the other hand, a greater BOLD response when comparing extensively rehearsed actions to generally familiar actions (see [47,74,75]) might be explained by the fact that for rehearsed actions, the participants can make very strong and specific predictions about how an action will continue based on prior experience, which in case of slight deviation of sensory input might lead to a higher prediction error compared to observation of ‘generally familiar’ actions. Thus, it might be possible that the relationship between the activation of the MNS and action familiarity is not linear. Instead, in comparison to generally familiar actions, MNS might be stronger activated when observing extensively familiar [47,74,75], non-intended [29,71] or surprising actions [177].

However, I have to note that a very unnatural, mechanical movement might also lead to a reduced activation of the MNS. A recent study investigated how the MNS-activity is modulated due to the unnaturalness of an observed action [260]. The authors inserted short pauses in the middle of the presented action. Interestingly, they revealed that although the MNS activity was still present when two pauses were inserted, it was significantly reduced by the jerkiness of movement when four additional pauses were added. The discrepancy between my results and findings from [195] and [276] might be thus explained by the fact that a slightly deviated, but smooth action, like in case of JUSTIN, may enhance the MNS activity during action observation, while a highly unnatural action like in [195] and [276] would lead to a deactivation of the MNS. The smaller number of joints and the more restricted range of motion of each joints might have impaired the motility of robots used in these two experiments, leading to a smaller degree of motor resonance when observing them [175].

Attentional explanations of the increased MNS activity

In the present study, the increased activation of the MNS for the robot might additionally result from the participants’ engagement in an explicit intention attribution task. Indeed, an fMRI-study has shown that the request to explicitly attend to the emotion of the agent led to significantly increased response to robot, but not human facial expressions in the left IFG [66]. Further, [29] demonstrated an increase of activation in the MNS in the group of participants who had to judge whether the observed action was intended or not in comparison to the participants who were simply asked to observe the presented actions. Thus, observation of less predictable actions in comparison to familiar actions could lead to stronger MNS activity due to the effort to create an action representation where there is less prior information available. In line with this, a recent study has shown that movement prediction during hand-over is impaired when the prior knowledge about the usual movement kinematics (velocity and trajectory) acquired during the daily interaction does not correspond to the observed movement kinematics [144].

Finally, there are also several alternative explanations for the higher BOLD signal during observation of robotic actions compared to human. Due to motor constraints and lacking familiarity, it is possible that simulation of robotic movements might have required greater muscle tension compared to performing the natural human style movements. Another reason for a stronger activation in the MNS might be a higher 'engagement' of the participants by the more salient robotic actions, since it is possible that actions not belonging to the motor repertoire capture attention stronger than actions we see and perform more frequently.

5.1.4 Role of movement variability, self-propulsion and capability to interact

Some studies claimed that movement variability is a crucial factor in triggering MNS-activity [112] and perceiving someone's action as being goal-directed [226]. Likewise, although infants did not attribute goals to a moving box because it repeated exactly the same movements in consecutive trials, in the same setup 6.5-month-old infants were capable of doing so if it moved along a different path in every trial [79]. Although I have used monkeys and not human infants, my results do not support this later study, since despite having a slightly different starting point and trajectory in each habituation trial, the box was not perceived as an intentional agent. Also the results from the MI study show that MI can be evoked even by robotic monotonous movements, indicating that movement variability is not a crucial factor for motor resonance. Thus, when designing robots for interactions with humans we do not have to take this factor into account.

Although my results indicate that certain morphological cues are necessary for intention attribution, they cannot rule out the possibility that self-propulsion is also required for it, as previously claimed in [116,180,226]. However, since the monkeys were not able to attribute intentions to a moving box, this study provides additional evidence that self-propulsion is not sufficient for triggering categorization of the object as an 'intentional agent' as suggested by [10,226] when the required morphological cues are absent. Likewise, [161] demonstrated that young infants do not attribute goals to a self-propelled box (but see [185]).

The looking time study further indicates that interaction with the object is not required for goal attribution. In my experiment, the monkey attributed goals to the robot, although it did not interact with the object after approaching it. This finding is in contrast to [7], who used the looking time methodology to show that infants interpret only an interactive humanoid robot but not a non-interactive robot as a biological agent.

5.2 Neuronal activations related to understanding actions and attributing intentions

5.2.1 Common system for action execution and action observation

The areas which were active during both action observation and execution and therefore are likely to be classified as MNS were located in the ventral part of the pars opercularis of the left IFG, bilateral supramarginal gyrus, AIP and the PMC. Thus, my results support the account that observation of a hand action performed by another individual triggers activity within a network of areas which broadly matches some neural systems relevant to hand action execution [31,112] and thus underlies action understanding through motor simulation [107,238]. These results are widely in line with findings from the recently performed meta-analysis of studies incorporating observation of visual images of actions and/or a requirement to execute motor actions [196]. These findings yielded significant clusters in the IFG, ventral and dorsal PMC, SPL and IPL in the conjuction analysis of action observation & action execution. The sum of voxels activated during action execution and action observation separately was larger than the number of voxels which were active during both conditions and thus can be categorized as the MNS.

5.2.2 **Differentiating action types**

When observing grasping actions performed by both the human and the robotic agent in the fMRI-experiment, bilateral PMC and the IPL (aIPS) were activated more than during pointing (see Figure 22c). Activity in the area IPL was also demonstrated during action recognition and action planning [263]. The activity in this region was further shown by [219] and [122], who compared observation of grasping and pointing actions performed by a human agent. When performing actions, IPL was activated more during grasping than reaching or pointing movements [80,109], which can be explained by increased demands on motor control required by precise finger coordination during the grip and lifting phase after grasping. In my experiment, increased activity in the IPL during observation of grasping can be explained in the following way. During action observation, the observers simulate the actions by activating motor circuits which they would recruit while performing this action themselves. The simulation of grasping would require a more precise motor coordination than the simulation of pointing. The stronger IPL activation during observation of robot’s grasping pointing indicates that we might recognize actions of conspecifics and even inanimate agents by simulating them with our own MNS.

