Imitation and observational learning of hand actions: Prefrontal involvement and connectivity

S. Higuchi [a, b, c], H. Holle [d], N. Roberts [e], S.B. Eickhoff [f, g], S. Vogt [a, b]

[a] Department of Psychology, Lancaster University, [b] Magnetic Resonance and Image Analysis Research Centre, University of Liverpool, UK, [c] Center for Experimental Research in Social Sciences, Hokkaido University, Japan, [d] School of Psychology, University of Sussex, UK, [e] Queens Medical Research Institute, University of Edinburgh, UK, [f] Department of Psychiatry, RWTH Aachen University, Germany, [g] Institute for Medicine, Research Center Jülich, Germany

The first aim of this event-related fMRI study was to identify the neural circuits involved in imitation learning. We used a rapid imitation task where participants directly imitated pictures of guitar chords. The results provide clear evidence for the involvement of dorsolateral prefrontal cortex, as well as the fronto-parietal mirror circuit (FPMC) during action imitation when the requirements for working memory are low. Connectivity analyses further indicated a robust connectivity between left prefrontal cortex and the components of the FPMC bilaterally. We conclude that a mechanism of automatic perception-action matching alone is insufficient to account for imitation learning. Rather, the motor representation of an observed, complex action, as provided by the FPMC, only serves as the 'raw material' for higher-order supervisory and monitoring operations associated with the prefrontal cortex. The second aim of this study was to assess whether these neural circuits are also recruited during observational practice (OP, without motor execution), or only during physical practice (PP). Whereas prefrontal cortex was not consistently activated in action observation across all participants, prefrontal activation intensities did predict the behavioural practice effects, thus indicating a crucial role of prefrontal cortex also in OP. In addition, whilst OP and PP produced similar activation intensities in the FPMC when assessed during action observation, during imitative execution, the practice-related activation decreases were significantly more pronounced for PP than for OP. This dissociation indicates a lack of execution-related resources in observationally practised actions. More specifically, we found neural efficiency effects in the right motor cingulate–basal ganglia circuit and the FPMC that were only observed after PP but not after OP. Finally, we confirmed that practice generally induced activation decreases in the FPMC during both action observation and imitation sessions and outline a framework explaining the discrepant findings in the literature.

Under my skin (I've got you…)

E. Barile [a], M. Ardizzi [b], F. Ferri [b], V. Gallese [b]

[a] University "Vita-Salute" San Raffaele, Milano Italy; [b] University of Parma, Parma, Italy

In the footsteps of the **neurophenomenological** tradition (Varela F. 1996) (or, better, the so called '**front loaded phenomenology**' (Gallagher- Zahavi, 2008) we address the topic of the **'bodily' self,** conceived as the common ground of the multy layered phenomenon of self-consciousness (Bermudez J.-L. 1995). We focus on **interoception** proper (the perception of *viscera* and of the internal *milieu* of the organism (Sherrington 1907)) that is mainly neglected or at least underestimated in neuroscientific and philosophical approaches to bodily self-perception (cfr. Gallagher 2005).

At an **empirical** level, we consider here the study case of **touch**: Differences between **tactile experience** *in first person* and as *observed* in the others at a subcortical level, namely in the insula, have already been discovered (Ebisch et *al.* 2008, 2010), following **mirror neurons** theory tradition and its developments (Gallese V. - Sinigaglia C. 2011). Nevertheless, it remains unclear if there are also **physiological** underpinnings at **autonomic** level, that might be considered **distinguishing** criteria for **self/other** differentiation, shaping our ability of building up the sense of '**own-ness**' as distinct from others.

In the experimental conditions here provided, we consider the 'approaching' process, starting from the '**other**' - *extrapersonal* - space, moving randomly closer and closer to the so called *peripersonal* space or to the **cutaneous** space - that is mainly considered the '**self**'- *personal* - space, while registering autonomic feedbacks. By the way, the *personal* space itself has been recently recognized as 'plastic' (cfr. Gallese - Sinigaglia 2011): It may also include the traditionally considered *peripersonal* space (7/35 cm, cfr. Ladavas 2004). The personal/peripersonal space is here considered as '**interaction**' - rather than 'action' – space only. Differently from other approaches, testing just one channel of autonomic responses (see Chritchley H. *et al.* 2005, or Pollatos O. - Schandry 2004), **RSA** technique will be used here, in line with Porges' polyvagal theory (2001, 2009), that is based on a **multichannel integration** (heart period - breathing).

At a **theorethical** level, the role of the **skin,** as the main organ involved both in **touch** experience **(**skin considered from its *surface*, constituting the *cutaneous* - strictly *personal* - space) and in **interoception** (skin conceived as its 'thickness' is also the main *viscus* of our body) will be therefore investigated, in order to assess if skin surface itself constitutes the *border*, the **boundary** in between **self/other** differentiation (not only physiologically, but, when symbolised, also psychologically (Anzieu D. 1995)) or if the boundary (if any) is the **peripersonal** space redefined, rather. These results might eventually be used in order to constitute the control group references to compare to **psychosomatic** patients with **skin lesions**, whose pathological behaviours are mainly psychologically connected to disorders on personal **identity** (Anzieu D. 1985, Ulnik J. 2005).

Beyond mu rhythms: Decoding action observation from scalp EEG using a neural interface approach

Carlos and Pepe Contreras

MNS activity during an action planning task is modulated by learning and working memory span

L.P. Behmer Jr. & L.R. Fournier

Activity in the mirror neuron system (MNS), a frontal-parietal network active when individuals observe meaningful, goal-directed biological actions, as well as abstract stimuli which have become associated with learned motor programs, has been reliably measured in humans using a variety of brain imaging techniques. For example, in EEG, mu-ERD over the rolandic strip is indicative of MNS activity. Recent evidence suggests that differences in MNS activity between experts and novices may be a measure of neural efficiency. For example, studies have demonstrated that expert athletes show less alpha-ERD than novices when observing meaningful biological actions associated with their sport. However, evidence from other studies appear to contradict these findings. For example, fMRI revealed that trained dancers showed increased MNS activity when viewing dance moves from their dance repertoire of expertise compared to other dancing styles. Also, musicians showed increased mu-ERD when viewing sheet music compared to non-musicians. To better understand this discrepancy in the literature, our study examines how cognitive ability modulates MNS activity during skill acquisition (i.e., learning action plans associated with abstract stimuli). More specifically, we examined whether mu-ERD changes with task training, and whether these changes are similar for persons with high or low working memory spans. To our knowledge, no studies have examined how cognitive ability modulates MNS activity during skill acquisition. The current study used EEG to measure mu-ERD over the rolandic strip during an action planning task. The AOSPAN was used to assess memory span and separate participants into a high-span (top 25%) and low-span (bottom 25%) groups. Consistent with the neural efficiency hypothesis, we predicted that low-span participants would initially show significantly more mu-ERD than high-span participants during intervals where they planned and maintained an action in working memory. Also, we predicted that mu-ERD would decrease in this task with additional training (i.e., a second day) for both span groups; however, we observed the opposite. This uptick in MNS activity with training for both span groups may be a result of novel motor skill acquisition where action planning and maintenance is transitioning from a declarative to a procedural representation.

SOCIAL GRASP: Interpersonal perception modulates predictive simulation and mutual adjustments during a joint-grasping task

L.M. Sacheli [a, b], M. Candidi [a, b], E.F. Pavone [a, b], E. Tidoni [a, b], S.M. Aglioti [a, b]

[a] Department of Psychology, University of Rome "La Sapienza", Rome, Italy; [b] IRCCS, Fondazione "Santa Lucia", Rome, Italy.

Prediction of "when" a partner will act and "what" he is going to do is crucial in joint-action contexts. However, studies on face-to-face interactions in which two people have to mutually adjust their movements in time and space are lacking. Moreover, while studies on passive observation have shown that somato-motor simulative processes are disrupted when the observed actor is perceived as an out-group or unfair individual, the impact of interpersonal perception on joint-actions has never been directly explored. In the present study we aimed at investigating whether the behaviour and kinematics of healthy humans engaged in a joint-grasping task is modulated by co-agents' reciprocal interpersonal perception. We compared the ability of pairs of participants who may or may not undergo an interpersonal perception manipulation procedure to synchronize their reach-to-grasp movements during: i) a guided interaction, requiring pure temporal reciprocal coordination, and ii) a free interaction, requiring both time and space adjustments. Results demonstrate that a negative interpersonal relationship disrupts co-agents' coordination in self-organized free interactive grasping. Crucially, this disruption was paralleled by the absence of movement corrections and low movement variability, indicating that partners cooperating within a negative interpersonal environment executed the task ignoring the partner instead of reciprocally adapting their motor behaviours. Nevertheless, subjects' performance improved over the sessions and partners became interdependent as suggested by higher movement variability and appearance of interference between the self-executed actions and those observed in the partner. Our study expands current knowledge on on-line motor interactions, providing an effective method to investigate shared representations in the motor domain with a genuinely 'dual' perspective and by showing that interpersonal perception modulates joint-motor prediction and learning mechanisms.

Mirroring others: an rTMS study of hand-triggered reflexive social attention

G. Porciello [a, b], F. Crostella [a], M.T. Liuzza [a, b], E. Valentini [a, b] & S.M. Aglioti [a, b]

[a] Department of Psychology, University of Rome "La Sapienza", Rome, Italy; [b] IRCCS, Fondazione "Santa Lucia", Rome, Italy.

Averted gaze and hand-pointing gestures powerfully capture the attention of observers. Behavioral and fMRI studies indicate that: i) observing directional gaze or hand-pointing in a model influences the responses of an onlooker according to eye- or hand-centered coordinate systems; ii) gaze- and hand-related effects are preferentially linked to frontal and parietal activity, respectively, suggesting an effector-specific activation. To investigate the causative influence of frontal and parietal structures on reflexive shifts of social attention triggered by the observation of directional hand-pointing we used a repetitive, dual pulse transcranial magnetic stimulation (rdpTMS) to interfere with the Frontal Eye Field (FEF) and the Posterior Parietal Cortex (PPC), which play a role in gaze- and hand-following behavior, respectively. Fourteen subjects (4 males; mean age 24; SD 2.8) were asked to perform a leftward or rightward pointing movement according to the color change of a central imperative signal. 75ms before the onset of the imperative cue subjects saw one of three different directional cues (gaze, hand pointing or arrow) which pointed in the same (congruent) or opposite (incongruent) direction with respect to the central cue. We found that interfering with PPC activity increased the detrimental effect of incongruent direction during the observation of hand-pointing stimuli. Thus, reflexive shifts of attention triggered by social signals are coded according to effector-specific mapping rules. Moreover the parietal and not the frontal cortex is preferentially involved in mapping hand-triggered shifts of social attention when hands and not eyes are used as effectors.

