1

General introduction

1

1

Computers that act like humans have been in science fiction movies for decades. How great (but also very dangerous) would it be if we could recreate a human being? Record signals from our brains and read them into the computer, as simple as that. This may sound very plausible, and is demonstrated in movies very realistically, however we are not quite as far yet. We can nowadays record signals from the brain in various ways, through fMRI, EEG, MEG, and we are just starting to figure out which part of the brain is active during different kinds of activities. However to make sense of the signals of the brain – to go from the recorded signals, to reconstruction of the brain - we have to know what these signals represent. We need to decode the brain.

Where do we start to decode the brain? There are many things we do in daily life, such as perceive, think, feel, speak, walk, listen, eat, and so on. The most important thing we need our brains for, as argued by Daniel Wolpert[1], are movements. He argues that the largest purpose for living beings to have brains are movements. A nice example for this is the Sea squirt, once it does not have to move anymore it release the brain into the water. If movements are the most important purpose for our brain, it is a logical step to start figuring out how the brain codes them.

This thesis is about movements and how they are coded.

What kind of movements?

There are many ways we can investigate movements and how they are coded. We can look at specific brain structures; we can record signals and evaluate how these signals change with different activities. However to know how the brain processes these activities we need to know how we respond to different types of input. That is why I looked at how humans behave, how they move under different types of circumstances.

There are different types of movements; one type of movements are reflexes. These movements are very quick, and therefore the motor commands are thought to be generated in the spinal cord, and not through the brain (only afterwards). The movements I look at in this thesis are movements that are voluntary, they are assumed to have a movement plan prepared in the brain before the movement is executed. The movements that are studied in this thesis are voluntary movements toward a specific place: goal-directed movements. Because most movements towards specific objects we make in daily life are hand movements, we examined these movements.

Why do we move the way we do?

Humans are very similar on the one hand, we all stand upright, have arms and legs, etc. At the same time we are very different: the muscles of for example a swim-

mer are very different than the muscles of a speed skater. Specifically looking at arms, different people have different lengths of arms, different strengths of the muscles, etc. Despite all these differences most humans move in similar ways from a start position to a target[2]: approximately straight, but a little bit curved. This similarity is a surprising finding, especially when you take into account that there are infinite possibilities to make a movement, also known as the degrees of freedom problem[3]. The question is: Why do we move the way we do? There are two possibilities: the trajectories are like this because we intended it to be this way, because it is in some way optimal. On the other hand it might be that we intended it otherwise, but constraints like biomechanics, differences in reference frames or perceptual misjudgments cause the trajectory to deviate from our plan. In this paragraph I will discuss these possibilities.

We move the way we do because we intend it to be this way
Do we optimize something?

The answer to the question why we move the way we do might be that it is in some way the optimal way to do it. We might have a purpose to make a small curve in our trajectory. This purpose could be an optimization principle. We might move in a certain way because that is the trajectory that results in the least energy[4,5], effort[6,7], torque change[8,9], jerk[10,11] or joint rotation[12]. However, studies showed that energy consumption and torque change were not being optimized in fast planar arm movements[13]. The entire range of movement trajectories in human behavior could not be explained by optimizing models[14.] So it might be that we optimize something, but it might not be the only explanation.

We move the way we do because other factors cause differences in the way we intended to move
Are there mechanical constraints?

One of the reasons that movements are executed differently than that they are planned might be related to the biomechanics of the arm[15-17]. Boessenkool et al.[15] compared fast movements of the left and right hand. They found that movements of the left hand are the mirror image of movements of the right hand. In this case it is likely that biomechanics played a role, because the anatomy of the hand is also mirrored for the right and the left arm. The influence of biomechanical factors is supported by the fact that trajectories in a certain part of space show different curvature than in other parts of space[18,19]. Biomechanical constraints might be particularly important when moving fast, but biomechanical constraints cannot explain all curvature. For movements that have the same start and endpoint there are differences in curvature found, for instance when moving in opposite direction[20]. It has also been

shown that participants can move more straight if they are asked to do so[16,21,22]. From this we can conclude that it is clear that biomechanics are a major constraint on our movement behavior, but not the only reason why we move the way we do.

Are there different coordinate frames?