One might argue that apart from higher requirements for finger coordination during grasping, the increased activation in the PMC and IPL might be caused by attributing generally different “prior global intention” to pointing vs. grasping actions. Thus, pointing differs from grasping not only through visual characteristics, but besides might have a different final goal (e.g. grasping the object vs. indicating the presence of an object). In contrast to grasping an object, when the person points to an object, this might mean that (i) the person indicates the desire to later interact with the object or that (ii) he/she wants the observer to interact with the object. In my experiment, 10 subjects attributed the intention (i) to the agents and 10 other subject the intention (ii). I assigned these subjects to two groups and performed a t-test using individual contrast images for “pointing” to find out whether the brain activity was different according to the intention attributed to pointing. However, this test did not reveal any difference between the groups indicating that my findings for the contrast “grasping-pointing” were not due to different intentions attributed to the hand action but due to different movement patterns of the two action types.

5.2.3 Attributing action goals

All tool and food items had different size and all three object categories were presented in every trial, independent from the action goal, thus allowing us to minimize the possibility that goal-related activity was caused by different physical and visual features of objects. Thus, in contrast to the previous studies [130,230], in my experiment, the goal of grasping was not defined by the form or color of a certain object (which would have made the differentiation between grasp configuration and goal object impossible) but by its belonging to a certain functional category defining the widely known purpose of the object. In most daily life situations, grasping something is just an initial component of a broader action, in which the object is likely to be used to achieve a subsequent final goal. I therefore supposed that, after the agent grasped a certain object, the subjects would expect the agents to act upon it based on the range of possibilities which this object offers [145,301]. I characterized this expected further action stream (e.g. “eating something” or “fixing something with a tool”) as a primitive form of intention attribution and argued that it will be reflected in the differential activity within the MNS, depending on the action goal. Even if these expected actions are not seen, occlusion mirror neurons and sequence selective neurons could add to differential activations [99,148,293]. Indeed, in my study, the debriefing after the action observation experiment revealed that observation of grasping of every item suggested a further stream of actions. Accordingly, during action observation, the MNS was differentially activated depending on the goal of grasping.

During observation of both human and robotic agents, for the comparison of grasping actions directed at tools with those directed at food items, I find increased activation for tools in the bilateral IPL, PMC but not left pIFG (BA 44, see Figure 23a). For attributing intention to grasping familiar specific objects (tool/food) versus unspecific objects (block, see Figure 23b, c) I find additional increased activation in the left pIFG. This increased activation was present for the observation of actions of both agents.

Activations in PMC and IPL are consistent with studies demonstrating repetition suppression of brain activity in these regions when repetitively observing an action which has the same intention [130,131,132,209,230]. Further, [294] found robust activation in the bilateral aIPS during discrimination of action intentions for actions aimed at displacing or using a tool-object. Finally, there is some evidence for more abstract goal representations in the inferior parietal cortex from studies of patients with apraxia [42,128] and from studies which use transcranial magnetic stimulation for disrupting goal processing [288]. Therefore, I suggest a central role for the left aIPS/IPL in representing and interpreting the goals of observed hand actions irrespective from the agent nature and biological velocity. I further argue that the stronger activation in the IPL and PMC for observation of tool grasping in comparison to food grasping is elicited by expectation of a more complex action chain following grasping a tool (which suggest using a tool in a further complex action) vs. grasping a food item (which is less abstract and most likely suggests direct eating action).

The (i) absence of difference in pIFG activity when comparing grasping tool with food items and (ii) increase of pIFG-activity for observation of grasping directed at familiar and specific items (tool and food) vs. the geometric shape (block), might be explained by the following. First, the actions performed with the block might be less meaningful than those performed with tools and food. A recent study of object-directed actions revealed that although all actions led to increased activity in the bilateral IPL, the bilateral IFG differentiated between meaningful and meaningless actions [202]. However, since another study revealed no difference in the IFG activity when comparing observation of grasping actions (both robotic and human) directed at meaningful objects (e.g. cocktail glass) in comparison to simple geometric shapes (e.g. a cylinder) [112], this explanation seems to be unlikely. An alternative explanation could be related to hand configurations during grasping. In contrast to trials with tool- and food-items, where I have used multiple objects, grasping a block resulted in the repeated grasping of one item. Thus, when comparing grasping tool and food items to grasping a block also resulted to comparing various hand configurations with only one hand configuration. This could have led to an increased pIFG activity for tool and food items. Consistent with this assumption, [132] have shown that although the IPL activity is modulated by the goal of grasping, the activity in the IFG is modulated by observation of different grasp configurations. Supporting this suggestion, it has been shown that in monkeys, the area F5 (congruent to human IFG) has direct connections to primary motor cortex and neurons specializing for different grasp configurations [237]. The proposal, that IFG is involved in processing grip configuration is at odds with some studies which have attempted to link IFG to more abstract action understanding functions, such as the interpretation of goals [293] and intentions [177]. However, I have to note that these studies either did not distinguish between the configuration of the hand and the identity of the goal object [293] or did not control for context [177].