The role of the inter-speaker articulatory variability in the motor contribution to speech perception: a TMS-MDS study

E. Bartoli, A. D'Ausilio and L. Fadiga

The ability to perceive speech can be viewed not only as a purely auditory task, but also as the ability to recognize a special type of motor act, therefore suggesting a critical involvement of the mirror neurons system, as it supports the ability to match perception and execution of complex motor sequences. A recent TMS study (D'Ausilio et al., 2009) investigated the functional contributions of the motorarticulatory systems to specific speech-perception processes. The stimulation of a given M1 representation led to better performance in recognizing speech sounds produced with the concordant effector. This effect was present only if the speech sounds were embedded in white noise, suggesting that the cross talk between auditory and motor areas becomes central under "noisy" conditions, when the auditory analysis has not enough information to fulfill task requirements. However, the main critique raised against these findings is that embedding speech stimuli in white noise encourages participants to adopt atypical strategies, including atypical reliance on motor centers. The present TMS experiment is aimed at demonstrating that the role of the motor system in speech perception is not related to the use of artificially degraded stimuli. Therefore, we introduce inter-individual speech differences as a tool to create an ecological source of noise. Our results confirm that the phono-articulatory variability induces a somatotopic effect on the recruitment of motor areas during speech perception, as predicted by a functional role of motor cortex in the recognition of speech motor acts. The degree of recruitment of the specific motor areas normally involved in the production of that particular speech sound is related to the task demands ("noise", both artificial and ecological). This evidence strongly supports the hypothesis of a functional and causal role of motor areas during the perception of other's speech to increase performance by reducing system uncertainty.

Human and robotic actions evoke motor resonance

A. Sciutti [a], A. Bisio [a], F. Nori [a], G. Metta [a], T. Pozzo [a, c], G. Sandini [a] and L. Fadiga [a, b]

Motor resonance, i.e. the automatic activation of motor control systems during action perception, is a central phenomenon in understanding social behaviors. It seems to have a physiological basis in the mirror neurons, cells which are activated both during action execution and action observation (Rizzolatti et al. 1996). In the last decade motor resonance has been investigated in presence of both humans and humanoids robots (reviews: Chaminade and Cheng 2009; Sciutti* et al. 2012) with contrasting results. Indeed, although several behavioral (Kilner et al. 2003; Oztop et al. 2005), neurophysiological and neuroimaging (Gazzola et al. 2007; Tai et al. 2004) experiments have addressed the question whether mirror neurons could be activated by the observation of a robotic agent or not, there is not yet a clear understanding about the response of MNS to humanoid artifacts.

In our study we aimed at investigating whether robotic actions can induce motor resonance by exploiting two socially relevant behavioral phenomena associated to MNS activation: proactive gaze and automatic imitation. When subjects observe a human action – but not just a predictable object motion - their gaze predicts forthcoming events rather than reactively tracking actor's motion (Falck-Ytter et al. 2006; Flanagan and Johansson 2003). These findings were explained in the framework of the direct matching hypothesis (Rizzolatti et al. 2001). Similarly, neurophysiological studies suggest that the automatic contagion induced by motion observation in subsequent actions is a behavioral manifestation of MNS activation (Iacoboni 2009). In a series of action observation and execution tasks we compared the effects of observing a human or the humanoid robot iCub as actor. Our results show that the observation of robotic actions elicits both proactivity in subjects' gaze and automatic imitation, as much as human actions do. However, automatic imitation significantly decreases in presence of non-biological motion, thus underlying the relevance of biological kinematics in eliciting motor resonance in human observers.

Dynamic simulation and static matching for action prediction: Evidence from body part priming

A. Springer [a] & W. Prinz [b]

[a] University of Potsdam, Department of Sport and Exercise Psychology, Potsdam, Germany;
[b] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

Accurately predicting another individual's action seems to depend on the observers own motor activity. Previous research suggests that two processes may enable action prediction: real-time simulation (i.e., dynamic updating), and matching recently perceived action images (i.e., static matching). We tested the impact of body part priming on action prediction performance. Participants played a motion-controlled video game with either their arms or legs. They then observed briefly occluded arm movements of a point-light actor, followed by a static test pose, and judged whether or not this depicted a coherent continuation of the previously seen action. Evidence of real-time simulation was obtained after compatible effector priming (i.e., arms), whereas incompatible effector priming (i.e., legs) revealed evidence of static matching. These results support action prediction as involving two processes: dynamic simulation and static matching and indicate that their relative contributions depend on contextual factors like compatibility of body parts involved in performed and observed action.

Therapy of functional voice disorder assisted by mirror neuron activation: a combined treatment and fMRI study

K. Sakreida, J. Heller and F. Binkofski

Division of Clinical and Cognitive Neurosciences, Department of Neurology, Medical Faculty, RWTH Aachen University, Aachen, Germany

Everyone has already experienced transient disturbance of the own voice as for instance hoarseness or loss of voice. People with a functional voice disorder have these problems every day. Attending to physiological or disordered voice could influence voice performance corresponding to the heard phonation. Mirror neurons are discussed as a reason for that. Beyond the focus on the effects of using mirror neuron activation within conventional voice therapy this study aimed at identifying possible differences in neural correlates of normal and distorted speech production. For this reason ten people with functional voice disorder received conventional voice therapy from a speech and language therapist twice a week. Four patients were assigned with regular homework, whereas six patients had to listen to audio tapes of good voice performance twice a day for about 25 minutes instead. Effects were controlled according to the recommendations of the European Laryngological Society by using a general logopedic diagnostic, a stroboscopic investigation of the larynx as well as a voice field examination. Additionally, the Voice Handicap Index served as a self-assessment scale. To control for mirror neuron activation five patients were measured by functional magnetic resonance imaging in a pre-post-treatment design. Even though first results revealed significantly improved phoniatric findings along the timeline in both groups, the self-assessment seemed to interact with the way of therapy. This study will contribute to a better understanding of functional voice disorders and point to a therapeutic improvement by extension to mirror neuron activation.

Decreased cognitive empathy for facial expressions of pain in high functioning autism

O. Rogier [a], N.R. Zürcher [a], L. Hippolyte [a], B. Russo [a], T. Ruest [a], E. Lemonnier [b], N. Hadjikhani [a], [c]

[a] Brain Mind Institute, EPFL, Lausanne, Switzerland; [b] CRA Bretagne, Brest, France; [c] Athinoula A. Martinos Center for Biomedical Imaging, Massachusetts General Hospital, Harvard Medical School, Charlestown, Massachusetts, USA

Autism spectrum disorders (ASD) are neurodevelopmental conditions characterized by difficulties in social interactions. Empathizing, which involves understanding others and sharing their affect, is a crucial skill for adaptive social behaviour. So far, no study has explored the neural processing associated with the perception of facial expression of pain in ASD. The aim of this fMRI study was to investigate brain areas involved in empathy for pain in participants with ASD (high functioning autism or Asperger's Syndrome) compared to age and IQ matched typical controls. Twenty-two adults with ASD and 18 controls underwent functional MR scanning. While in the scanner, participants viewed short movies of facial expressions of shoulder pain patients examined in a clinic, while either their painful arm (painful condition) or their healthy arm (control condition) was moved. To ensure attention, participants were asked to press a button every time a fixation cross, present on the screen between movies, changed color. Neural responses evoked by expressions of pain were compared with those of the control condition. Both groups displayed activation in regions involved in pain perception, notably in the insula. However, controls showed more activation than ASD in the medial prefrontal cortex, important for perspective taking, and the subcallosal cortex. ASD participants, on the other hand, showed increased activation in the amygdala, pulvinar and cerebellum. When viewing expression of pain in others, both ASD and controls show activation in areas involved in pain perception, implying the presence of a simulation mechanism and affective empathy. Controls, in addition, exhibit increased activation related to perspective taking, a key aspect of cognitive empathy. Remarkably, ASD participants display increased activation in the fast processing subcortical route for face perception and in the cerebellum. Our data show that cognitive empathy is affected in ASD, but that affective empathy may be preserved.

Training the human motor cortex by observing others' actions.

Bassolino M. [a], Campanella M. [a], Bove M. [b, c], Pozzo T. [a, d, e], Fadiga L. [a, f]

[a] Department of Robotics, Brain and Cognitive Sciences, Istituto Italiano di Tecnologia, Genova;
[b] Department of Experimental Medicine, Section of Human Physiology University of Genova, Italy;
[c] Centro Polifunzionale di Scienze Motorie, University of Genova, Italy; [d] INSERM, U1093, Cognition Action Plasticité sensorimotrice, Dijon, F-21078, France; [e] Institut Universitaire de France, Université de Bourgogne, Campus Universitaire, UFR STAPS, Dijon, France; [f] DSBTA, Sezione di Fisiologia Umana, Università di Ferrara, Italy.

Motor practice and motor inactivity may lead to long-lasting modifications of human motor cortex (Sanes & Donoghue, 2000). In this framework, it has been recently demonstrated that even a short period of limb non-use, induced by immobilization, reduces the contralateral motor cortex excitability in healthy subjects (Huber et al., 2006; Avanzino et al., 2011). Here, we investigated whether action observation and motor imagery, that has been largely demonstrated to enhance corticospinal excitability (e.g. Fadiga et al., 2005; Lotze M. & Halsband U., 2006), may prevent the non-use-dependent corticomotor effects. To this aim, we compared hand muscle motor maps and recruitment curve assessed by transcranial magnetic stimulation before and after 10 hours of right arm immobilization in 24 participants divided in three groups according to the type of task they had to perform during non-use. The first group was requested to watch some scenes extracted from nature documentaries (ND) without human actors; the second group observed videos of reaching-to-grasp right hand actions in first-person perspective (AO) and the third group mentally simulated the same actions showed to the AO participants, upon visual presentation of the target objects on a computer screen (MI). Hand muscle motor maps and recruitment curve reliably show that action observation but not motor imagery prevented the corticomotor atrophy measured in the ND group after the non-use period. Our results support the existence in humans of a visuomotor mechanism, linking together action observation and execution, able to affect cortical plasticity in a facilitating way. This facilitation seems to not depend upon action simulation because it cannot be induced by explicit motor imagery. With important implication for neuro-rehabilitation, these findings strengthen the feasibility of a visual training of the motor system in the framework of new therapeutic strategies and suggest different mechanisms underlying action observation and motor imagery.

The neural basis of joint attention deficits in autism spectrum disorders

N.R. Zürcher [a], O. Rogier [a], J. Boshyan [b], L. Hippolyte [a], B. Russo [a], T. Ruest [a], E. Lemonnier [c], N. Hadjikhani [a, b]

[a] Brain Mind Institute, EPFL, Lausanne, Switzerland; [b] Athinoula A. Martinos Center for Biomedical Imaging, Massachusetts General Hospital, Harvard Medical School, Charlestown, Massachusetts, USA; [c] CRA Bretagne, Brest, France.

Joint attention deficits belong to the earliest markers of autism spectrum disorders (ASD), a neurodevelopmental condition affecting approximately 1% of children. Joint attention, a triadic social skill, refers to the non-verbal ability to coordinate attention between individuals and to share awareness of an object. The aim of the current study was to investigate the neural basis of joint attention deficits in ASD using a gaze cue implicitly signaling danger.

We collected functional MRI data while 22 adults with high-functioning autism or Asperger's syndrome and 21 typical controls, matched for age and intelligence quotient, viewed grayscale pictures of faces with a fearful facial expression, either looking straight at the participant (direct gaze) or looking downwards to the left or right (averted gaze). Previous research has shown that an averted fearful gaze is a salient signal indicating a potential environmental danger that increases activation in a network of brain areas involved in gaze and emotion processing.

