7

Summary and epilogue

This thesis is about movements and how they are coded.

The movements we investigated are voluntary goal-directed arm movements. All humans move in approximately the same way, despite all their individual differences and the infinite possibilities to make a movement. That humans make approximately the same movements suggests that the brain codes movements in higher order parameters. Two information sources that are required to make a movement plan are the information about where the target is, and the information about how to get to the target.

Humans move towards objects in a typical way; in a slightly curved trajectory, even if they are instructed to move in a straight line. To investigate what information we use when making a movement, we used the observation that in free space movements are more curved than movements over a surface[21] (**chapter 2**). The reason for this might be that there is less information available for movements in free space (unconstrained) than for movements over a surface (constrained). We asked participants to move towards haptic targets (their other finger) in different settings. We found that participants' trajectories were more curved for unconstrained movements than for constrained movements when they moved towards a haptic target, even if they were instructed to move in a straight line towards the target. Strongly reduced tactile information did not have an effect on the movement trajectories. Also for a surface with a high compliance there was a strongly reduced curvature compared to an unconstrained movement. Therefore we concluded that the amount that participants needed to control the movements did not influence the movement trajectory. Extra information that the surface gives about the third dimension and information about the direction of the movement provided by the additional force needed to overcome friction might be two additional sources of information that can explain differences between movements over a surface and movements in free space.

Information about how to get to the target might be coded in higher order parameters. In this thesis we investigated whether a movement is coded as a position or a vector. When a movement is coded as a vector, movement direction is a parameter we use when planning a movement. We therefore related errors in initial movement direction in movements when participants moved as straight as possible towards a targets with errors in setting a pointer towards the same targets (**chapter 3**). We did this for movements towards visual and haptic targets. The results showed a modest correlation between initial movement direction and perception of direction. The amount of correlation depended on the orientation of the setup. That there is a modest relation might suggest that not only vector coding is used, but also position coding. The question whether movements are coded as positions or vectors was directly investigated in **chapter 4**. We assumed that repeating movements towards the same position would increase precision if movements are coded as a position and repeating movements with the same direction would increase precision if movements are coded as a vector. Participants made movements towards visual targets on a table without being able to see their hand. We compared blocks of repetitions of endpoints and of movement vectors with a third block with the same movements in random order. We found no benefit for repeating a position or repeating a direction. We repeated the experiment with a different setup where participants saw the target and the feedback on a vertical screen and made the movement on a table. Participants were more precise in the repeated position block than in the random block. We therefore conclude that participants benefit from repeating a position when acting in an unusual visuo-motor mapping.

Taking these two chapters together suggests that both vector and position coding is important to consider in order to understand human movements.

There are several models with different ideas on how to determine where a target is. In **chapter 5** we considered a model in which both the position of the target and the position of the moving hand are based on a combination of a visual and a proprioceptive estimate. It has been shown that you combine visual and proprioceptive information to localize your hand precisely[45]. It has been suggested that you do the same to localize a target[46]. To investigate whether a proprioceptive estimate of a visual target is relevant, we studied repetitive movements towards visual targets when participants did not see their hand. If vision of the hand is prevented, the proprioceptive memory of the target will degrade when the hand is moved. We investigated whether humans were able to keep this proprioceptive estimate by placing a non-informative finger of the left hand near the target. This unseen left hand did not add new information; it only copied the visual information of the target to proprioception. Placing the left hand near the target improved the accuracy of the movements. The rate at which the endpoints drifted away from their original positions was higher which suggests that participant had a more precise estimate of the target. This is evidence for a model where both for the target and the hand a proprioceptive estimate and a visual estimate are combined.

