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Summary in English

Neural correlates of action perception

When observing others we usually do not require a verbal explanation to understand what they are doing and, in many cases, why they are doing it. Specific brain regions are involved in the processing of observed actions and some of them belong to the motor system, which is mainly involved in the planning and production of movements. Intensive research of these regions suggests, that the same neurons are active during action observation and execution. It has been proposed that these neurons, so called mirror neurons, allow the simulation of observed actions in a person's motor system. This simulation may help to understand the actions of others'. This theory of motor simulation is an intriguing way to explain certain aspects of action perception, as learning by observation, but many questions remain, some of which have been addressed in this thesis.

The spatial extent of the areas that potentially contain mirror neurons is picked out as a central theme in Chapter 2. In humans, mirror neuron activation can typically not be recorded directly as this requires invasive electrode implantation. Instead, techniques such as functional magnetic resonance imaging are used to visualize brain regions that are activated both during action observation and execution, so called shared voxel regions. While several shared voxel regions have been described in the cerebrum, less is known about the existence and spatial localization of shared voxel regions in the cerebellum. The cerebellum is involved in motor planning, execution and learning, and is therefore a good candidate region to contain mirror neurons. In Chapter 2, we show that choices in data processing have likely led to an underestimation of the number of cerebellar shared voxel regions. Standard data acquisition and analysis settings exclude parts of the posterior cerebellum and data smoothing may have led to merging of activated regions in the cerebrum and cerebellum, leading to a neglect of cerebellar activations. Importantly, several shared voxel regions were found in different parts of the cerebellum (Lobule VI, VIIb and VIIIa). Functional magnetic resonance imaging also allows to evaluate which brain regions are likely to communicate with each other using so called function resting-state connectivity analyses. We concluded that the cerebellar shared voxel regions communicate with the ventral and dorsal sub-regions of the cerebral shared voxel network. Based on these findings the cerebellum should be considered part of the human mirror neuron system.

In Chapter 3, we looked at the type of information processed within the human mirror neuron system. It has been proposed that the mirror neuron system can compute the goal of an action, for example grasping a glass in order to drink water. However, there is another brain network, the so-called theory of mind network, that activates when we think about another person and take his or her perspective. If we see a person reaching towards a glass of water, which brain network is necessary to understand that he wants to grasp the glass and that he is thirsty, the mirror neuron system or theory of mind network or both? In Chapter 3, we are using a technique called transcranial magnetic stimulation (TMS) to determine the contribution of both networks during action perception. TMS evokes small perturbations in specific brain networks. If participants perform worse or slower on a given task after TMS, you can conclude that this brain network is necessary to perform the task efficiently. We found evidence that the mirror neuron system is necessary to understand the goal of an action. In order to understand the mental state of a person (wants to drink because he is thirsty) the theory of mind network is needed in addition.

This interaction of mirror neuron system and theory of mind network during action perception leads to the question how these mechanisms develop in children, which is subject of Chapter 4. Here, we were interested if 2-year olds would automatically associate a hesitant hand movement with unreliability compared to a confident hand and if this skill was associated with movement analysis (within the mirror neuron system) and/or theory of mind skills. We found some evidence that toddlers tend to expect that a confident rather than a hesitant hand will correctly indicate the position of a hidden object. However, this effect was only found for one out of two experimental conditions. Additional tests are necessary to determine which clues are important for toddlers to identify a motion as being hesitant. While there was no strong association between hesitation detection and movement analysis and/or theory of mind skills in toddlers, adults who showed a stronger tendency to trust a hesitant hand, also showed a stronger tendency to discriminate between a hand lifting a heavy or a light object. Both processes are likely to depend on motor simulation within the mirror neuron system.

Finally, Chapter 5 is looking at the association between action perception and social functioning. The diagnosis autism spectrum disorder (ASD) often implies difficulties to feel at ease in social situations. This symptom may be based on a difficulty to perceive actions, potentially due to differences in activations of visual and/or motion processing brain areas. We showed that a group of adult participants diagnosed with ASD had a neurotypical level of activation when watching actions, even though there was no instruction to attend to them. There was even an

increased activation in brain areas tuned to motion and shape processing. Given that children diagnosed with ASD experience stronger difficulties for example in reading emotions from faces than adults, this increased brain activation may reflect a compensatory mechanism in adults diagnosed with ASD.