In the ASD group, averted gaze compared to direct gaze in a fearful face did not modulate activation in three networks involved in emotional gaze perception and understanding others' actions and intentions. Contrary to what was observed in typical controls, response to joint attention was not present in the dorsal attention network (intraparietal sulcus, motion area MT, frontal eye fields), in the ventral attention network (superior temporal gyrus, supramarginal gyrus and middle frontal gyrus), nor in the areas involved in social and emotional aspects of face processing including the amygdala, insula, cingulate cortex, and fusiform face area.

In conclusion, individuals with ASD did not modulate brain activation in response to salient communicative gaze cues signaling implicit danger. Our data suggest that the neural response to emotional joint attention for an implicit object is deficient in ASD.

Towards a neural basis of action-based music processing

Jin Hyun Kim

In cognitive neuroscience of music, the increasing number of studies indicating neural mechanisms of action-based music processing has recently been conducted. This poster considers some important results and discusses them as related to mirror mechanisms.

1) The network of anterior cingulate cortex (ACC) and anterior insula (AI), which is activated while both experiencing one's own pain and recognizing the pain of others (Decety 2011), is involved in tempo and loudness processing of music (Bernardi et al., 2006) and part of an "emotion circuit" consisting of the orbitofrontal cortex (OFC), the anterior cingulate cortex (ACC), the nucleus accumbens (NAc), the basolateral Amygdala (Am (BL)), corticomedial Amygdala (Am (CM)) including the central nucleus, the hippocampal formation, the parahippcampal gyrus and the temporal pole as interacting structures (Koelsch, 2010; Omar et al., 2011).

2) Cognitive neuroscience of music has found that the activity in BA 44, which is considered as part of human "mirror system" (Gallese et al., 2004; Rizzolatti & Craighero, 2004), is also essential to the brain's processing of meaningful musical events: a) Pasternak et al., 2011 found that the right hemisphere's homotope of Broca's area, BA 44 in the inferior frontal gyrus IFG of the left hemisphere, dorsolateral prefrontal cortex dlPFC, BA 40 (supramarginal gyrus SMF) of the left hemisphere and the insula were activated in dealing with prediction, expectation, and surprise in processing music; b) Babiloni et al., 2011 found that alpha rhythms in the right ventral-lateral frontal regions (BA 44/45) reflected affective empathy in musicians playing in ensemble while observing own performance; c) Other studies indicate the involvement of the right homotope of BA 44 in connection with studies indicating the involvement of Broca's area and the premotor cortex in music processing (e.g. Maess et al., 2001; Koelsch, 2006, 2011; Fadiga, Craighero & d'Ausilio, 2009).

Infants' Processing of Continuous vs. Non-Continuous Movement: Evidence for Action Simulation from ERPs

C. Bache, F. Kopp, A. Springer, W. Stadler & U. Lindenberger

Recent studies have indicated that infants' neural activity during action production and action observation overlap, which supports the assumption that infants internally simulate an action they observe, possibly by means of mirror neuron activity. This internal action simulation has been interpreted to serve the prediction of observed behavior which is crucial to coordinate in social interaction. From the action simulation point of view, the neural signature of action prediction should differ between human and object movement as only movement that is within the observer's own motor repertoire can be simulated. In the present study, a total of N=79 10-month-old infants were repeatedly shown short video clips of human movement (same-aged child) and object movement (geometrical figure). Each video clip was occluded (black full-screen occluder for 500 ms) and continued afterwards. The movement predictability was manipulated by presenting continuous (high predictability) or non-continuous (low predictability) movement prior to the occluder. Throughout the experiment, neural activity (EEG) was measured. The neural activity during the occluder was assumed to vary as a function of movement predictability prior to the occluder, although the visual input during occlusion was identical in all conditions. Event-related potential (ERP) analysis revealed that at occipital and centro-parietal regions neural activity was enhanced for human compared to object movement which may reflect higher cognitive engagement in human movement. In late neural processing, human continuous and non-continuous movement differed indicating that maintained internal simulation is facilitated in highly predictable human movement. The results contribute to the discussion about the existence of an early mirror neuron system in infants.

Hyperbrain Networks in Guitar Duets

J. Sänger, V. Müller and U. Lindenberger

Max Planck Institute for Human Development, Berlin

In search of the neural code of interpersonal action coordination, synchronous oscillatory brain activity has been associated with joint action (Astolfi et al., 2010; Cui, Bryant&Reiss, 2011; Dumas et al., 2010; Lindenberger et al., 2009; Yun et al., 2008). To test and explore in how far this synchronous oscillations built up functional hyperbrain networks, the brain activity of each of 12 guitar duets repeatedly playing a modified Rondo in two voices by C. G. Scheidler was recorded in an EEG-hyperscanning study. Indicators of within-brain and between-brain phase coherence were obtained from complex time-frequency signals based on the Gabor transform. A graph analytical evaluation of the phase coherence was performed for the delta (1-4 Hz) and theta (4-8 Hz) frequency bands, where highest coherence values were found. It showed that (a) within- and between-brain connection strengths were enhanced at frontal and central electrodes during periods that put particularly high demands on musical coordination, (b) within-brain and hyperbrain networks showed small-worldness properties that were enhanced during musical coordination periods, (c) community structures included so called hyperbrain modules, i.e. groups of strongly interconnected electrodes from both brains (hyperbrain modules). Accordingly, non-random hyperbrain networks, involving electrode sites that suggest a participation of the mirror neuron system, are proposed as a neural mechanism of interpersonally coordinated behavior. Additionally, an outlook on single-trial coupling analyses offering the possibility to relate the degree of neural synchronization to the quality of behavioral synchronization will be given.

Imitation without attention: imitative compatibility is immune to perceptual load

C. Catmur

Department of Psychology, University of Surrey, Guildford GU2 7XH, UK - c.catmur@surrey.ac.uk

Automatic imitation (Stürmer et al., 2000; Heyes, 2010) is the tendency for response times to be faster when observing the same action as one is performing, as opposed to when viewing a different one. This effect is thought to rely on the mirror system (Catmur et al., 2009) and may underlie mimicry, a key behaviour during social interaction (Chartrand & van Baaren, 2009). However, the extent to which automatic imitation is truly "automatic" – that is, occurs without attention (Shiffrin & Schneider, 1977) – is currently unclear. Participants performed a perceptual load task (Lavie, 1995) in which finger movements were presented as distractors. Responses were performed by means of finger movements which could therefore be imitatively compatible (response required the same finger movement) or incompatible (response required the opposing finger movement) with the distractor movements. Attention to the distractor movements was manipulated by altering perceptual load. If automatic imitation requires attention, then at high levels of perceptual load, imitative compatibility should have no influence on response times. In contrast, the distractor movements were found to influence response times at the highest level of perceptual load. Two follow-up experiments were performed. The first confirmed that non-movement distractors in the same experimental configuration produced standard perceptual load effects, whereby an influence on response times was observed only at the lowest level of perceptual load. The second demonstrated that it was the movement of the fingers, rather than effector compatibility, that produced immunity from perceptual load. These results suggest that automatic imitation can occur without attention and as such is truly automatic.

Mirroring Movements or Goals: Exploring the Somatotopic Topography of Mu Rhythm Desynchronization during Action Execution and Observation in Infants

J.N. Saby, P.J. Marshall, & A.N. Meltzoff

What aspect of an observed action is reflected in infant mu rhythm desynchronization? Is it the overall goal or the precise means used to attain the goal? The current study aims to address this question by examining the somatotopic response of the infant mu rhythm during action execution and action observation. In an interactive, turn-taking protocol, 14-month-old infants activated a toy object with his/her hand and then observed an experimenter activate the object using her foot. Halfway through the experimental session, the effectors used by the infant and the experimenter were reversed so that the infant now executed the action with his/her foot and observed the experimenter activate the toy with her hand. This design allowed us to examine EEG responses to observed actions in which the means, but not the goal, differed from the means currently used by the infant. Which condition (execute-hand or execute-foot) was presented first in the experimental session was counterbalanced across participants so that half the infants first executed hand and observed foot and half the infants first executed foot and observed hand.

The analysis focused on the mu rhythm (6-9 Hz) at central electrode sites overlying hand (C3, C4) and foot (Cz) areas of the sensorimotor cortex. The analysis of the mu rhythm during action execution revealed a somatotopic (effector-specific) desynchronization during the early phase of the action. During action observation, mu rhythm desynchronization was more related to the typical means used by the infant to achieve the goal rather than to the specific means used by the actor.

The effect of induced walking experience in infants on their motor activation for observation of walking

J.C. Stapel, S. Hunnius & H. Bekkering

Radboud University Nijmegen, Donders Institute for Brain, Cognition and Behaviour

Action observation activates motor areas in adults, which is thought to be a reflection of the human mirror neuron system (MNS) at work. How the mirror neuron system develops during infancy, is still an open question. Previous research has provided indications that the MNS is initialized by action experience, such that motor activation is stronger during observation of motorically familiar acts (Calvo-Merino et al., 2005, 2006; Falck-Ytter et al., 2003; van Elk et al., 2008; Cross et al., 2006). Van Elk and colleagues (2008) found that a sample of experienced crawlers who were about to learn to walk, displayed stronger motor activation for observation of crawling compared to walking. This difference was stronger with longer crawling experience. The current infant EEG study examined whether training of walking movements would change the motor activation for observation of walking versus crawling. Twenty-five infants of 11 months of age were presented with the original stimuli of the Van Elk study while their EEG was measured during two measurement sessions. In-between sessions, the infants received a walking training at home for one week, using an infant walker device. Preliminary analyses of the second session suggest that the motor areas of the infants do no longer respond differently to observation of crawling versus walking, as there was no significant difference for walking compared to crawling stimuli in power in the 6 and 7 Hz frequency of the EEG signal overlying sensorimotor areas (C3 and C4). Results of the complete sample, including analyses of the EEG of both sessions, will reveal whether this is a systematic effect of training. These results will be shown at the conference.

Two Goals are Better than One: Comparison of Familiar and Unfamiliar Actions Facilitates Goal Imitation in 7- and 10-month-old Infants

S.A. Gerson & A.L. Woodward

University of Chicago

In this work, I provide evidence for a novel mechanism that drives the generalization of action understanding. As an example of the progression of action understanding, I examine 7- and 10-month-old infants' recognition and imitation of the goal of a tool-use action. At these ages, infants recognize the goal-relation inherent to a grasp but do not yet recognize the goals underlying embedded sequences such as tool-use actions. In three studies, I present evidence that comparisons between familiar and novel actions allows infants to extract and imitate the goal objects of novel, tool-use actions.

Each study uses a goal imitation paradigm in which infants see an experimenter act on one of two toys and can then select one of the toys themselves. In previous work (Hamlin et al., 2008; Mahajan & Woodward, 2009), infants imitated the experimenter's goal object when they recognized the intention of the action she used to select the toy, but not when the action was ambiguous or unfamiliar. In the current work, infants saw an experimenter choose between two toys using a claw, an action they would not naturally view as intentional.