We investigated the origin of the visuo-proprioceptive biases in **chapter 6**. More specifically, we studied whether only sensory biases are involved when vision and proprioception are combined, or whether there are also other sources of errors. We performed different matching tasks to investigate if there are differences in matching errors in tasks involving the same sensory biases. For example when participants moved with their unseen right finger towards a visual dot, or moved the visual target towards their unseen finger. In this case there is both an unseen hand and a visual dot, but the order differs. When there are only sensory biases, moving with the left hand towards a visual target versus the right hand towards a visual target should give rise to the same matching errors as matching the left with the right hand. We found that tasks were not reproducible for the comparisons where vision and proprioception were aligned. However the errors in these tasks were more reproducible within participants than between participants. This suggests that the matching errors are not due to sensory biases alone, but might arise from transformations between the senses. The model we assumed in **chapter 5** could not explain these results. **Chapter 6** study suggests that the visual and proprioceptive estimates in the model we suggested in **chapter 5** could not only arise from a memory where these estimates were before, but might also arise from transforming information from one sense to the other.

These studies suggest that there are not only biases in the senses that are combined for both the hand and the target, but that there are also errors in the transformation of information.

Information about WHERE the target is

When making a movement plan, we need to go from observed information towards a motor command. This process is described in many ways. One of the possibilities is that what we see is transformed into proprioceptive coordinates. In a model by Flanders et al.[42] a reach plan in proprioceptive coordinates is proposed, because we need our motor command in proprioceptive coordinates. Another possibility is that information about the location of the hand is first transformed into visual coordinates, and after that this reach plan is transformed into motor commands. Evidence for this model is found for example in a study by Pouget et al.[41]. They found a significant effect of eye position on the direction of reaching movements aimed toward a proprioceptive target. Also Blangero et al.[112] showed that when moving with the unseen hand towards a proprioceptive target, non-informative gaze influences the endpoints of the movements.

An alternative explanation for gaze to influence movements with the unseen hand towards proprioceptive targets is a reach plan in combined coordinates. It has been argued that transforming sensory signals into a common representation would simplify reach planning[124-127]. Such studies argue for both eye-centred[41,55,128,129] and hand- or body-centred[56,130] planning. One example of these models is that there are always both a visual and a proprioceptive estimate of the target and the hand[46,131]. The amount on which the estimates are taken into account depends on how certain we are of this estimate. We found evidence for this theory in **chapter 5**, where we show that a non-informative finger at a visual target influences the way we move towards it with the unseen finger of the other hand. The results of **chapter 4** are also in line with this theory. We found in **chapter 4** that participants benefit from repeating a position when the targets are displayed on a computer screen and the movements were made on a horizontal table. The benefit of a remembered proprioceptive estimate is larger when the moving hand and the visual target are not in the same plane than when the moving hand and the visual target are in the same plane. We found that repeating a position when moving the unseen finger to the visual target itself did not significantly increase the precision of the movements.

A model that has both a visual and a proprioceptive estimate of the hand and the target[46] can however not explain the differences we find in **chapter 6**. If there are always two estimates of both the target and the hand, we do not expect differences between conditions with the same final end-configuration (when we move with our finger to a dot, or with a dot towards our finger). In **chapter 6** we show that there are differences between tasks in which the same sensory biases are involved, but the order in which they were performed differed. Probably there are systematic errors introduced when information is transformed. We show that these systematic errors are higher when information is transformed between modalities than within the haptic modality.

In **chapter 6** we measured matching errors in different tasks. Previous research suggests that these matching errors are specific to the participant and are stable over time[100,101]. In a set of experiments that were not included in this thesis we found that matching errors were not as reproducible over days as has been suggested in the literature. We found that the difference between the matching errors in the same task when they were measured a few weeks later were larger than the magnitude of the errors itself. When the same tasks were also measured a few months later, it seems that the errors were less similar to the original errors. Although we did not measure this systematically, this might suggest that matching errors are not stable over time, but might involve a more a dynamic process that evolves over time depending on the activities we do everyday. More research is needed to find out whether and how each participants' matching errors develop over time.

Information about HOW to get to the target

A combination of position and vector coding?

The question how the brain codes to go to a target is proposed to be either in terms of vectors or in terms of positions. However recently also a combination of vector and position coding is proposed[64], just as we combine vision and proprioception when determining where a target is[45]. It might be that the brain considers all available information, but weights the information that is most certain more heavily than the information that is less certain. In **chapter 2** we show that we might use force that tells us the direction of movement. In **chapter 3** we show in an indirect way that vector coding and position coding might be combined. We found that not all the errors in the initial movement direction that were made when moving towards a haptically defined target could be explained by the errors that are made in the perception of direction towards the same targets. If you assume that vector and position information is combined to make a movement plan, this would explain the results: the part of the errors that could not be explained by a misperception of direction could be explained by the fact that not only direction information is used for our movement plan, but also position information.