5.2.4 Present results in light of studies investigating the mentalizing network[25]

The conjunction analysis between action observation and action execution revealed common activations in the ventral part of the pars opercularis of the left pIFG, bilateral supramarginal gyrus, aIPS and PMC. Despite using an intention attribution task, in contrast to [65,170], I found no activation in the brain areas which are supposed to be involved in mentalizing when comparing human to robotic actions. These studies have demonstrated a stronger activation in the mentalizing regions - the medial prefrontal cortex and right temporoparietal junction (see Figure 26) - for human agent in comparison to humanoid robot during playing a rock-paper-scissors game [65] or an iterated prisoner's dilemma [170]. I argue that the usage of different methods serves as an explanation for the difference in findings between these studies and my study. Similarly to my experiment, studies investigating the MNS typically use photographs and videos of articulated body parts in interaction with objects or whole-body movements performed in contextually impoverished contexts [31,76,112,148,177,230,253]. These studies do not explicitly manipulate and investigate the extent to which participants make mental state inferences (beliefs, desires, and intentions). On the other hand, for investigation of the mentalizing system as in [65,170], researchers often use interactive games, verbal or abstract visual stimuli such as cartoons or animations (e.g., geometric shapes, see [138]) and present

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[25] Mentalizing is a psychological concept that describes the ability to understand the mental state of oneself and others which underlies overt behaviour.

the participants only seldom with stimuli showing embodied actions or observable behaviours [55,210]. In me experiment, however, the output of the actions was not an unobservable mental state but rather anticipating the further not yet executed chains of actions as in [131], which lead to an observable physical change. Therefore, modulation of activity in the mentalizing areas by observed videos of human and robot action was not expected.

We argue that attribution of intentions and mental states (associated with the mentalizing network) are processed in different brain regions and take place on different levels. One of the possible mechanisms by which the mirror system interacts with the mentalizing system is that mirror neurons provide rapid and intuitive input to the mentalizing system. In fact, the mirror neuron mechanism captures the motor intentional dimension of action, common to both the agent and the observer, supporting the process of mentalizing. Thus, we would not be able to explain the actions of others in terms of beliefs or desires were we not able to recognize immediately their intentional motor meaning; that is, to understand the goal-centeredness that specifies that a particular movement is part of this or that action. Similarly we would not be able to explain the behavior of others in terms of intentions (in the “propositional” sense of the term) and foresee their possible consequences, if we did not possess the motor knowledge that regulates the various goal-centered representations involved in both executing and understanding actions. I therefore argue that the first level of intention understanding involving a visuomotor analysis of the scene is mediated by the MNS [112], whereas the second level of intention understanding, involving a more abstract and descriptive content might be mediated by the metalizing network [117,181].

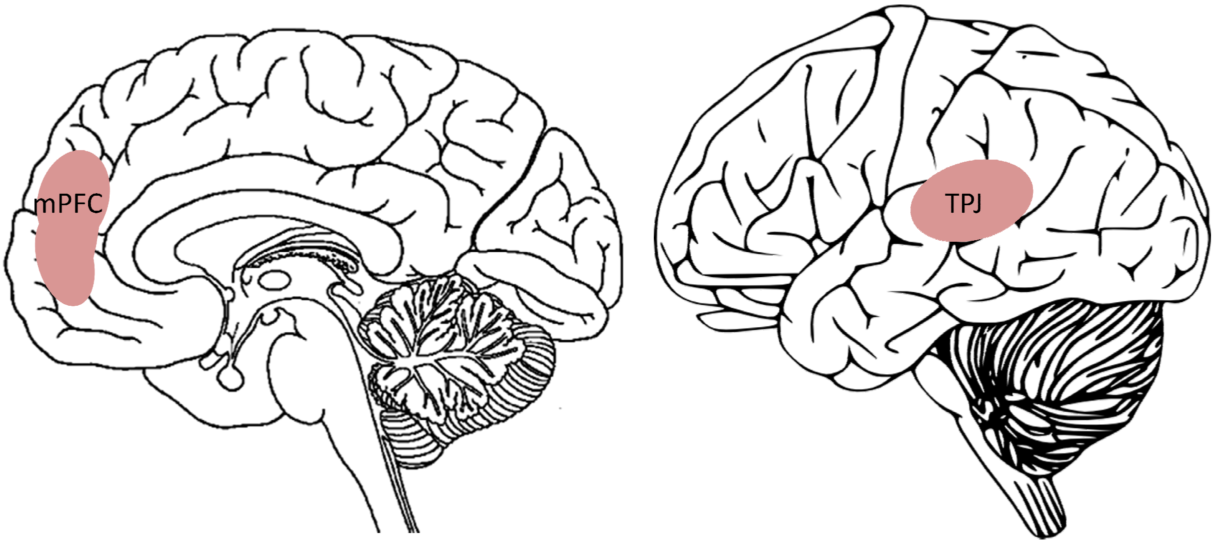

Figure 26: Brain regions supposed to be involved in the process of mentalizing. The regions involved in mentalizing are drawn based on [210]. Abbreviations: mPFG (medial prefrontal cortex), TPJ: temporo-parietal junction.

It is important to note that attribution of goal-directedness and intentions also operates independently from attribution of animacy and mental states to an agent. Likewise, in my case a robotic action might be perceived as goal-directed simply because it follows the principle of rational action [78], since (i) the functions of actions are to bring about future goal states, and

(ii) goals are achieved through the most rational and efficient action available, given the constraints of the environment [115]. However, based on the results of the debriefing and differential activation of the MNS depending on the goal of grasping (as seen in the behavioral data and supported by the imaging data) this assumption of rational action seems unlikely.