In Study 1, prior to test trials, infants had the chance to physically align their reaches for each toy with the experimenter's tool reaches. The opportunity to physically align and compare the familiar (own grasp) and unfamiliar (tool-use) actions led infants to imitate the experimenter's toy choice during test-trials. In Study 2, infants either aligned their reaches with the experimenter's tool actions or observed two experimenters align hand and tool reaches. Active engagement in alignment was more beneficial than observation of alignment. Finally, Study 3 showed that adding a common label to the aligned actions of the two experimenters allowed infants to compare and imitate the goal after observation of alignment.

Training the human motor cortex by observing others' actions.

M. Bassolino [a], M. Campanella [a], M. Bove [b, c], T. Pozzo [a, d, e], L. Fadiga [a, f]

[a] Department of Robotics, Brain and Cognitive Sciences, Istituto Italiano di Tecnologia, Genova;
[b] Department of Experimental Medicine, Section of Human Physiology University of Genova, Italy;
[c] Centro Polifunzionale di Scienze Motorie, University of Genova, Italy;
[d] INSERM, U1093, Cognition Action Plasticité sensorimotrice, Dijon, F-21078, France;
[e] Institut Universitaire de France, Université de Bourgogne, Campus Universitaire, UFR STAPS, Dijon, France;
[f] DSBTA, Sezione di Fisiologia Umana, Università di Ferrara, Italy.

Motor practice and motor inactivity may lead to long-lasting modifications of human motor cortex (Sanes & Donoghue, 2000). In this framework, it has been recently demonstrated that even a short period of limb non-use, induced by immobilization, reduces the contralateral motor cortex excitability in healthy subjects (Huber et al., 2006; Avanzino et al., 2011). Here, we investigated whether action observation and motor imagery, that has been largely demonstrated to enhance corticospinal excitability (e.g. Fadiga et al., 2005; Lotze M. & Halsband U., 2006), may prevent the non-use-dependent corticomotor effects. To this aim, we compared hand muscle motor maps and recruitment curve assessed by transcranial magnetic stimulation before and after 10 hours of right arm immobilization in 24 participants divided in three groups according to the type of task they had to perform during non-use. The first group was requested to watch some scenes extracted from nature documentaries (ND) without human actors; the second group observed videos of reaching-to-grasp right hand actions in first-person perspective (AO) and the third group mentally simulated the same actions showed to the AO participants, upon visual presentation of the target objects on a computer screen (MI). Hand muscle motor maps and recruitment curve reliably show that action observation but not motor imagery prevented the corticomotor atrophy measured in the ND group after the non-use period. Our results support the existence in humans of a visuomotor mechanism, linking together action observation and execution, able to affect cortical plasticity in a facilitating way. This facilitation seems to not depend upon action simulation because it cannot be induced by explicit motor imagery. With important implication for neuro-rehabilitation, these findings strengthen the feasibility of a visual training of the motor system in the framework of new therapeutic strategies and suggest different mechanisms underlying action observation and motor imagery.

What you see is what you get: motor resonance in peripheral vision

R. Siugzdaite [a, c], A. Leonetti [a], G. Puglisi [a], G. Cerri [b], P. Borroni [a]

[a] Dept. of Health Sciences and [b] Dept. of Biotechnology and Translational Medicine, University of Milano, Medical School, Milano, Italy; [c] MEDISIP, Dept. of Electronics and Information Systems, Ghent University Hospital, Ghent, Belgium.

Observation of others' actions evokes a motor resonant (MR) response, mediated by the mirror neuron system, which reflects the motor program encoding the observed actions. Presumably factors internal (attention, motivation, emotion) or external (location, salience) to observers, can modulate MR responses. We have started a series of studies evaluating the role of some of these factors, such as attention (Cerri et al. 2010) and emotion (Borroni et al. 2012). Here we explore the importance of location of the action in the visual field of observers.

A grasping action was presented in the mid-peripheral vision of subjects (10° from fixation point), who were asked to maintain their gaze on a fixation point in the left lower corner of a computer screen while, on the right, a short video showed an avatar hand grasping a ball. Motor-evoked potentials (MEPs) were elicited in the right Opponens Pollicis and Abductor Digiti Minimi muscles by transcranial magnetic stimulation of primary motor cortex, at different delays during the observed action. Two different grasping actions were shown to two different groups of 20 subjects: a normal (palmar finger flexion) or an impossible grasping (dorsal finger flexion). After the experiment, subjects were questioned about the action they had observed.

Motor responses were elicited by observation of an action in peripheral vision, though the corresponding subliminal motor program was grossly imprecise. MEP modulation was virtually identical in for both normal and impossible actions, with significantly larger MEPs at all dynamic delays compared to baseline. Peripheral vision did not provide enough visual information to evoke distinct MR responses in the different conditions and delays. Interestingly, all subjects, whether they had observed the normal or the impossible movement, reported seeing a normal grasping action, suggesting that motor resonance in the primary motor cortex is a faithful representation of observed movements rather than of the meaning (or intention) of observed actions.

Infants' Understanding of Goal-Directed Reaching Behaviors: Evidence from an Action-Anticipation Study

S. Krogh-Jespersen & A. Woodward

Infant's understanding of the goal-directed behavior of others was the focus of this action-anticipation study. Eighteen 14- to 16-month-old participants (Mean age: 15.03 months) viewed videos featuring a female actress reaching for toys. She first demonstrated that she could reach for a single toy on both sides of the table. Next, in a single familiarization trial, she reached for one of two toys (i.e., a giraffe or bear), with the target object counterbalanced across participants. In two test trials, the objects switched locations from the familiarization trial and the actress did not complete the reaching behavior; rather, her hand paused in mid-air centered with her body and between the two objects. Infants correctly predicted that she would reach for the target object in the new location on an average of 70% of trials (SD=.39), which was above chance (set at.5), $t(17)=2.41$, $p=.03$. This finding replicates previous findings (Cannon & Woodward, 2012; Paulus, 2011) indicating that infants anticipate the goal-directed reaching behaviors of others. AOIs included the objects, the actress's face, and her hand that was performing the reaching action. Future directions will focus on infant's use of gaze cues from the actress as markers of intention.

Controlling automatic imitative tendencies: proactive and reactive mechanisms

K.A. Cross [a, b], M. Iacoboni [b, c]

[a] Neuroscience Interdepartmental Program, [b] Ahmanson-Lovelace Brain Mapping Center & [c] Department of Psychiatry & Biobehavioral Sciences, University of California, Los Angeles

Humans have an automatic tendency to imitate actions observed in their environment. This phenomenon is thought to result - at least in part - from the link between observed and executed actions provided by the human mirror neuron system. Although unconscious imitation has been shown to promote positive social interactions, there are also many situations when imitative behavior is not ideal and must be inhibited. Indeed, there seems to be some active mechanism that keeps unwanted imitation in check as demonstrated by patients exhibiting reflexive or impulsive imitation after frontal lobe damage. Recent work examining this imitative control mechanism argues that a specialized mechanism - one that is distinct from other mechanisms of cognitive control - may be responsible for controlling imitation.

The cognitive control literature in general, and the relatively small imitation control literature specifically, has paid little attention to the temporal structure of control mechanisms. However, there are likely differences between control mechanisms depending on whether control is implemented proactively, in advance of a stimulus, or reactively, in response to a stimulus. In proactive or preparatory control, information about the need for control can be used to bias perception in advance of a specific stimulus. This might mean that, in situations where imitation would be detrimental, the action specific visual input to the mirror neuron system may be reduced. Alternatively, the mirroring mechanism itself may be attenuated for proactive control. In contrast, when the need for control is unpredictable this type of preparatory mechanism cannot be relied upon. Instead, if a non-imitative response is preferred, control over the more automatic imitative response must be implemented after it is evoked by the stimulus. While several studies suggest that proactive and reactive control mechanisms may be distinct in non-imitative domains, little is known about these mechanisms during imitation and its control. Using fMRI and TMS, we are examining the neural systems involved in proactive and reactive control over automatic imitative tendencies.

Neuronal activity in area AIP/PFG related to visual feedback during hand manipulation.

K. Maeda [a], A. Murata [b]

[a] Graduate School of Medicine, Kinki University; [b] Faculty of Medicine, Kinki University

Many hand manipulation neurons in area AIP of the macaque showed visual properties. Some of these neurons encoded object 3D properties responding with object presentation (object type). On the other hand, another type of visual neurons was not active during object presentation (non object type), implicating response to the hand image. Furthermore, it is known that mirror neurons were recorded in a part of the inferior parietal cortex (area PFG). Since both non object type neurons and mirror neurons were likely related to visual configuration of the hand, we speculated that both type neurons concerned to monitoring self-generated action. In this study, we try to investigate visual properties of these neurons during hand manipulation. The monkey performed the hand manipulation task fixating on a monitor screen that was presenting object and hand movement on line. The monkey also performed fixation task in that a movie of the monkey's own hand action or experimenter's hand action were presented. We found that some AIP/PFG neurons related to the hand manipulation task responded during fixation on the movie of the monkey's own hand movement (hand type) and during movement in the dark. Some of these neurons also showed mirror neuron properties responding to hand action by experimenter. We consider that some of hand manipulation neurons and mirror neurons were related to monitoring on going own hand action in AIP and/or PFG. Further, for these neurons, we also introduced time delay for visual feedback to make some gap between actual movement and sensory feedback during hand manipulation task, and we found some modulation in response to visual feedback. This may be the result of influence by efference copy during active movement. We would discuss embodiment representation in the inferior parietal cortex.

Joint actions in early childhood: Behavioural development and underlying neurocognitive changes

M. Meyer, S. Hunnius, H. Bekkering

Donders Institute for Brain, Cognition and Behaviour, Radboud University, Nijmegen, The Netherlands

Adults master joint actions with apparent ease and sophistication. Yet, for young children performing successful joint actions is a non-trivial challenge. The question arises how joint action performance develops and which neurocognitive mechanisms are underlying its development. To investigate this, we designed a joint action game feasible for young children. In this game, two buttons had to be pushed alternately. In a behavioural experiment, we found that 2½- and 3-year-old children performed equally well when playing bimanually on their own. However, only by the age of three children coordinated their actions with a partner as well as when acting individually[1]. In a subsequent EEG study we investigated the role of the motor system for young children's joint action performance[2]. In adults, the involvement of the motor system has been suggested to play a key role in joint actions. Motor-related brain activity is observed both during action execution and action observation. Moreover, a recent study [3] has shown that motor system activity is more enhanced when observing the actions of a joint action partner than those of an individual actor. Consequently, we tested 3-year-olds during a live joint action set-up using the same joint action game. We measured both, motor-related brain activity by means of EEG and behavioural performance. In one condition, the children played together with an adult experimenter. In the other condition children watched the experimenter play with someone else. Power changes in mu- and beta-band activity over motor areas were analyzed during periods when children were not moving but observing either their joint action partner or the same person acting when they were not involved in the joint action. As a result, stronger motor activation (as indicated by attenuated sensorimotor mu- and beta-power) was found when the 3-year-olds observed their joint action partner. Interestingly, this enhancement in motor activation was related to better joint action performance. Taken together, the data suggest that context-specific involvement of the motor system might have important consequences for developing success in joint actions.