Another reason that movements might be executed differently than planned might be that movements are planned in terms of positions or in terms of joint angles. Humans can plan their movements in different coordinate frames: frames relative to the workspace or frames relative to joint space. There is a nonlinear relation between positions in workspace and joint space[2,23]. If movements are planned to be straight in joint space, they will be curved in the workspace[24-28]. However, movements may also be planned in the workspace rather than in joint space[2,10,25,29-32], or in a combination of the two[33,34]. So again, one theory cannot explain the whole range of experiments.

Is there a perceptual misperception?

A last reason that humans execute movements in a different way than they plan are planned is because of a misperception. The reason that movement trajectories are actually curved, might be that there is a distortion of visual space[19,35,36]. Wolpert et al.[36] showed that humans prefer a movement to be visually straight, even though the actual movement they made was curved. It might also be that not visual space is distorted, but only the direction of the target is distorted. Many studies suggest that a misjudgment of direction could cause movement trajectories to be the way they are[37-40]. That direction is misjudged might suggest that this is also one of the parameters that we use to plan a movement. What other parameters might be involved?

Information sources required for movement planning

That we do not know the full input/output relation of the brain suggests that the brain must have a smart design. This is obvious if we look at how robots are controlled; their movements are not nearly as perfect as human movements. We believe that the brain codes movements in simple higher order parameters. This higher order information can be divided in two parts that are required to make a movement plan; the information about where the target is, and the information about how to go to the target.

Information about WHERE the target is.

There are several ways our brain can code where a target is in space. We can code the coordinates of a target relative to our eyes (visual)[41], or relative to our body (proprioceptive)[42] (for example shoulder or hand). These different types of coding

are called reference frames. Depending on what frame of reference we want to make our final reach plan, we need to combine information in a different way. However, we cannot combine different kinds of information. This problem can be solved in different ways; we can either transform one kind of information to another kind of information, so we are able to combine the two. It might also be that the information is always present, but the certainty of the information differs. In the next section I illustrate these differences in three simplified examples.

Different ways to combine target and hand information

In diagram A and B of figure 1.1 the final reach plan is coded in a visual or a proprioceptive reference frame, depending on the coordinates in which we need our reach plan. It has been proposed that we make a reach plan in proprioceptive coordinates[42], but also reach plans in visual coordinates have been proposed[41]. We transform one estimate to other coordinates, and we can then compare them to each other to calculate the relative distance (if the movement is coded as a vector, or transform position information in the required coordinates if the movement is coded as a position, whether position or vector coding is used is described in the next section). For example for diagram A: we know the coordinates of the hand in a proprioceptive frame of reference, so we know the posture of our arm, and therefore the coordinates of the hand relative to our body. We know the coordinates of our head on our body and the coordinates and the direction of our eyes in our head, so we can – with all these steps – calculate the coordinates of the hand relative to our eyes. When we know both the target's and the hand's position in visual coordinates, we can combine them to calculate the relative distance, required for a movement.

Diagram C of figure 1.1 needs extra reasoning: this diagram assumes that we always have the target and the hand in visual and proprioceptive coordinates, so we can combine them in an optimal way. Suppose that you have your mobile phone in your left hand, and want to touch the number 7 on it with your right hand. To
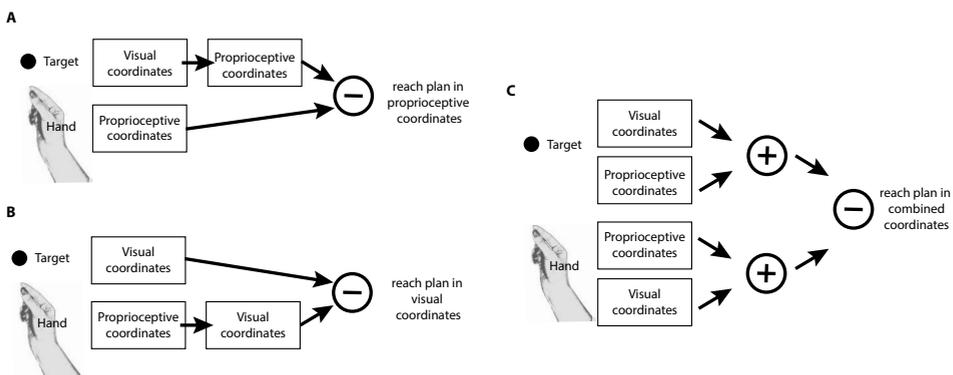