5.2.5 **Limitations of classical fMRI design**

There is no reason to believe that the premotor and parietal cortices are the only MNS-areas in the human brain that have mirror or simulation properties. Until recently, studies investigating the neural basis of the MNS have used experimental designs such as passive observation and active imitation protocols for various tasks. Thus, the researchers could demonstrate areas which are more active during a certain condition (e.g. gesturing, hand-object interactions, symbolic hand movements, or emotional facial expressions) compared to a control condition (e.g. random hand movements or rest). However, it is possible that certain regions of the brain include neurons with simulation properties that cannot be displayed by conventional methods, since their activity might be not higher than during the control task. Thus, since most fMRI studies compare activation patterns to a rest baseline, the seeming lack of activation of the MNS (as for example in autism spectrum disorder), may result as a consequence of a greater resting state [85]. The second problem with using classical control tasks used for studying the MNS is that in the test condition the active areas sum over the responses of many neural populations which might be involved in processes other than simulation (such as vision, motor planning, motor execution, working memory, and emotion).

Mirror neurons make up only about 10%-20% of the neurons that respond either during movement observation or execution in monkey mirror system areas [99]. Thus, one of the early studies on the MNS found that only 92 out of 532 neurons (17%) in F5 of the macaque had so-called “mirror” properties [106]. Since during action observation and execution, MNS matches one’s actions with resonant actions of other people, the temporal changes in brain activity in a certain brain voxel (MRI voxels typically represent a brain volume of 27 mm^3) of a person who performs an action should modulate the “ups” and “downs” in the activity of the same voxel in the person who observes the action almost simultaneously. The concept of simulation entails more than only “going on and off together” at the beginning and end of a single action - it involves a continuous tracking of the more subtle changes in activity during the execution and observation of entire streams of action. Single cell recordings [199] show that the temporal profile of the mirror neuron activity is indeed similar during action observation and execution, potentially providing a neural basis for resonance. However, the usage of conventional fMRI designs makes it possible to display only the location of activation in certain brain areas during a certain task.

Conventional fMRI experiments are classically analyzed using general linear modeling (GLM) which requires a highly controlled setting and predefined, isolated stimuli. This analysis uses the GLM for each voxel indexed against a specified experimental design but does not explicitly involve measuring highly structural temporal dynamics of neuronal responses. For these reason, [135] moved away from the classical experimental MRI design, where a predefined stimulus is used to locate brain regions. Instead, in order to define preferred stimuli, the authors recorded brain activation during a free viewing of a movie and examined its temporal dynamics. The authors coined the term “inter-subject synchronization” a method of voxelwise temporal correlation between subjects performing the same “naturalistic” task that is now called inter-subject correlation analysis (ISC). In contrast to classical MRI analysis, in the ISC analysis, hemodynamic response of one subject serves as reference to predict the hemodynamic response of another subject. The correlation coefficient of the corresponding voxels is calculated between the time series of the hemodynamic activity in two subjects. Therefore, for the future study of mirror neuron activity some studies might prefer using a ISC method.

5.3 Goal attribution in non-human primates is innate and subject to morphological similarity

In accordance with my expectations, in all three experiments with marmoset monkeys, looking times decreased significantly during the first three habituation trials (see Figure 24a, b, c). Further, when the subjects were presented with the conspecific and the robot models, all subjects displayed a higher recovery of attention in the incongruent condition. This indicates that they expected the model monkey and the monkey-like robot to adjust their grasping/path to the change of the object position in the test events. In contrast to the first two experiments, in the third experiment, the subjects looked longer if the agent (box) changed its trajectory than if it changed its goal, indicating that the monkeys did not attribute intentions to it. Thus, that the generalization mechanism for goal attribution in monkeys required at least some resemblance of the model to a conspecific (which could be for example a head or torso).

But why did the monkeys look longer when the box changed its trajectory? The explanation for this kind of behavior might lie in the fact that after observing the box repeatedly perform one and the same movement toward the same direction with no significant modification in the path, the monkeys had formed an expectation about the box and its physical movement pattern. Therefore, they were likely to expect an inanimate entity to repeat its behavior from the habituation phase during the test phase and understandably looked longer when it changed its previous trajectory.

Our results suggest that in monkeys, goal attribution to inanimate agents is possible, but limited only to agents possessing conspecific-like features like similar body shape and presence of limbs. This goal-attribution capability might allow the monkeys to predict the behavior of predators and prey, and of conspecifics in contexts related to hierarchy and food retrieval. Thus, it enables the animals to respond appropriately to objects and animate agents (e.g., run away from a predator, approach a piece of fruit that has dropped from a tree and rolled next to a rock) and might provide some of the relevant building blocks for the development of the theory of mind during evolution [222].

Our results bring us closer to answering one of the central questions in the cognitive development which concerns the nature of our understanding of intentionality. Thus, my study provides evidence in favor of an innate vs. learned-by-experience mechanism of intention understanding proposed by [99,51,157,180,224,226]. Based on certain morphological and behavioral features, monkeys are able to positively attribute goals to robots without having any previous experience with them, indicating that the capacity to understand goals is something which does not need to be learned as long as the agent possesses conspecifics-like features. The sensitivity of goal attribution ability to certain morphological features might explain why monkeys do not attribute intentions to a moving box. Additionally, the increasingly demonstrable overlap between infants and primates in early intention understanding capacity strengthens the view for the idea that inferring goals is an innate ability, shaped by our evolutionary heritage [245,303]. However, since adults attribute intentionality even to moving geometric figures [138], it seems that the innate goal attribution capacity can be widened by experience and extended by the mechanisms of the mentalizing system (see section 5.2.4).

The innateness of goal understanding indicates that when designing robots for interaction with humans, implementing basic human features into their appearance might facilitate intuitive understanding of their actions by untrained users.