Kinematics of intransitive action in adults with autism spectrum conditions

C. Press and J. Cook

It has been proposed that there is a core impairment in autism spectrum conditions (ASC) to the mirror neuron system. However, evidence of impairment is mixed. A likely source of experience for development of mirror representations of action is observation of the visual effects of our own actions. If individuals with ASC move with a kinematic profile different from typically developing individuals, they may develop dissimilar mirror representations. Apparent impairments to the mirror neuron system in ASC may therefore reflect the fact that the actions observed in these studies possess a different kinematic profile from that with which actions are typically executed; not an intrinsic inability to mirror. To test the plausibility of this hypothesis, we investigated the kinematic profile of simple intransitive actions in adults with ASC and matched control participants. Participants were required to execute horizontal sinusoidal arm actions and we recorded the kinematics with a Vicon motion tracking system. We analysed the velocity, acceleration and jerk profiles of the movements. We found several differences in the kinematics of action in the two groups and discuss the findings with reference to the literature on mirror neuron system functioning and action control in ASC.

Infants' Processing of Continuous vs. Non-Continuous Movement: Evidence for Action Simulation from ERPs

C. Bache, F. Kopp, A. Springer, W. Stadler, & U. Lindenberger

Recent studies have indicated that infants' neural activity during action production and action observation overlap, which supports the assumption that infants internally simulate an action they observe, possibly by means of mirror neuron activity. This internal action simulation has been interpreted to serve the prediction of observed behavior which is crucial to coordinate in social interaction. From the action simulation point of view, the neural signature of action prediction should differ between human and object movement as only movement that is within the observer's own motor repertoire can be simulated. In the present study, a total of N=79 10-month-old infants were repeatedly shown short video clips of human movement (same-aged child) and object movement (geometrical figure). Each video clip was occluded (black full-screen occluder for 500 ms) and continued afterwards. The movement predictability was manipulated by presenting continuous (high predictability) or non-continuous (low predictability) movement prior to the occluder. Throughout the experiment, neural activity (EEG) was measured. The neural activity during the occluder was assumed to vary as a function of movement predictability prior to the occluder, although the visual input during occlusion was identical in all conditions. Event-related potential (ERP) analysis revealed that at occipital and centro-parietal regions neural activity was enhanced for human compared to object movement which may reflect higher cognitive engagement in human movement. In late neural processing, human continuous and non-continuous movement differed indicating that maintained internal simulation is facilitated in highly predictable human movement. The results contribute to the discussion about the existence of an early mirror neuron system in infants.

Does action simulation facilitate categorization learning in infants?

S. Hunnius [a], M. Meyer [a], D. Mandell [b] & H. Bekkering [a]

[a] Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, The Netherlands
[b] University of Amsterdam, The Netherlands

From early in life, infants learn about objects and begin to organize them in terms of categories. Various studies demonstrate that how categories are presented influences infants' categorization learning. Neurocognitive research, on the other hand, has shown that the infants' motor system gets activated when observing others' actions (van Elk et al., 2008). This action simulation mechanism is thought to play an important role for cognitive processing (Iacoboni et al., 2005). Yet, it is unknown whether action simulation enhances learning, especially categorization learning. We hypothesized that presenting categories in terms of actions would facilitate infants' learning of novel categories.

In a between-subjects design, 10-month-old infants were presented with stimulus movies from two conditions. In the human action condition, infants observed an actor picking up an object. After this ambiguous period, the object was placed in one of two buckets to his left or right. The object's colour was predictive of which bucket was selected as target location. In the non-human movement condition, movies with the same objects and movement trajectories were presented, but objects moved into the respective buckets in a self-propelled manner. Infants watched a pseudo-randomized series of 14 training stimuli followed by 3 test trials. Here, differently shaped objects were used to test whether infants generalized the learned colour categories to novel shapes.

To assess categorization learning, visual anticipations were measured using an infrared eye-tracker. Eye-movements were considered anticipatory if infants shifted their gaze to a target bucket already during the ambiguous lifting phase. Anticipation frequencies to correct targets were compared between conditions. Infants who observed a human action tended to show more frequent correct target predictions than infants in the non-human movement condition. Moreover, presenting categories in terms of human actions facilitated generalization to novel exemplars. These findings suggest that action simulation facilitates infants' categorization learning.

Mirror neurons and dual ontology. From mind-body to person-body

A. Volonnino [a] e G. Basti [b]

[a] Dottorando in Filosofia presso la Pontificia Università Lateranense con una tesi su "Dal gesto al pensiero. Neuroscienze, intenzionalità e ontologia della mente" andrea.volonnino3@tin.it
[b] Ordinario di Filosofia della Natura e della Scienza e Decano della Facoltà di Filosofia della Pontificia Università Lateranense. Da oltre trent'anni ricercatore nel campo dell'intelligenza computazionale (reti neurali) e delle scienze cognitive

In this poster we present a synthesis of the actual debate in the physical, biological and neurocognitive sciences about the reality and the role of information in the physical, biological and neural systems. Such a notion of information as a fundamental physical magnitude like energy, is compatible with a dual ontology of the physical being in the wider sense:

a. The dual ontology - Aristotle first, then Scholastic and then phenomenological - the "mind" or "soul" as a "form of matter" of the body, is a third way between:

b. The ontology of "spiritualist dualism" - the mind or soul as a "spiritual substance" separate and independent from the brain and "material substance" of the body - and

c. The ontology of "materialist monism" - the mind and consciousness as "function", "product" of parts of the brain and the body reduced to mere matter.

In a second step, we illustrate the transition from the original "representational approach" or "functionalist", which followed the metaphor of the brain as a computer and then the mind as "software" of the cerebral "hardware", to "intentional approach" in cognitive neuroscience. According to the intentional approach, the mental contents, rather than "representations" of the "outside" world, are the result of internalizing "intentional actions" of the subject, with an unavoidable component intersubjective, as showed fundamental discovery of "mirror neurons" in the cerebral cortex of primates and humans.

In a third part, we illustrate the close relationship that exists, first, between "representational approach" to the cognitive functions and "deductive logic" (extensional logic), and, secondly, between "intentional approach" to cognitive function and "inductive logic" (intentional logic). Between modal and intentional logics, the system KD45 of epistemic logics, in a specific interpretation, is the base system of "knowledge based", as distinct from "belief". The studies on mirror neurons (cf. Gallese, Ortigue, Rizzolatti, Sinigaglia) and chaotic systems (cf. Freeman) are an example.

All this motivates an anthropology of the person as a psychophysical substance, and with a redefinition of the classical mind-body problem in the more appropriate terms of the person-body relationship.

Anticipatory Reaching Ability And Action Observation: Do 13-month-olds make goal predictions based on the orientation of a person's hand?

C. Filippi and A. Woodward

University of Chicago

Previous research has shown that by 13 months anticipatory reaching is a robust behavior. As such, one would expect that if infants use specific motor experiences to understand others' actions, then at this age infants' ability to predict an actor's goal should also be robust. The current study used an eye-tracking procedure to measure infant attention to goal directed reaches. Infants in the current study watched both a reach that anticipated the shape of the object prior to the midpoint of the reach (i.e., a congruent reach) and a reach that did not anticipate the shape of the object prior to the midpoint of the reach (i.e., an incongruent reach). Preliminary analyses suggest that when infants watch a congruent reach they make faster goal predictions than when they watch incongruent reaches. Future studies will examine whether there are individual differences in infants' abilities to use motor cues and whether this directly correlates with infants' own motor behavior. Implications for mirror neuron research are considered.

The neural correlates of "vitality forms" recognition: an fMRI study

G. Di Cesare [a]*, C. Di Dio [a]*, M.J. Rochat [a], C. Sinigaglia [b], N. Bruschweiler-Stern [c],
D.N. Stern [d, e], G. Rizzolatti [a, f]

[a] University of Parma, Department of Neuroscience, Parma, Italy. [b] University of Milan, Department of Philosophy, Milan, Italy. [c] Centre Brazelton Suisse, Clinique des Grangettes, Geneve, Switzerland. [d] University of Geneva, Section of Psychology, Geneva, Switzerland. [e] Cornell University Medical School, Department of Psychiatry New-York Hospital, USA. [f] IIT (Italian Institute of Technology) Brain Center for Social and Motor Cognition, Parma, Italy. * These authors contributed equally to this work.

The observation of goal-directed actions performed by another individual allows one to understand what that individual is doing and why he/she is doing it. Important information about others' behavior is also carried out by the dynamics of the observed action. Action dynamics describes the "vitality form" of an action, that is the cognitive and/or affective relations between the performing agent and the recipient. Here, using the fMRI technique, we assessed the neural correlates of vitality forms presenting participants with videos showing two actors executing a series of actions. The actions were carried out with two vitality forms: energetic or gentle. The participants were asked to perform two tasks. In one task (what), they had to focus on the goal of the presented action; in the other task (how), they had to focus on the vitality forms. In both tasks activations were found in visual areas and in the action observation/execution circuit. Most interestingly, the contrast how vs. what revealed activation in right dorso-central insula, highlighting the involvement, in the recognition of vitality forms, of an anatomical region connected with the medial temporal areas. This insular-limbic circuit should underlie the observers' capacity to understand the vitality affects intrinsic to action observation.

Varieties of Learning in Macaques:
Modeling List Learning, Task Learning and Observational Learning Effects

B. Gasser & M. Arbib

Macaques have been shown to be able to reproduce simultaneously presented images in an arbitrary order through trial-and-error learning. Slowly, across many lists, they develop task expertise that increases learning rate and performance on novel list instances. Expert monkeys passively observing other expert monkeys executing novel lists subsequently perform at higher rates on those lists compared to other novel list instances in control conditions. Additional probe lists support the conclusion that the monkeys learn to use ordinal representations to organize their performance. Here, we present a computational model demonstrating these varieties of learning and the representations the monkeys use to organize their behavior. We provide explanations for the development of task expertise and show how distributed regions in parietal and frontal cortices contribute to the performance of the animal. Crucially, we explain the observational learning effects not as a form of 'cognitive imitation' as first proposed, but as an enhancement of attention to learned, task-relevant features which develop associations to the cognitive structures only an expert monkey would have developed. We consider data on gaze-following, and neural responses sensitive to others' gaze direction, such as recently discovered LIP 'mirror neurons', as supporting the notion that monkeys are sensitive to the attentional states of others. We hypothesize this sensitivity contributes to the observational learning effects demonstrated. We also offer possible links between this work and other non-human primate data important to the discussion of the evolution of the neural and cognitive structures necessary for linguistic competency.

Do Mirror Neurons exist in Macaque Primary Motor Cortex?

G. Vigneswaran, R. Philipp, S. Waldert, R. Lemon and A. Kraskov

Sobell Department of Motor Neuroscience, Institute of Neurology, UCL, London UK

Mirror neurons were discovered in macaque premotor cortex over 15 years ago but their identity remains a puzzle. Recently we showed that pyramidal tract neurons (PTNs) in macaque premotor cortex (area F5) also exhibit mirror activity, modulating their activity during both action execution and action observation. This implies that some mirror neurons are able to influence downstream spinal targets. Importantly, there was no overt movement during observation of grasp (detectable by EMG recorded simultaneously in hand and arm muscles) even though F5 PTNs were firing.