Evidence for a combination of position coding and vector coding comes from the study of Hudson and Landy[64]. They show that participants optimize their movements in a different way when either positions or vectors were repeated for movements on a table, when they saw the targets on a vertical screen. Movements were optimized in both the direction of the movement as well as orthogonal to the movement direction when the same endpoint was repeated. Movements were more precise in the direction orthogonal to the movement direction than in the movement direction when a vector was repeated. We replicated this study in **chapter 4** but found that for movements with the same movement direction, movement were always more variable in the direction of the movement. We only found that participants were more precise when repeating a position, but this could also be explained by the proprioceptive estimate of the target being more certain when the targets are not presented in the same plane as the movements are made.

Future research?

Position coding has been suggested in the literature many times[53-59]. However vector coding has been in the literature for a longer time[47,49]. Our studies show that position and vector coding might both be important for movement planning (**chapter 3** and **4**). Especially when learning a new visuo-motor mapping, participants became more precise when they repeated a position (**chapter 4**). We find differences in the extend to which the initial movement direction correlated with the perceived direction for different setups (**chapter 3**). If participants repeated a vector or a position instead of a random order of movements, a different setup also caused different benefits. More research must be done to investigate how vector and position coding might be combined to form a movement plan, and also when one type of coding might be more beneficial than the other type of coding.

What can we do with this information? An example where the vector-coding hypothesis is used is in the control of a prosthetic arm[132]. A sensor records signals from the brain that is converted to a signal to control a prosthetic arm or a cursor on a computer screen. This signal is tuned for a directional map, so that specific brain parts correspond to specific directions. As is found in **chapter 3** and **4**, position coding might be more important for arm movements than vector coding. It has been shown before when combining both visual and proprioceptive information[133] and optimizing the place of the neural sensor[134] improves the performance of a prosthetic arm. When we know how a movement is coded in the brain, it might be better to use that information to control a prosthetic arm. For example what happens when instead of electrodes that correspond to certain directions, they correspond to positions, or an optimal combination of position and direction.

Conclusions

In this thesis

This thesis is about movements and how they are coded. I show that the amount of control and tactile information does not influence the way we move but that we might use information about the third dimension and information about the direction of movement (**chapter 2**). That we move the way we do might involve both vector and position coding (**chapter 3**), however position coding seems to be a more important component, at least when acting in a unusual visuo-motor mapping (**chapter 4**). I show that to move towards a target, we use both a visual and a proprioceptive estimate of both the hand and the target to determine their position (**chapter 5**). To get these two estimates, information is transformed, which induces systematic errors. (**chapter 6**). These errors are larger for transformations between modalities than for transformations within the proprioceptive modality.

This thesis suggest that models of motor control should be adjusted to consider both position and vector information. It also suggests that there are not only biases in the senses that are combined for both the hand and the target, but that there are also errors in the transformation of information.

Why do we move the way we do?

Making a movement plan might involve higher order parameters, such as separate estimates for the target and the hand, but also position and vector information. In some circumstances we are not able to use certain information, for example when we have no vision of the moving arm. Different circumstances, for example how long ago we have seen the arm, alters the certainty of the information, which alters our movements. Repeating information sources and changing the order of a task also changed how we moved to a certain position. Lastly, the presence or absence of information available during a movement also change the movements.

In the future... can we reconstruct a human brain?

Unfortunately the brain is still a black box to us, for now… When we are able to understand the whole input/output relation of the brain, we might be able to reconstruct a human brain. We are already able to record signals from the brain to control a robotic arm! However the movements of this arm are not nearly as fine-tuned as human movements. In this thesis the planning of goal-directed movements was investigated, by decoding actions we found evidence for different kind of parameters in which the brain may code movements. When we know what parameters are used to code a movement we may be able to improve those movements.