5.4 Goal attribution is a precondition for social learning

Apart from investigating goal attribution to inanimate agents, the second goal of the looking-times study was to investigate whether the capability of marmosets to recognize goals of an entity has an effect on their readiness to accept such an entity as a model in a social learning context. Social reward-learning from a conspecific model has been demonstrated in a number of studies with marmosets [34,44,84], even if the model was presented in video-clips rather than in real life [39]. In [34], it could be shown that after observing a monkey demonstrator perform a certain task-solving technique for a food reward, some of the observer monkeys showed a stronger tendency to use this technique to reach the goal. Also [296] have shown that monkeys who observe a conspecific used certain method to solve a task for getting food reward (opening a canister with their mouth), they are more likely to use this method instead of a different one which is equally effective (opening a canister with paws).

It has been shown that imitation might be linked to goal attribution [178,280,282]. However, it is not clear whether goal attribution is also a precondition for more simple forms of social learning, such as stimulus enhancement. As expected, I could demonstrate that in case of intentional agents (conspecific and a robotic conspecific-like agent), the monkeys were more likely to prefer the object which has been previously approached by the agent (see Figure 24d) and spent more time exploring it than the second object (see Figure 25). Additionally, when intention attribution was present, the number of monkeys who showed interest in at least one of the objects was higher than when it was absent (see section 4.3.6). In contrast, in the third experiment, when the monkeys did not attribute intention to the agent, they did not show any preference in approaching the objects and explored both objects for equal amounts of time (see Figure 24d and Figure 25). Thus, the monkeys were more likely to learn from a model, which they considered an intentional agent (conspecific or robotic model) than from an entity to which they did not attribute goals (a moving abstract shape). My data imply that the capability of social learning by stimulus enhancement is subject to goal attribution. These results indicate that also in humans, intention attribution to robots might be a precondition even for learning simple tasks from a robot.

5.5 Novelty of the present research and implementation of results

5.5.1 Better understanding of factors contributing to motor resonance and goal understanding

The results from the motor interference study demonstrate that MI and thus the process of simulation can be elicited while observing a robotic arm moving with a stereotyped quasi-biological velocity profile. The fMRI study has supported these findings since observation of robots moving with artificially generated, although quasi-biological movement velocity led to similar activation of the MNS as human action (at least for pointing movements). This is a novel finding since previous studies have compared only constant vs. biological movement velocity and did not test the effect of smooth artificial velocity. A further novel finding is that the motor resonance during action observation does not require movement variability which is a characteristic aspect of human motion and has been suggested to be crucial for motor resonance [112]. Finally, while none of the studies has tested the influence of agent's appearance on motor resonance in the observer, results of the MI-study demonstrated that not human-like appearance, but human-like motility is a precondition for motor resonance when observing actions of inanimate agents. Altogether, I have shown that the combination of a human-like joint configuration and at least quasi-biological motion of the observed agent, i.e., its motility, rather than its human-like appearance is the most important precondition for perception of an inanimate agent as a partner in joint interaction.

The results of the fMRI-study have demonstrated that the MNS-activity is modulated by action goals of artificial agents indicating that intention attribution operates in an agent-independent manner. This is a novel finding since previous studies have investigated MNS-activity only in response to either different intentions from the same human agent or human vs. artificial agents having the same intention. My results show that MNS-activation can be modulated by attributing various intentions to artificial agents, although these agents clearly do not have mental states. Thus, the processing of actions and goals does not depend on whether an agent is animate or artificial as long as we are tempted to attribute intentions to it. Concerning the functional activations I could show that when we observe actions of both conspecifics and human-like inanimate agents, the type of actions and their goals are both processed in the bilateral IPL and PMC. In contrast, another MNS-area, pIFG, might play a role in processing different hand grasp configurations during observation of hand actions. Thus, the fMRI study shed light on how the function of mirror neurons in various brain regions differs. Further, there was an increased activity in IPL and PMC when contrasting grasping actions of the robot vs. human. However, this difference disappeared when contrasting the activations elicited by observation of static pictures of both agents and also pointing actions produced by them. Thus, I propose that activity of MNS is not sensitive to the agent's appearance or to its movement velocity. Instead, I argue that increased activity when observing robot's grasping actions in comparison to human actions is caused by artificial appearance of the grasping action, which led to a higher prediction error on the part of the observer.

In contrast to [276] and [195], which demonstrated stronger involvement of the MNS in covert simulation of human action than in action of artificial agents, my data indicates that MNS activity is not reduced when observing robotic actions in comparison to humans. In fact, it can even be increased when observing actions that look unnatural. Thus, I suggest that, in contrast to [47,48] which claim that the MNS is stronger activated by familiar actions, the relationship between the activation of the MNS and action familiarity is non-linear. Therefore, observing extensively familiar [47,74,75], non-intended [29,71], and surprising [177] actions might activate the MNS stronger than generally familiar actions.

The looking-times study on marmoset monkeys indicated that the ability to attribute goals is most likely shaped by evolution and is bound to certain morphological features of the observed agents. Until now, there were only two studies which investigated how monkey process actions of inanimate objects [136,218]. However these studies have not investigated which cues (e.g. presence of a body with a head, biological motion, monkey shape and size, ability to manipulate objects) an entity must exhibit in order to be perceived by monkeys as an intentional agent. I demonstrated that although marmoset monkeys attribute intentions to their conspecifics and can extend this capacity to infer goals of inanimate, conspecific-like agents, they seem not to be able to do so in case of objects with only a small degree of morphological similarity. Thus, presence of at least some basic degree of monkey-likeness, such as limbs and head, might be a precondition for goal attribution. My study indicates that the dependence of goal-attribution capacity on the agent’s morphology is shaped by our evolutionary heritage. Further, my results indicate that goal understanding is a requirement for simple forms of social learning (social enhancement). This result is interesting, since up to now it was assumed that intention attribution was required only for cognitively demanding forms of social learning such as true imitation [45,282].