In this study we investigated whether PTNs in primary motor cortex (M1), whose discharge is closely associated with movement onset, also show mirror activity. We carried out recordings from identified PTNs in a macaque monkey trained to both perform a reach-to-grasp task, and observe the same task executed by a human experimenter. We found evidence of both types of mirror neuron: 'classical' and 'suppression'. 'Classical' mirror neurons increase their firing rate during both action execution and action observation, whilst 'suppression' mirror neurons are active during execution but suppress their discharge during observation. The monkey performed and observed three different grasps: precision grip (of a trapezoid object), hook (small ring) and whole hand grasp (sphere). The objects were grasped, held for one second and than released. No overt EMG activity was present during observation. We found that the discharge of 73% (32/44) of M1 PTNs were significantly modulated during active execution and observation of the task (anova, $p<0.05$). We also found that the selectivity of M1 PTNs for grasp of different objects was much higher during execution (75 % (24/32)) than during observation (50% (16/32)). Interestingly, it was quite common that the grasp associated with highest firing rate during execution did not show the highest rate during observation, and vice versa. In conclusion, we have found evidence that M1 PTNs can be active during action observation without producing any overt movement. Thus the macaque mirror neuron system is more extensive than previously thought. Given that M1 PTN activity has generally been implicated in the generation of active movement, these results prompt fresh questions about dissociation of PTN and muscle activity and the role of the mirror neuron system in this dissociation.

Inhibition during action observation: spinal or cortical?

Alexander Kraskov, Ganesh Vigneswaran, Roland Philipp, Stephan Waldert and Roger Lemon

Sobell Department of Motor Neuroscience, Institute of Neurology, UCL, London UK

The defining property of mirror neurons is that they modulate their firing rate both during action execution, when a subject is moving, and during action observation, when the subject remains still. Simultaneous recordings from subcutaneous EMG electrodes implanted in hand and arm muscles of macaque monkey confirmed that while mirror neurons are modulating their discharge during action observation, there is no detectable change in EMG above that recorded in the baseline period. This finding unequivocally proves that activity of cortical neurons during action observation does not result in overt movement. Since some of these mirror neurons are M1 output neurons projecting to the spinal cord, this implies that there is an active mechanism which suppresses movement during action observation. This mechanism could operate at cortical, subcortical and/or spinal levels. We have developed different experimental protocols in the macaque monkey to try to uncover the origins of the inhibition during action observation. To attempt to disentangle cortical and spinal origins of inhibition we analysed EMG responses to stimulation of the pyramidal tract (PT). Although the monkey is sitting quietly during action observation, it is still possible to evoke small EMG responses in many digit and wrist muscles by delivery of single PT shocks with intensities of 300µA. These responses are of course very much smaller than those observed during action execution (typically less than 5% in peak amplitude), but they provide a direct test of the excitability of different motoneuron pools in response to corticospinal input at different stages of the task, allowing detailed comparison of responses during baseline, object presentation, action observation and execution. At the cortical level, it is possible to assess the excitability of mirror neurons by delivery of single pulses of intracortical microstimulation (sICMS). These stimuli are delivered through one electrode of a multiple electrode system, while recording from a mirror neuron through a neighbouring electrode (Kraskov et al., 2011). When tested in this way, several mirror neurons, including some pyramidal tract neurons (PTNs), showed a much longer sICMS-evoked suppression during observation of a grasp than during execution of the grasp, despite the fact that a given mirror neuron was similarly active during both task conditions. This result could reflect a higher level of activity in intracortical inhibitory interneurons during action observation, allowing for disfacilitation of cortical outputs to digit and wrist muscles. We will present our preliminary findings using these two approaches to identify some of the potential mechanisms that allow movement to be withheld during action observation.

Reference: Kraskov, A. et al. J. Neurosci. 31, 8812-8821

Macaque gaze behaviour during a grasping task: action execution vs. action observation

R. Philipp, G. Vigneswaran, R. Lemon and A. Kraskov

Sobell Department of Motor Neuroscience, Institute of Neurology, UCL, London UK

Paying visual attention to an object which is going to be manipulated is an essential requirement for most tasks performed in everyday life of primates. Here we analysed the coordination between gaze behaviour of a macaque monkey while it executed different visually-guided grasps, and during observation of the same grasps mirrored by a human experimenter. We monitored the eye movement pattern of the monkey by means of a non-invasive infra-red eye tracking system (ISCAN ETL-200, 120Hz). The monkey executed and observed three different types of skilled grasp: precision grip (trapezoid object), hook (small ring) and whole hand grasp (sphere). After an inter-trial waiting period, one of the three objects became visible either in the monkey's peripersonal space (execution trials) or in its extrapersonal space (observation trials). After a short period (epoch 1, visual presentation), a green light around the object (Go cue) (epoch 2, reaction time) instructed either the monkey, or the experimenter sitting opposite the monkey, to reach out and grasp the object, displace it against a spring load (epoch 3, movement), and hold it for 1s (epoch 4, hold), and then release it. The task did not require any particular eye movement or fixation, which allowed us to investigate the natural eye movement pattern during execution and observation of the task. In 13 sessions, we estimated, for each of four epochs, the median fixation time on the object relative to the length of the epoch. We found that the monkey's overall gaze pattern was similar during execution and observation trials (correlation across sessions and epochs, 0.66, $p<0.001$). The monkey started to fixate at the object shortly after it became visible, and then returned to it near the GO cue and then continued to fixate it for short periods both during the reach-to-grasp movement, and during grasp itself. During visual presentation (epoch 1), the monkey spent significantly ($p<0.05$) longer looking at the object during execution vs observation trials. We simultaneously recorded mirror neurons in M1 and F5 (Vigneswaran et al., this meeting). In the mirror neuron literature, it is generally assumed that the observer is paying attention to what the actor is doing. We will present results comparing mirror neuron firing rates for trials when the monkey attended the object for longer vs. those for shorter periods of fixation. We will also present data comparing the influence of longer vs. shorter periods of eye fixation on mirror neuron activity in M1 versus that in area F5.

The *'Arches'* before the *'Mirrors'*: an historical perspective on a French-Italian connection on *arceau*/mu rhythm

C.A. Tassinari [a, b], G. Cantalupo [c, d], P. Avanzini [b], J. Bert [a]

[a] Service de Neurophysiologie Clinique, Hôpital de la Timône, Marseille, France; [b] Dipartimento di Neuroscienze, Università di Parma, Parma, Italy; [c] Dipartimento Materno-Infantile, Neuropsichiatria Infantile, AOU di Parma, Parma, Italy; [d] Dipartimento di Scienze della Vita e della Riproduzione, Neuropsichiatria Infantile, Università di Verona, Verona, Italy

Since the advent of electroencephalography, the oscillations recorded from the scalp, and used for both clinical and experimental studies, have been classified in different *'EEG rhythms'* according to three indissoluble characteristics: <u>frequency</u> spectrum, <u>topography</u> and <u>reactivity</u> to specific stimuli. The first *EEG rhythm* described – an oscillation at about ten cycles per second, with occipital preponderance and reactivity to visual stimuli – was identified early on by Hans Berger in his pioneering recordings. For this reason it was referred as 'Berger Rhythm' or 'alpha rhythm' – as the first letter of the Greek alphabet (α) – to suggest it would be the first building block of a *new language*. The primacy of occipital alpha rhythm was largely due to the practice of performing recordings on subjects while they were keeping the eyes closed.

Discovery: looking at the EEG with the 'eyes opened'
At the *Hôpital de la Timône* in Marseille, in the EEG lab directed by professor Henry Gastaut, there was a keen and special interest to look at the EEG recordings while the patients kept the eyes opened: indeed, Yvette Gastaut had just (1951) described for the first time the *«pointes occipitals survenant pendant l'ouverture des yeux»* since then referred to as *lambda* (λ) waves.

So, Henry and Yvette Gastaut, together with an Italian neurologist, Hrayr Terzian, a few months later were thrilled by a 8-11 rhythm appearing intermittently over rolandic regions, best evident when the eyes were kept open, thus reducing the predominant occipital alpha rhythm. The 'new' rhythm was blocked by movements to reappear with a rebound at the end of the movement itself. It was a little bit morphologically different from the occipital alpha rhythm: it looked like *'en arceau'* (Gastaut, Terzian and Gastaut, 1952). Based on cortical recordings (Gastaut, 1952), it was considered as an half-frequency or *'dedoublement'* of the beta activity.

From mu rhythm to brain-computer interface
<u>Thinking or programming a movement</u>: *«Le fait d'imaginer un mouvement volontaire suffisait même a provoquer une réaction (blockade) complete du rythme en arceau»* (Gastaut, 1952).

<u>Phantom Limb</u>: *«mental mobilization of the phantom limb can block the arceau»* (Gastaut, Naquet, Gastaut, 1965). Both these observations constitute the cornerstone of the modern BCI techniques, that will likely allow humans with severe motor disabilities to interact with the environment by controlling robotic arms.

From mu rhythm to action understanding
<u>Rhythm *'en arceau'* while observing a movie</u>: *«It disappears when the subject identifies himself with an active person represented on the screen»* (Gastaut and Bert, 1954). Although this observation was appealing, it remained difficult to explain the physiological basis of this reactivity until the discovery of mirror neurons by Rizzolatti and co-workers (di Pellegrino et al., 1992).

Fortuitous meetings of minds
Hrayr Terzian held the Chair of Neurology at the University of Padua; beside coauthoring the earliest report of the 'en arceau' rhythm, he first described the Kluver-Bucy syndrome in humans. Infact, notwithstanding he was mainly a skillful *'clinical'* electroencephalographer, he recognized the relevance of experimental neurophysiology for the basic understanding of clinical neurology. For this reason, few years later, he advised a young neurologist to work – for a while – with the physiologist Giuseppe Moruzzi (at that time in Pisa). The young neurologist, Giacomo Rizzolatti, accepted the suggestion and 'few' years later, in Parma, discovered the Mirror neurons, shedding new light on the 'old' rhythm *'en arceau'*.

What are you doing? Experience, social context and acquisition of a new task

B. Regaiolli [a, b], P. Furlan [c], C. Spiezio [a]

[a] Research Department, Parco Natura Viva, Garda Zoological Park, Italy; [b] Department of Evolutionary and Functional Biology, University of Parma, Parma, Italy; [c] Department of Biology, University of Padua, Italy
barbara.regaiolli@gmail.com

Social learning could be defined as the modification of an individual's behaviour through the observation of others, although it could take place with different mechanisms, ranging from local and stimulus enhancement to imitation and goal emulation. Imitation has been considered a peculiar characteristic of humans. However, it is important to understand how it evolved by studying social primate species such as monkeys. In literature there is some evidence that social and gregarious animals might learn from each other. In this study we investigate the social learning strategy adopted by vervet monkeys (*Chlorocebus aethiops*) in acquiring new behaviors to solve tasks through observation. Fourteen vervet monkeys, hosted at two different Italian zoos, were presented with five different boxes to open in order to retrieve a reward. Nine monkeys (the experimental group) saw a human demonstrator opening each box several times, whereas the remaining five vervet monkeys (control group) did not. The results of this study show that the performance of vervet monkeys was significantly better when they observed a demonstration than when they did not. Thus, it seems that *Cercopithecus aethiops* can learn new behaviours by observing others. As the experimental group did not reproduce the sequence of the behaviours observed, our findings suggest that local and stimulus enhancement have certainly played a role in learning new behaviours and it seems that emulation may be the strategy adopted by these monkeys to acquire new tasks.