Figure 1.1

make a movement towards the number 7 with your right hand you have to know where the right hand is in space. You can feel it because you know how your posture is in space[43]. If you see the arm you know where it is in visual coordinates, or when you saw your arm, you might have a memory of it's visual coordinates. How do you know where the number 7 is in space? You can see the number 7, so you know where the target is in visual coordinates. How do you know where it is in proprioceptive coordinates? You have a memory of where the hand was before, or maybe use the coordinates of the other hand that is holding the phone. Previous research showed that you can combine visual and proprioceptive coordinates in an optimal way to have a more precise estimate of where a target is[44,45]. In diagram C, it is assumed we do this for both the target and the hand, this diagram is previously shown to accurately describe human behavior[46].

Information about HOW to go to the target.

When we have an accurate measure of where we are and where we need to go, we also need a reach plan how to get there. There are two theories in the literature on how the brain makes a reach plan to go from a start to a target position: vector coding and position coding.

Vector coded reach plans have a lot of support in the literature[30,42,47-52]. Convincing evidence for vector coding is the existence of the population vector[49]. The vector coding hypothesis describes that every neuron has a preferred direction. When we move in a certain direction, neurons in the primary motor cortex with that specific preferred direction fire the most. Combining the firing rates of all neurons reconstructs a population vector; this vector accurately describes the direction of the movement. Other evidence for vector coding is that the direction or the length of a movement is a parameter we use in movement planning[30,38,47].

Recently, the existence of position coded reach plans gained more evidence[53-59]. In a study by Graziano et al.[54] the primary motor cortex and premotor cortex of a monkey were stimulated for a longer period of time; the time it usually takes to make a reaching movement. Stimulation of a particular site of the cortex always resulted in arm movements towards the same end position, regardless of the direction and the start position of the arm. This suggests that there might be a map of the workspace that codes position.

Why does it have to be either vector or position coding? It could also be a combination of the two types of coding[60-63]. Scheidt and Ghez[62], showed that learning movements focused on the movement trajectory only showed little transfer when a movement was made towards a specific position. This suggests that participants may use different types of coding for the different types of movements. Another study showed that only a small part of errors in movements could be explained

1

by errors made by perceiving the length of the movement (vector coding theory). That only a part of the errors could be explained by misperceiving length might be because vector coding is combined with position coding[60]. Recently was found that participants can learn the same movement when repeating the same position as well as repeating the same vector, which might also suggest a combination of vector and position coding[64].

How we investigate these movements?

Redundancy in ways to move

Humans move in approximately the same way despite differences between them. Moreover, there is a large number of degrees of freedom in the arm, so there is a redundancy in the way we can make an arm movement. That humans make movements in a similar way, despite all their differences and despite all the different possible solutions we can make a movement, may provide information on how a movement is coded in the brain.

Curvature

That humans like to move in a visually straight line[19] might suggest that they plan a straight line towards the target. However, when we look at trajectories of human movements: we see that they are curved even if the movements are very slow. This curvature has been explained in different ways. The curvature in movement trajectories was used to study trajectories of goal-directed movements in **chapter 2** and **3**. In **chapter 2** we removed information when participants moved towards a target to see if this caused curved trajectories. In **chapter 3** we compared movements with perceptual estimates to see if they were related.

Redundancy of information

When we move with our visible hand towards an object that we have in our other hand we have redundancy of information about the hand and the target, since we have both proprioceptive and visual information of the hand. It is known that when we have two sources of information, we are able to optimally combine these two sources and perform more accurately than when we have either of the sources alone[44,45]. When we remove available information when people have to perform a task, they start making errors. In this thesis we used the setup where people move toward visual targets, without seeing their hand. This setup causes large visuo-proprioceptive matching errors. The way people make these errors when there are different sources of information available may reveal which sources of information and to which extent people use these sources of information.

In **chapter 4, 5** and **6** we use this setup to study human movements. In **chapter**

4 the same kind of movements with different information sources were repeated, to see if participants learn from these different sources of information. In **chapter 5** we added an extra source of proprioceptive information to see if participants used this and in **chapter 6** participants performed tasks with different hands and in a different order, so we could reveal the origin of visuo-proprioceptive errors.

In this thesis I contribute to the question how the human brain codes movements. When we know why humans move the way they do, we might know how movements are coded in the brain. I studied the planning of goal-directed movements; by decoding actions we might discover the fundamental input/output relation of the brain.

1