While the robot used in the fMRI study was clearly inanimate, it was similar in overall form to a human and displayed human-like motion. Since I did not use robots with different morphological features in this study, the present data do not provide any hints which particular morphological characteristics of the (robotic) agent are crucial for modulation of the MNS-activity by goal-directed actions. Future studies will need to address this issue in a more detailed way using even more disparate forms of artificial appearance. Another interesting issue would be to test the role of the subjects’ experience with artificial agents on the activity of neural markers of motor resonance.

5.5.2 Applications of present results in the medical sector

The area of humanoid robotics develops very fast and has a promising future. But is it a realistic that in the future some percentage of human caregivers and therapists will be replaced by robots for accomplishing at least some tasks? If so, which morphological factors influence our perception of robots as intentional beings and enable us to learn from them? Further, which human-like features should be present in a robot so that the observational therapy used in stroke patients can be effective? This therapy is based on the assumption that observing actions of a person will facilitate the execution of these actions since during action observation we simulate the observed actions with our motor system. Thus, people with physical impairments will profit from using robotic models in the observational therapy only if the simulation is successful. In this thesis, I therefore not only examined whether humans perceive artificial robots with human like appearance as intentional beings but also whether they simulate the robot's action using the same mechanism as they use to simulate actions of other humans during action observation. To this end, participants were scanned by means of functional magnetic resonance imaging enabling us to measure cortical activation during observation or robots' actions. I further investigated what aspects of the robot's appearance and movement kinematics are important for using them in clinical and household settings. For this purpose, I tested the importance of morphological features (presence of human-like body shape), joint configuration (motility) and movement kinematics (biological velocity, movement variability) for engaging the observer's motor system during observation of the robot's actions.

Based on the results described above I suggest following recommendations for the design of robots for human-robot interaction:

i. As long as the robot is designed only for use in the observational therapy or teaching humans certain motor skills during rehabilitation therapy of an upper limb, the overall human-like appearance (like presence of human body shape, head and other extremities) is less important than human like motility (joint configuration) of the observed limb. The similar appearance and motility of the to be trained limb will enable the patients to simulate the robot's actions internally and learn from them.
ii. However, during a dyadic interaction with artificial agents for the purpose of care giving or entertainment, the absence of features characterizing a human body shape of an artificial agent (like presence of a head, arms and torso) might have a negative effect on action prediction and also intention attribution to them. Thus, our results provide indications that robots designed for close human-robot interactions should exhibit at least main human-like features like presence of a body, limbs and a head. The human-like appearance will enable people to use their behaviour models and experience from social interaction with other humans in the interaction with robots. It will also facilitate intention attribution to humanoid agents and therefore have a positive effect on learning skills from these agents.
iii. Although biological velocity and movement variability are not required for triggering the activation of motor system during action observation, I advice to use at least an approximation of biological velocity to minimize the jerkiness of the robot's movements.

5.5.3 General recommendations for designing humanoid robots

In a nutshell, this dissertation has shown that humanoid robots which convey anthropomorphic cues and move smoothly are more advisable for use in robot-human interaction than robots with machine-like appearance. However, the high degree of anthropomorphism of a robot is not a necessary precondition for building every artificial agent - it rather depends on the context and purpose. People with bad vision will need robots for guidance and support in the everyday living, people with chronic illnesses like diabetes will need a robot that can help them with shots; people with deadly diseases will need a robot to entertain them, people with motor deficits will need a robot to provide them with therapy and help them to re-learn motor tasks. Therefore, not in every scenario it is the best idea to create human-like robots. For example, robots designed to perform a certain automatic task, like dishwashing, do not have to be similar to the human person they replace. Thus, cleaning the floor can be accomplished by machine-like service robots like “Roomba” [100]. Further, while robot`s appearance might be important at the start of an interaction, its behaviour might become even more important during the course of the interaction. Indeed, a recent study suggested that although both the appearance and the behaviour of robots play a significant role, if they are contradictory to each other, the robot’s behaviour is more crucial than its appearance [214]. Another study has investigated how robot’s behaviour influenced the user’s evaluation during a dyadic interaction in a route guidance situation [162]. When the robot showed human like behaviours like eye contact, arm movement and head nodding, the users evaluated the robot as more reliable. Thus, in a real-life scenario, not only the human-like behaviour, but also human-like expressiveness and cooperative behaviour play a role. Therefore, robots should be designed for specific purposes and their appearance will have to support the correct estimation of the robot’s real competence by the users.

5.5.4 **Future directions**

Although a number of studies investigated the neural correlates of social cognition and its dysfunctions, many fundamental questions remain unanswered. At present, detailed knowledge is lacking about the neural correlates of circuits supporting different aspects of social cognition and the neuronal bases underlying impairments of social cognition in neuropsychiatric conditions such as autism, psychopathy or schizophrenia. Further studies on healthy subjects are required to facilitate the characterization of atypical developmental pathways and improve our ability to develop more effective interventions and early identification of difficulties in social information processing. As mentioned in the introduction, in the future, functional neuroimaging and behavioural techniques may provide means for assessing the efficacy of treatment in these disorders.

My thesis has shown that there are similarities between perceiving human and artificial agents. The questions is whether there are still some aspects of agent perception that are uniquely dedicated to processing of human actions, and whether there are specific neural processes which allow humans to use their social knowledge acquired in interactions with conspecifics with unfamiliar agents. An answer to these questions will require inputs from multiple disciplines and profit from the integration of data collected in studies on human and nonhuman animals. By combining neuroscientific and behavioral studies with a developmental perspective we will enhance our understanding of the representation of actions, intentions and agents.