Action- and goal-specific activation of the mirror-neuron system during action observation of artificial agents

A. Kupferberg [a, b], V. Flanagin [a], S. Glasauer [a, b]

[a] Center for Sensorimotor Research, Clinical Neurosciences, University of Munich; [b] Graduate School for Systemic Neurosciences GSN, Ludwig-Maximilian University Munich, Germany

Upon perceiving a body movement, we map it into our own motor system and understand it when its observation leads to "resonance" of the motor system based on the activity of the MNS. However, how does the MNS react if the observed agent does not only possess a different motility and shape but is a non-biological entity and therefore has no intentionality? Previous studies investigating this question lead to inconsistent results. We used fMRI to study the flexibility of the MNS during observation of hand actions of a humanoid inanimate agent focusing on recognizing different action types and attributing goals/intentions to them. 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) and therefore suggesting 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 the different object categories themselves thus enabling us to localize the regions active during action observation and execution by conducting a conjuction analysis. This analysis revealed four regions of interest: the bilateral premotor cortex and inferior parietal gyrus and finally the left inferior frontal gyrus. During action observation, the participants were required to indicate whether they were able to attribute an intention to every action by pressing a button after each trial.

The analysis of the button presses and the debriefing after the experiment revealed that the subjects were able to attribute a certain intention to the actions of both the human (in 95% percent of all trials) and the robotic agent (in 94% percent of all trials). For action understanding, the imaging analysis revealed a significant signal increase in the bilateral IPL and premotor cortex when contrasting grasping with pointing actions for both the robot and the human indicating that the MNS is involved in differentiating hand actions performed by artificial agents to the same extend as differentiating human actions. For contrasting grasping and pointing actions directed at different object categories we found activations in the bilateral IPL, premotor cortex and the left IFG, again, for both agents, suggesting that despite artificial body shape and movement velocity, MNS was sensitive to goals of robotic actions.

Brain syntax of the Mirror Mechanism activation in Children. An EEG source imaging study.

C. Berchio [a], M.A. Umiltà [a], T.A. Rihs [b], C.M. Michel [b], F. Apicella [c], F. Muratori [c, d], V. Gallese [a]

[a] Dept. of Neuroscience, University of Parma, Italy. [b] Functional Brain Mapping Laboratory, Genève, Switzerland, [c] IRCCS Stella Maris, Italy, [d] IRCCS Stella Maris & University of Pisa, Italy.

Several studies have shown that in the human brain specific Parietal and Frontal areas become activated during motor acts execution and observation ("Mirror Mechanism", for review, see Gallese 2009, Psychol Res, 73(4):486-98.). The activation of this fronto-parietal network is deemed to be at the basis of basic forms of action understanding. However, at the moment is still largely unknown how this network develops during ontogeny. In order to explore this issue, we recorded EEG signals from one group of 12 children (6 female, 6 male; average age:10,5: SD: +/-2,15).

Data were collected when children observed video clips showing hands grasping objects in two different experimental conditions: 1) Full Vision, in which the motor act was fully visible; 2) Hidden, in which the interaction between the hand and the object was not visible (Umiltà et al. 2001, Neuron, 31(1):155-65.). By means of EEG "traditional" Event-Related-Potentials (ERPs) and topographic map analyses we explored and described the temporal pattern of the evoked electrical potentials. Furthermore, using source-imaging methodology (Michel et al., Clin Neurophysiol, 115(10):2195-222.) we investigated the localization of the corresponding brain activations.

Results showed that the fronto-parietal network instantiating the mirror mechanism for motor act observation is already active in children and it overlaps with a similar network already demonstrated in adults. Moreover, the amplitude, topographic maps and source localization of the recorded ERPs are differently modulated in the two experimental conditions. Our results indicated that in children, the fronto-parietal network of mirror mechanism works differently in relation with the available amount of visual information.

Clinical Implications of Applied Mirror Neuron Research.
A Pilot Project Including Twelve TBI or Stroke Survivors

V. Macri, P. Zilber, V.J. Macri

One question in studies of sensory perception is what physical movement visual inputs are mirrored by the human brain. We expanded that question by asking how mirror neurons can be stimulated using non-invasive technology. Historically, physical events external to the viewer generated visual inputs to the mirror neuron system. Currently, we employ digital technology to support viewer-created inputs of simulated physical events. In our pilot project twelve viewers-survivors controlled anatomically realistic virtual upper extremities, having analogous true range of motion to generate graphic images of simulated physical movements. In effect, internal visualizations (abstract images) of intended physical movements were instantiated into real images (albeit, simulated physical movement images). The process represents a feedback loop in that what was mirrored derived from stimulated cortical processes, beginning with premotor planning, implemented by survivor image control/creation of simulated movements of virtual upper extremities, accompanied by viewing the self-simulated movements, thereby stimulating mirror neuron activation and cycling back into improved premotor planning and motor control. We submit that pilot project survivor-created mirror neuron activations contributed to improved motor and cognitive performance.

Autistic traits modulate the influence of reward on spontaneous mimicry: Implications for the mirror neuron theory of autism

B. Chakrabarti and T.B. Sims

Centre for Integrative Neuroscience & Neurodynamics,
School of Psychology & Clinical Language Sciences, University of Reading, Reading, UK

Spontaneous mimicry (SM) is an index of emotional contagion, a key component of empathy. Humans show greater SM of conspecifics who they like more, and want to affiliate with. This suggests that the subjective reward value of the target is a key determinant of the extent of SM, and hence, empathy. Research on rodents and sheep have further shown a considerable overlap between the brain regions involved in reward and empathy-related behaviour. In this set of studies, we tested if reward value of a face influenced a) the extent of SM of its happy expression (using facial EMG, study 1), and b) the magnitude of activity in brain regions involved in mimicry, such as the ventral premotor cortex and IFG (using functional MRI, study 2). For both studies, 4 neutral faces were associated with varying levels of rewards (high and low), using an implicit conditioned learning paradigm instantiated through a card game. In the test phase for both studies, participants were required to passively view happy and angry expressions of these conditioned identities. In Study 1, 33 participants from the general population showed greater SM for happy expressions of high-reward faces, compared to those of low-reward faces. Importantly, participants who scored high on autistic traits (and low on a trait measure of emotional empathy) did not show a significant difference in SM between happy expressions of high and low reward-conditioned faces. Conversely, participants low in autistic traits (and high on emotional empathy) showed a significant difference in the extent of SM between the different reward-conditioned faces. In Study 2, an independent sample of 30 participants showed greater activity in a cluster (defined below) in response to happy expressions made by high-reward faces compared to those made by low-reward faces. This cluster i) includes the ventral premotor cortex and Inferior Frontal Gyrus, iii) was defined using several independent studies of mimicry, and iii) is part of the putative human 'mirror system'. Importantly, the strength of connectivity between the ventral striatum and the IFG was negatively proportional to autistic traits. Together, these studies show that a) reward value modulates spontaneous mimicry of happy faces, as measured using facial EMG and fMRI, and b) the extent of this modulation varies as a function of autistic traits. These results can inform the ongoing debate about a fundamental deficit in mirror systems in autism. Our studies, although conducted in the general population, suggest that the autistic deficit may lie in an atypical modulation of the mirror system activity by the reward value of the stimulus. This is consistent with the social reward deficit hypothesis, which suggests that people with autism do not attend to and empathize with social stimuli, because they do not find them rewarding.

Somatosensory Experiences Modulate EEG Activity during Subsequent Action Observation

L.C. Quandt [a], P.J. Marshall [a], C.A. Bouquet [b] & T.F. Shipley [a]

[a] Temple University, Philadelphia, PA, USA; [b] Université de Poitiers, Poitiers, France

How does prior experience with action change how we percieve another person's performance of a similar action? Research has examined the role of sensorimotor and visual experiences in action mirroring during subsequent observation, however the contribution of somatosensory experiences to processing of observed actions has not been adequately examined. In the current study, we used EEG to measure how varied somatosensory experiences during reaching actions would change mirroring activity during the observation of similar actions. Participants reached into two boxes which varied both in their color (yellow or blue) and the presence of somatosensory stimulation (one box contained feather stimuli, one box was empty). Thus, they formed an association between the color of the box and somatosensory consequences of reaching into that box. Importantly, while somatosensory characteristics varied when reaching into each box, motor and visual aspects of the reaches were very similar for each box. Participants observed video clips depicting an actor reaching into the yellow or blue boxes, with no visual cue to whether there was any somatosensory stimulation within the boxes. Their prior experiences with the boxes (i.e. yellow is empty) would then lead them to predict whether the actor experienced any somatosensory stimulation during the reach. After observing a reach, the participant then reached into the box of the same color to reinforce the association. We predicted that varying the somatosensory consequences of the reaching actions would modulate regional oscillatory activity during observation of the video clips in the alpha and beta EEG frequencies, which are known to partly reflect mirror system involvement. Analyses revealed that alpha and beta rhythms varied significantly during the observation of reaches, depending on the prior somatosensory experience that participants had with the boxes of the same colors. The results presented here demonstrate that prior experience with somatosensation contributes uniquely to the neural processes involved in observing and understanding the actions of others.

Mirror neurons and simulation

S. Uithol

Radboud University Nijmegen, Donders Institute for Brain, Cognition and Behaviour

Mirror neuron activity is often interpreted as implementing the observer's 'simulation' of an observed action. This has lead to the idea that through simulating the mental state that caused the observed action, mirror neurons underlie the capacity of mindreading. I argue, however, that the persuasiveness of this idea is based on an overly rich interpretation of the notion of simulation. Alternatively, the embodied cognition thesis states that the representation of an action is implemented in the areas responsible for controlling and planning actions. Following this thesis, the reported activation of (pre-)motor areas upon action observation is a natural consequence of the embodied layout of the brain. In this light, a more parsimonious explanation of mirror neuron activity is closely related to Barsalou's interpretation of 'simulation': the re-enactment of a symbol. What is simulated here is a previous occurrence of the action—either perception or execution—, meaning that this form of simulation is a form of recognition, rather than a form of mindreading. This does not mean that mirror neurons do not contribute to our capacity to mindread at all. Yet, this contribution might be different, less direct and less important than the idea of 'simulating the other's mind' suggests.

Newborns differentiate between possible and impossible movements

I. Senna, E. Longhi, M. Addabbo, H. Bulf, N. Bolognini, V. Macchi Cassia, P. Tagliabue & C. Turati

Both primate and human adults possess neurophysiological mechanisms which allow to integrate action perception and execution within the observer's own motor representation. The aim of this study was to investigate whether these mechanisms are already present at birth by testing whether newborns can distinguish between observed movements differing only in their anatomical plausibility. Using a preferential looking paradigm, we explored whether 2-to-3-day-old newborns were able to discriminate between an observed plausible hand movement, which is already part of their motor repertoire, and a similar movement which violates the constraints of human anatomy. Newborns were presented with two videos of a hand closing in a possible (i.e. the fingers moving towards the palm) versus impossible manner (i.e. the fingers moving backward toward the back of the hand, violating the biomechanical properties of the phalangeal joints) (Experiment 1). Newborns looked longer at the impossible movement, suggesting that they discriminated between the possible and impossible movements, recognizing the first as familiar and perceiving the latter as novel and unexpected. In order to explore the role of movement in newborns' preferential response, in Experiment 2 two static images depicting a possible versus impossible posture of the closing hand were presented. Newborns did not manifest any visual preference. Hence, static images did not allow differentiating between possible and impossible hand postures. This evidence suggests that a mechanism linking motor representations of movements which are part of the newborn's motor repertoire and their visual representations is already present at birth. This visuo-motor link is active also for simple movements, which differ only for their anatomical plausibility.

Investigating the ontogeny of mirror neuron system: an emg study with 3- and 6-month-old infants

I. Senna, E. Natale, E. Longhi, M. Picozzi, N. Bolognini, V. Macchi Cassia & C. Turati

Although a large number of studies have examined the mirror neuron system (MNS) in human adults and monkeys, little is known about the origins of the human MNS and how it develops during infancy.

The present study aimed at investigating the muscular response of infants while observing different actions. In particular, using electromyographic (EMG) recording, we tested whether the final goal of the observed actions can modulate the activity of the corresponding muscles in 3- and 6-month-old infants. To this end, the EMG activity of the muscles responsible for mouth opening (i.e, suprahyoid muscles, SM) was recorded while the infants watched videos showing an actor reaching and grasping an object, and then bringing it either to the mouth or onto the head. Six-month-old infants' SM activity was modulated by the goal of the observed action. In fact, when the infants observed the object-to-the-mouth action an increase of SM activity was recorded. On the other hand, when the infants observed the object-to-the-head action a decrease of SM activation emerged. Unlike 6-month-old infants, 3-month-olds did not manifest any modulation of SM activity during action observation. Crucially, for 6-month-olds SM activity was specifically modulated during the bringing phase, i.e., when the goal is achieved, and not while infants observed the previous reaching and grasping phases. This suggests the presence of an on-line simulation, and possibly an understanding, of the observed action, rather than an ability to predict the action's final goal. Overall, our results support the hypothesis of an early involvement of the MNS in action understanding, but also show that the functional properties of mirror mechanisms develop gradually through experience.

The role of prediction in understanding goal-directed behavior

Sasha Ondobaka [a], Floris P. de Lange [a], Marco Wittmann [a], Chris D. Frith [b] and Harold Bekkering [a]

[a] Donders Institute for Brain, Cognition and Behavior, Radboud University Nijmegen
[b] University of Aarhus & University College London

Understanding goal-directed behavior entails processing of other individual's conceptual goals in addition to perceptuo-motor processing of their concrete movement goals. Recent accounts of action understanding stress the role of prediction, however, its contribution to inference of others' conceptual and movement goals remains unknown. Here, we examined which neural circuits underpin understanding of predicted object-related actions. In two tasks, participants underwent functional magnetic resonance imaging while they inferred conceptual or movement goals which either matched or mismatched their prediction. Predicted conceptual goals recruited the posterior cingulate cortex, a part of the default-mode network, irrespective of task and the observed movement-goal. In contrast, activation of parieto-frontal network reflected the synthesis of conceptual and movement-goal information, solely in the movement task. Results show specific contributions of default-mode and parieto-frontal circuits to prediction guided goal inference. Together, we demonstrate that understanding of goal-directed action entails a hierarchical mechanism in which conceptual predictions influence perception of concrete movement-goals.

Goal certainty modulates infants' goal-directed gaze shifts

I. Henrichs [a], C. Elsner [b], B. Elsner [a], N. Wilkinson [c] and G. Gredebäck [b]

[a] University of Potsdam, Germany; [b] Uppsala University, Sweden; [c] IIT, Italian Institute of Technology, Genova, Italy

We investigated whether 12-month-old infants rely on information about the certainty of goal-selection in order to predict observed reaching actions. In the current eye-tracking study, twenty-four 12-month-old infants' goal-directed gaze shifts were recorded while they observed a hand that reached for one of three goal objects. In one condition, the hand always reached for the same goal object between trials (frequent condition), whereas in the other condition it always reached for a new goal object in each trial (non-frequent condition). We found that 12-month-old infants exhibited gaze shifts significantly earlier when the observed hand reached for the same goal object in all trials compared to when it reached for different goal objects across trials. Infants in the frequent condition exhibited overall predictive gaze shifts, whereas infants in the non-frequent condition tracked the reaching action in a reactive manner. In addition, findings revealed rapid learning in the case of certainty and no learning in the case of uncertainty of goal selection over the course of trials. Together, our data indicate that by the end of their first year of life, infants rely on information about the certainty of goal selection to make inferences about the action goal, but the underlying mechanisms of action prediction are not yet fully understood. It might be that infants' goal anticipations are guided uniquely by a direct-matching process or by a statistical learning process. However, it is more likely that both processes are intertwined such that statistical learning feeds into the direct matching process by strengthening the motor representation of a perceived action.

Effects of early social experience on the mu-rhythm in infant macaques

R. Vanderwert [a], A. Paukner [b], S. Bower [b], S.J. Suomi [b], N.A. Fox [a], Ferrari P.F. [c, d]

[a] Department of Human Development University of Maryland, College Park, MD, USA; [b] Eunice Shriver Kennedy National Institute of Child Health and Human Development, NIH, Poolesville, MD, USA; [c] Dipartimento di Neuroscienze, Università di Parma, Italy; [d] IIT, Italian Institute of Technology, Parma, Italy

Differential experience has been shown to modulate the mu rhythm in the EEG of humans. Previous evidence (Ferrari et al, 2012) suggests that the mu rhythm (5-6 Hz) desynchronizes in week-old rhesus infants while they observe or execute lip smacking (LS) or tongue protrusion (TP) gestures compared to a disk control (DK) in a sample of infants separated from their mothers at birth. Over the first week of life infant rhesus macaques living with their mothers receive increasing amounts of experience with LS and TP. Mother-reared and nursery-reared 3-day-old rhesus macaque infants were tested using a modified neonatal imitation task under three conditions: (1) TP, (2) LS, and (3) DK, while EEG was collected. Event-related desynchronization of the EEG was computed for periods in which the infant sat still observing the stimulus and while they imitated the gesture presented (LS and TP conditions only). Results demonstrate desynchronization in the 5 – 7Hz band to the observation and execution of LS or TP. Moreover, there was an effect of rearing condition with mother-reared infants showing greater desynchronization to the observation of LS compared to their age-matched nursery-reared counterparts. These data suggest that mu rhythm desynchronization is dependent upon experience with meaningful biological actions.

From Hand actions to perceptual causality:
Physiologically-inspired model for the recognition of transitive hand actions

F. Fleischer [a], V. Caggiano [b], P. Their [b], M.A. Giese [a]

[a] Section for Computational Sensomotorics, Dept. for Cognitive Neurology, HIH and CIN, University Clinic Tuebingen; [b] Dept. for Cognitive Neurology, HIH and CIN, University Clinic Tuebingen, Germany

The visual recognition of biological movements and actions involves complex computational processes that link neural representations for action perception and execution. The processing of such complex visual stimuli has been even associated with highly abstract conceptual representations, which encode social intentions or the interpretation of causal events. The detailed neural mechanisms of the visual recognition of complex shapes have become increasingly clear over last decades. At the same time, the computational and neural mechanisms of the visual processing of body motion, and especially of goal-directed actions are much less clear, and this visual function has often been associated with internal simulation based on abstract information that is extracted by the visual system. However how such abstract information can be extracted from real images by physiologically plausible mechanisms has rarely been addressed. We present a physiologically plausible theory for the recognition of goal-directed hand actions, which largely exploits well-established cortical principles that have been shown to be relevant in visual and parietal cortex. We show that this theory correctly reproduces and partially predicts electrophysiological data about action-selective neurons in the STS and higher areas, such as premotor cortex. The model works on real video sequences and thus could be tested with stimuli that have been used in monkey experiments. Interestingly, the same model reproduces also a variety of psychophysical results on the perception of perceptual causality, even though the model was not developed for this purpose. Consistent with the model prediction, F5 mirror neurons show generalization between normal and very abstract action stimuli, as used in experiments for the assessment for causality perception. In this way, our model provides a neural theory for the perception of causality that is based on simple neural mechanisms and which does not require complex probabilistic inference mechanisms, whose implementation in terms of physiological plausible mechanisms is largely unclear.

Comparison of mirror neuron system function in hemiplegia with cortical versus subcortical lesions: two case vignettes.

E. Kirkpatrick, A. Basu, J. Eyre

Developmental Neuroscience Group, Newcastle University, UK.
e.v.kirkpatrick@ncl.ac.uk

Action observation has been suggested as an effective rehabilitation tool to aid recovery in stroke 1-3. This may also be a viable therapeutic approach for children with hemiplegia 4,5. The type or location of the lesion, as indicated by MRI, may be an important indicator of usefulness of this therapy. Additionally, EEG can provide an indirect measure of sensorimotor cortical function through mu suppression. Here we present two case studies, both female, tested at age 9 years. One has a right hemisphere cortical lesion, and one has a left hemisphere sub-cortical lesion. Both have good functional ability: ABILHAND-Kids questionnaire scores 33/42 and 36/42 respectively; Melbourne assessment of unilateral upper limb function scores 88% and 87% respectively. 21 channel EEG was recorded during rest and experimental conditions: observing pincer grasp with right and left hands, and performance of pincer grasp with right and left hands. Results indicate that the patient with the cortical lesion shows bilateral desynchronisation during performance of actions and when observing actions with the non-paretic hand. When observing actions with the paretic hand she shows ipsilateral desynchronisation (in the non-lesioned hemisphere). The patient with the sub-cortical lesion shows the expected pattern of contralateral desynchronisation when performing with the non-paretic hand and bilateral desynchronisation when performing with the paretic hand. During action observation she shows desynchronisation in the lesioned hemisphere. The mirror neuron system appears to be somewhat preserved in these cases. Future studies will explore if information from MRI and/or EEG can predict who will benefit from action observation as a therapeutic intervention.

Visual Attention and Person Recognition During Neonatal Imitation in Infant Monkeys

E.A. Simpson, A. Paukner, S.J. Suomi and P.F. Ferrari

We hypothesized that infants who imitate may be more attentive than infants who do not. To test this, we measured infant monkeys' (n = 49) visual attention and gestures—lip smacking (LPS) and tongue protrusion (TP)—in the first week of life, in a face-to-face interaction with a human experimenter. Imitators looked more to the face and a nonsocial control stimulus (disk), compared to non-imitators, p = .017. Interestingly, increased visual attention was associated with increased TP imitation, p = .001, but not LPS imitation, p > .05. This may be because LPS is a more natural gesture, and therefore less visual attention is required for LPS imitation, compared to TP imitation. In a second study, we examined whether infants (n = 107) were sensitive to the identities of the people with whom they were interacting, by measuring gesturing during a still-face immediately following gesturing, compared to a return-period after a one-minute delay. We found that imitators, but not non-imitators, exhibited decreased matching-gesturing when the return person was different, p = .02, but not when the return person was the same, p > .05. These findings suggest that there may be differences between imitators and non-imitators in how the brain codes gestures, which causes them to be differentially engaged by faces, influencing person recognition skills.