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3.1	1,2,3 and 5
3.2	7
3.3	4, 6

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Curriculum Vitae

Alexandra Kupferberg
Quiddestr. 86
81735 Munich
Deutschland
00 49 17 64 81 380 65
A.Kupferberg@gmx.de

Date of birth	03.02.1982
Place of birth	Tashkent (Usbekistan)
Citizenship	German, Usbek

Education

10.2007 – present	**Graduate School of Systemic Neurosciences (Ph.D.)** Ph.D. Title: Behavioral and neurological correlates of intention understanding in humans and non-human primates (LMU Center for sensorimotor research; Munich, Germany; University of Zurich, Department of Anthropology; Zurich, Switzerland)
10.2004 – 09.2007	**Elite-Study of Neuro-Cognitive Psychology (M.Sc.)** (Ludwig-Maximilians-Universität, Munich) M.Sc. after 6 Semesters; GPA: very good
10.2001 – 11.2006	**Biology (Diploma)** Diploma after 12 semesters; GPA: 1.1 (very good) Major : neurobiology; minors: anthropology, psychology, physiology
09.1999 - 07.2001	Oskar-von-Miller-Gymnasium (Munich, Germany) Qualification for university entrance; GPA: 1.4 (very good)
09.1998 - 07.1999	Werner-von-Siemens-Gymnasium (Munich, Germany)
12.1996 - 07.1998	Adolf-Menzel-Gymnasium (Halle/Saale, Germany)
08.1989 - 11.1996	English College (Tashkent,Usbekistan)

Research experience

10.2007-10.2012 **Doctoral thesis**

- Designing and conducting experiments on intention understanding using subjective (questionnaires) and objective (looking times, reaction times, motion trajectory analysis and functional brain imaging) methods

12.2006 - 09.2007 **Master Thesis** entitled: Feeling of presence in driving simulation (BMW Research Group, Munich)

- Developing and validation of a presence questionnaire for various driving simulation scenarios

09.2006 - 11.2006 **Internship:** Perception of velocity in driving simulation (BMW Research Group, Munich)

- Development and validation of a questionnaire assessing velocity perception in driving simulation

09.2004 - 01.2006 **Student research assistant** (Max-Planck-Institute for Cognitive Science, Munich)

- Planning and conducting experiments to investigate the aspects of bimanual coordination, data analysis with SPSS

11.2005 - 11.2006 **Diploma thesis** entitled: Behavioural and neural (fMRI) correlates of gravity perception (Ludwig-Maximilians-University, Munich)

- Designing, conducting and analyzing behavioral and functional experiments investigating perception of gravity in a tilt-chair and a magnetic resonance tomography scanner

4.2005 - 10.2005 **Bachelor Thesis:** Suppression of unwanted memories (Dept. of psychiatry, University Hospital, Munich)

01.2005 - 03.2005 **Internship:** Neuropsychological testing of patients with post-traumatic stress disorder (Dept. of Psychiatry, LMU University Hospital, Munich)

Work experience

02.2012-05.2012 **Internship** (IMS Consulting Group, Munich)

- Projects on in-licensing and launch excellence
- Proposal writing

05.2011-12.2011 **Part-time project assistant** (Intero-consulting, Munich)

- Support for project on management consulting and travel management
- Organization of retreats

10.2009 -10.2010 **Exhibition assistant** for "Deutscher Kunsthandelsverband"

- Preparation of presentations for Munich art fairs 2009 and 2010, customer service and technical support for the members

02.2001- 04.2007 **Exhibition assistant** in the Munich trade center

- Client service, German-English-Russian interpreter
- Promotional activities for foreign companies

07.1999 -01.2004 **Private teacher** for English language and mathematics
08.2001 -03.2002 **Swimming instructor** for children (DSV-München)
07.1999 -01.2002 **Private tour guide**

Teaching/supervision

04.2012- 07.2012 Lecture series (LMU): Mirror neurons and the theory of mind
02.2011- 05.2011 Supervision of 2 students (fMRI study) on a daily basis
08.2010 - 10.2010 Supervision of an AMGEN-scholar and a master student
03.2010 - 07.2010 Lecture series (LMU): Mirror neurons and the theory of mind

Language skills

German: fluent/native speaker
English: fluent
Russian: native speaker
Italian: basic knowledge

Software skills

MS-Office, SPSS, SPM, Interact, Adobe Premiere pro, Adobe Photoshop

Method skills

fMRI, EEG, Doppler Sonography, Motion tracking

Prizes and Scholarships

04.2007	Ph.D. Grant from the University of Bavaria: Graduiertenförderung nach dem Bayerischen Eliteförderungsgesetz
07.2001	Second best mark in the Qualification for University Entrance
07.1998	Best mark after finishing the 11th form

Conferences and talks

01-06.09.2012	Mirror neurons -20 years after discovery (Erice, Italy)
7.06.2011	Colloquium Talk at the University of Neuroinformatics (Zurich, Switzerland)
06.05.2011	Colloquium Talk at the Sensory-Motor-System Lab (Zurich, Switzerland)
07-08.05.2011	Implications of Research on the Neuroscience of Affect, Attachment and Social Cognition Conference (London)
17-19.04.2011	Talk at the workshop: Neurophilosophy and Neuroscience (Venice, Italy)
26.04.2011	Invited talk at Interdisciplinary College 2011: Mirror neuron system and the consequences of its dysfunctions (Soest, Germany)
02.12.2010	Colloquium Talk at the Department of Neurosciences (University of Parma, Italy)
08.2010	Invited talk on mirror neurons in the adult education center (Munich, Germany)
12-19.03.2010	Interdisciplinary College 2010. Focus Theme: Play, act and learn (Soest)
27-28.01.2010	The 4th International Conference on Cognitive Systems (Zurich, Switzerland)
12-15.08.2009	The 3rd International Conference of the European Federation of Primatologists (Zurich, Switzerland)
06-13.03.2009	Interdisciplinary College 2009, Focus Theme: Rhythm and Timing (Soest, Germany)
06-09.04.2009	Talk at: New frontiers in human-robot interaction Convention (Edinburgh, Scotland)
24-26.02.2009	The 11th Conference of the Gesellschaft für Primatologie (Hannover, Germany)
01-03.08.2008	IEEE Ro-Man. The 17th International Symposium on Robot and Human Interactive Communication (Munich, Germany)
07-14.2008	Interdisciplinary College 2008, Focus Theme: Cooperation (Soest, Germany)
17.02.2008	Colloquium Talk at the Artificial Intelligence Lab (Zurich, Germany)

List of publications

1. Kupferberg A, Glasauer S, Huber M, Rickert M, Knoll A, Brandt T. (2009) *Video observation of humanoid robot movements elicits motor interference.* In: Proceedings New Frontiers in Human-Robot Interaction (Dautenhahn K, Ed.), SSAISB: The Society for the Study of Artificial Intelligence and the Simulation of Behaviour ISBN - 190295680X, Edinburgh, pp 81-85.

2. Kupferberg A, Glasauer S, Huber M, Rickert M, Knoll A, Brandt T. (2010) *Biological movement velocity profile increases acceptance of humanoid robots as human partners in motor interaction.* AI & Society, 26 (4):339-345.

3. Kupferberg A, Glasauer S, Huber M. (2011) *Accessing robot acceptance by motor interference*. In: Advances in Interaction Studies (Dautenhahn K, Cangelosi A, Eds.), pp. 165–184.

4. Burkart J, Kupferberg A, Glasauer S, van Schaik C. (2012) *Even simple forms of social learning require intention attribution in marmoset monkeys.* Journal of Comparative Psychology, 126:129-138.

5. Kupferberg A, Huber M, Helfer B, Lenz C, Knoll A, Glasauer S. (2012) *Moving Just Like You: Motor Interference Depends on Similar Motility of Agent and Observer.* PLoS ONE 7(6): e39637. doi:10.1371/journal.pone.0039637.

6. Kupferberg A, Glasauer S, Burkart JM *Do robots have goals? How agent cues influence action understanding in non-human primates.* Manuscript under revision.

7. Kupferberg A, Iacoboni M, Flanagin V, Huber M, Kasparbauer A, Schmidt F, Borst C, Glasauer S *Action- and goal-specific fronto-parietal activation during observation of actions performed by artificial agents and humans.* Manuscript submitted for publication.

8. Huber M, Kupferberg A, Lenz C, Knoll A, Brandt T, Glasauer S *Spatiotemporal movement planning and rapid adaptation for manual interaction.* Manuscript submitted for publication.

9. Kupferberg A, Glasauer S, Stein A, Brandt T. *Influence of uninformative visual cues on gravity perception.* Ann NY Acad Sci 1164: 403–405, 2009.

Eidesstattliche Versicherung/Affidavit

Hiermit versichere ich an Eides statt, dass ich die vorliegende Dissertation „*Of men, monkeys, and machines. Behavioral and neural correlates of goal understanding in humans and non-human primates*“ selbstständig angefertigt habe, mich außer der angegebenen keiner weiteren Hilfsmittel bedient und alle Erkenntnisse, die aus dem Schrifttum ganz oder annähernd übernommen sind, als solche kenntlich gemacht und nach ihrer Herkunft unter Bezeichnung der Fundstelle einzeln nachgewiesen habe.

I hereby confirm that the dissertation „*Of men, monkeys, and machines. Behavioral and neural correlates of goal understanding in humans and non-human primates*“is the result of my own work and that I have only used sources or materials listed and specified in the dissertation.

München, den 28.11.2012

Munich, date 28.11.2012 Unterschrift/signature

Contributions

Contributions to programming and video recording

Chapters	Contributions
3.1; 4.1	The videos were recorded and edited by Aleksandra Kupferberg with the support of Bartosz Helfer, Markus Huber and Helmut Radich. Additional help for programming the robots was provided by Claus Lenz.
3.2; 4.2	The programming of the experiments was carried out by Markus Huber and Virginia Flanagin. The videos were recorded and edited by Aleksandra Kupferberg with the help of Christoph Borst and Florian Schmidt.
3.3; 4.3	The videos of monkeys were recorded and edited by Aleksandra Kupferberg

Contributions to data collection

Chapters	Contributions
3.1; 4.1	The data was collected by Aleksandra Kupferberg with the help of Bartosz Helfer and Markus Huber.
3.2; 4.2	The data were collected by Aleksandra Kupferberg with the support of Virginia Flanagin, Anna Kasparbauer and Markus Huber.
3.3; 4.3	The entire data was collected by Aleksandra Kupferberg.

Contributions to data analysis

Chapters	Contributions
3.1; 4.1	Data analysis was carried out by Aleksandra Kupferberg, Markus Huber and Stefan Glasauer.
3.2; 4.2	Data analysis was carried out by Aleksandra Kupferberg with the help of Virginia Flanagin.
3.3; 4.3	Data analysis was carried out by Aleksandra Kupferberg with the support of Judith Burkart, Stefan Glasauer and Sereina Graber.

Contributions to writing manuscripts

Article #	**Contributions**
1	Aleksandra Kupferberg, Stefan Glasauer
2	Aleksandra Kupferberg, Stefan Glasauer
3	Aleksandra Kupferberg
4	Judith Burkart, Aleksandra Kupferberg, Stefan Glasauer
5	Aleksandra Kupferberg, Stefan Glasauer
6	Aleksandra Kupferberg, Judith Burkart
7	Aleksandra Kupferberg, Stefan Glasauer, Marco Iacoboni, Virginia Flanagin

Signature of the lab head: