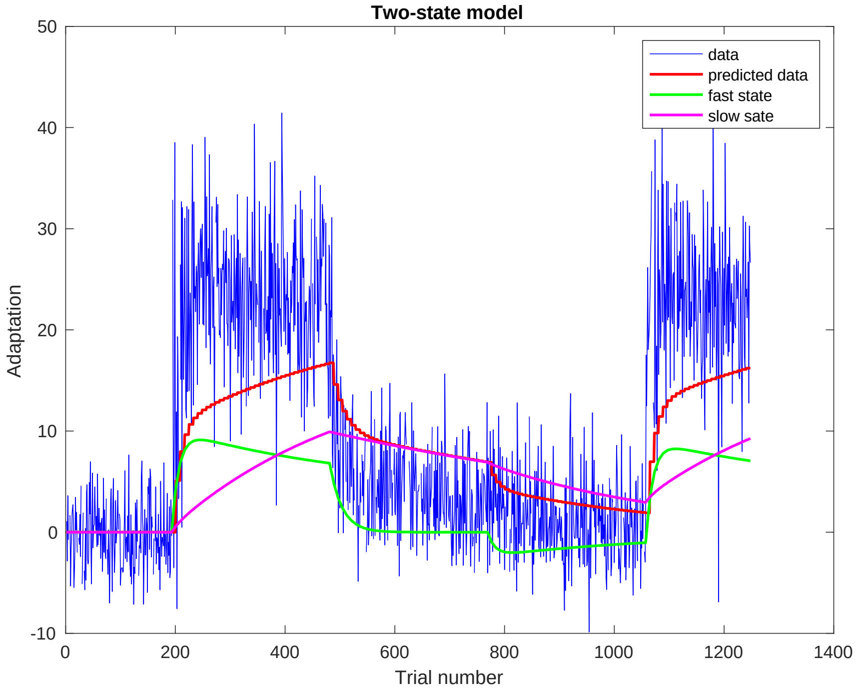
ID: 2227572

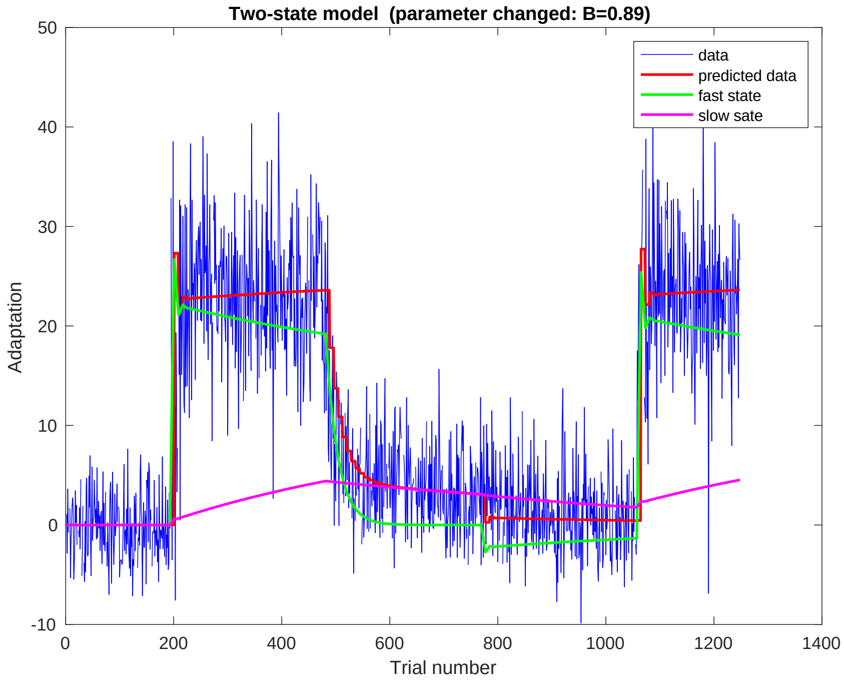
Lab 7 (Cerebellum)

3)



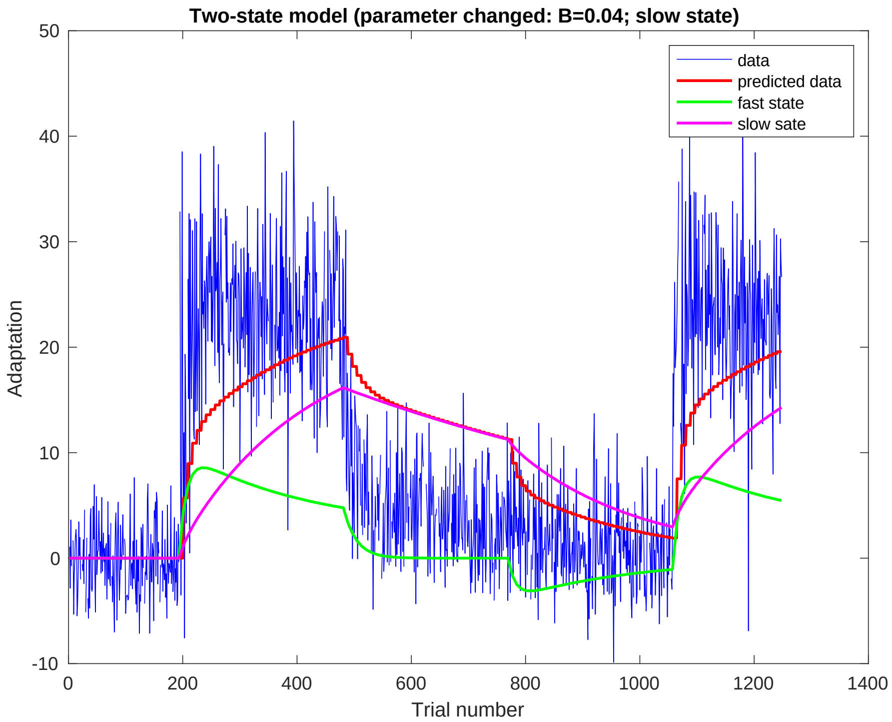
The figure shows the two state model with the raw data plotted against the predicted data. The values were kept the same as the original values (M.A = [0.7 0.99] M.B = [0.15 0.02]). The fast state (green) follows a rapid increase whereas the slow state (magenta) shows a gradual, slower increase indicating slower motor learning.

4) ***Two state model with B for the fast state changed to 0.89***



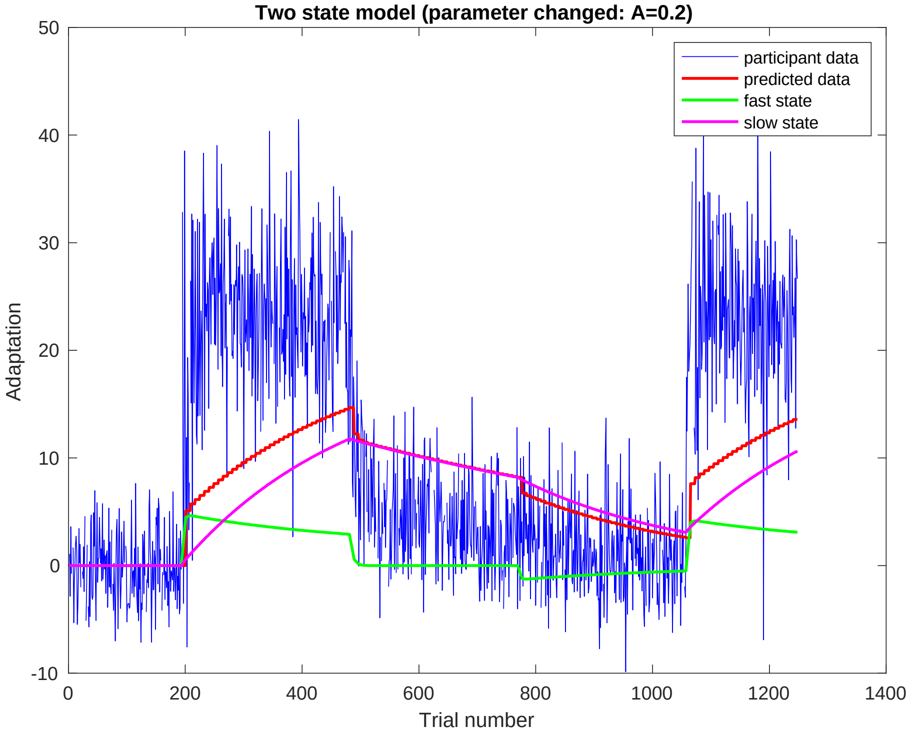
B is the learning rate. A is the retention parameter meaning the degree to which people can remember some previously practiced material (or skill) after an elapsed period. Only the B parameter was changed. Changing the learning rate for the fast state increased its amplitude and made it fit the participant data (blue line) better. This means that there was rapid learning of the task during the adaptation stage. As it can be observed, the fast state and predicted data follow the same oscillations and peak very close to each other further indicating a good fit. The slow state was significantly decreased.

Two state model with B for slow state model changed to 0.04



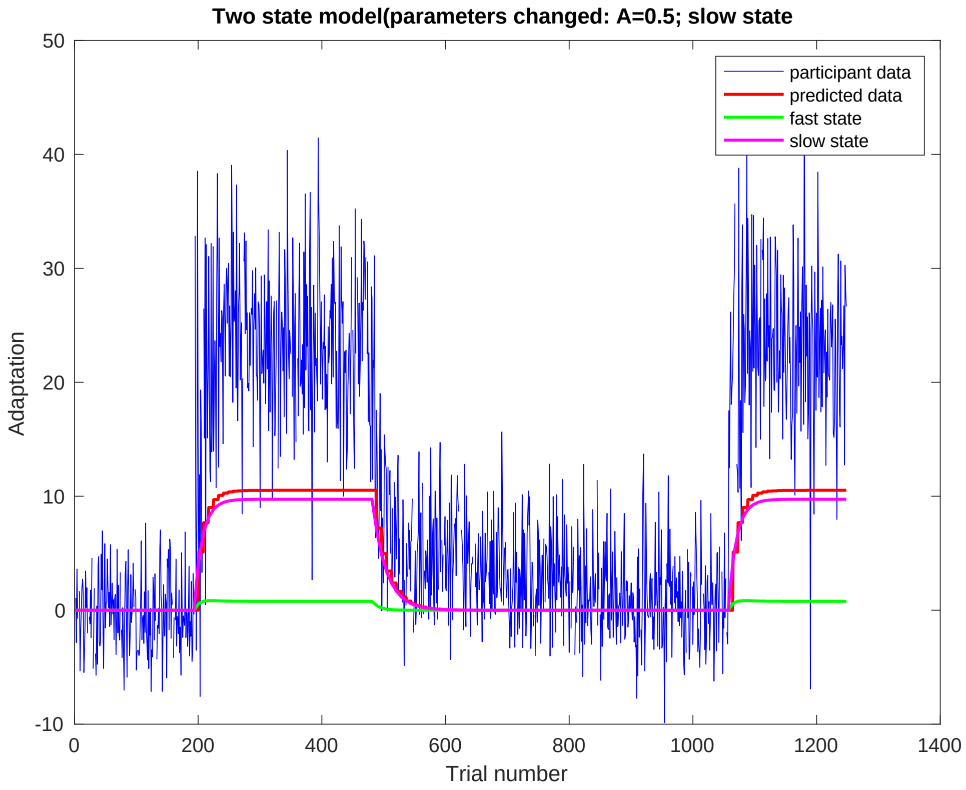
Conversely, when B for the slow state increased, the fast state decreased. This time as well, the predicted data increases and aligns with the slow state. This shows that it adapts to the model that better predicts the raw/original data.

Two state model with A for fast state model changed to 0.2



When A is decreased for the fast state model the learning goes down since the participants are not able to keep the learned information in memory making their performance worse. Similar results were observed when A was set to a low value for the slow state as well:

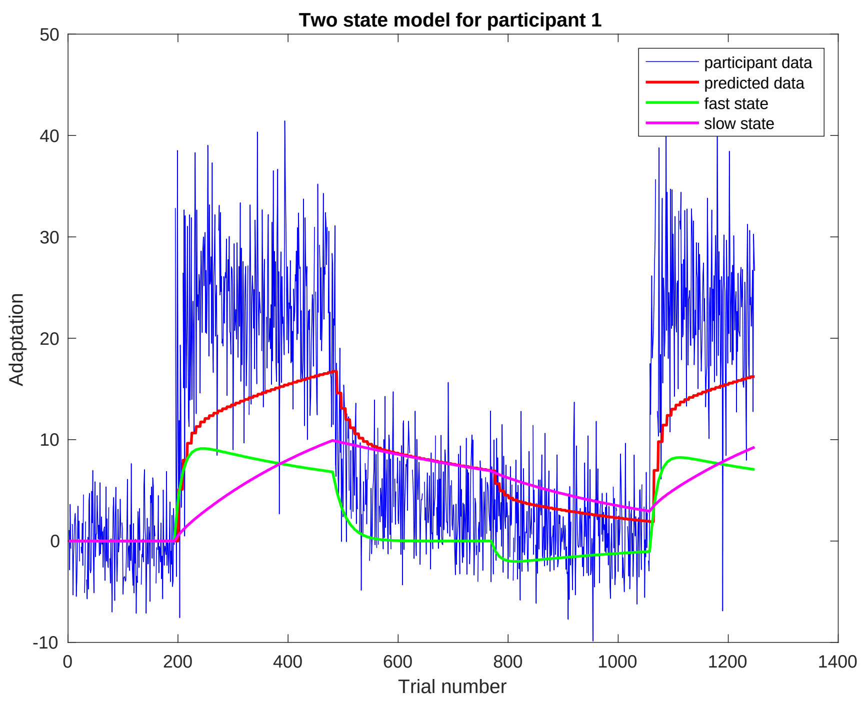
Two state model with A for slow state model changed to 0.5



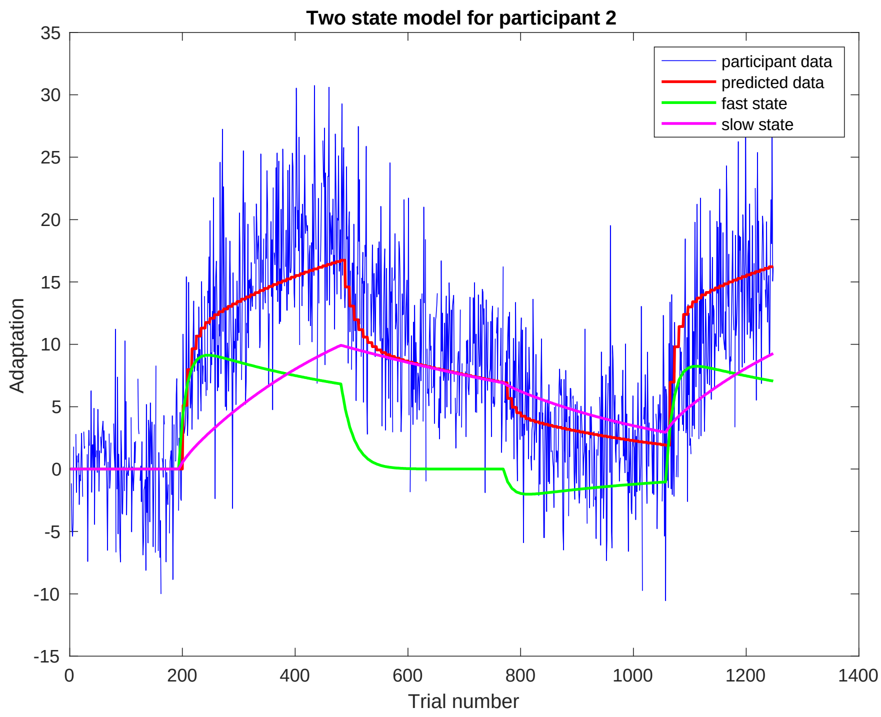
Compared to the previous figure where A for the slow state was unchanged, the slow state has decreased. Now it resembles the modelling of a fast state since there is a rapid initial increase that stabilizes and then rapidly falls again.

5) *Two state model for each participant:*

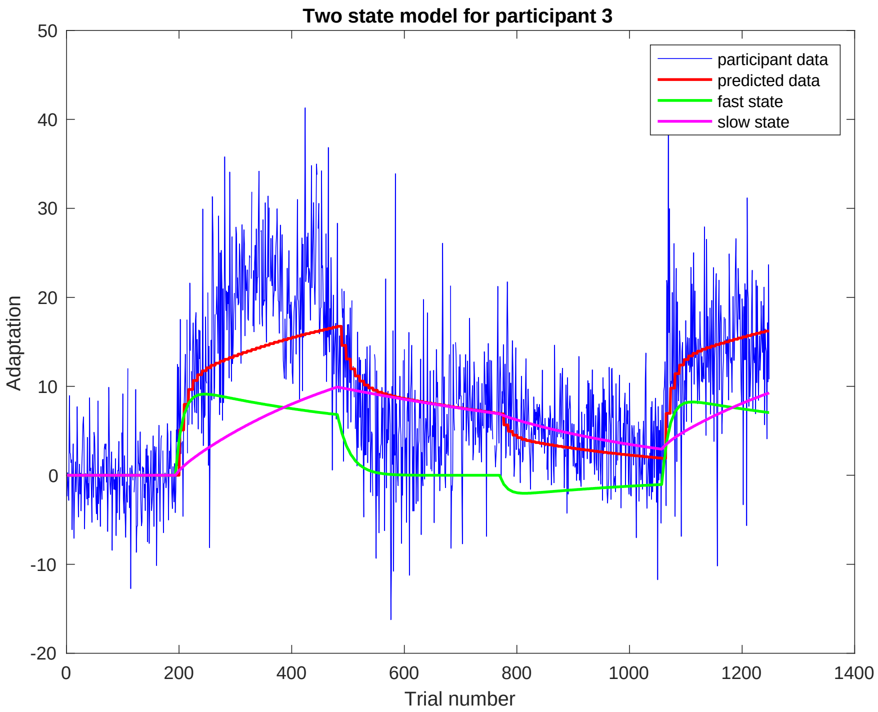
Participant 1



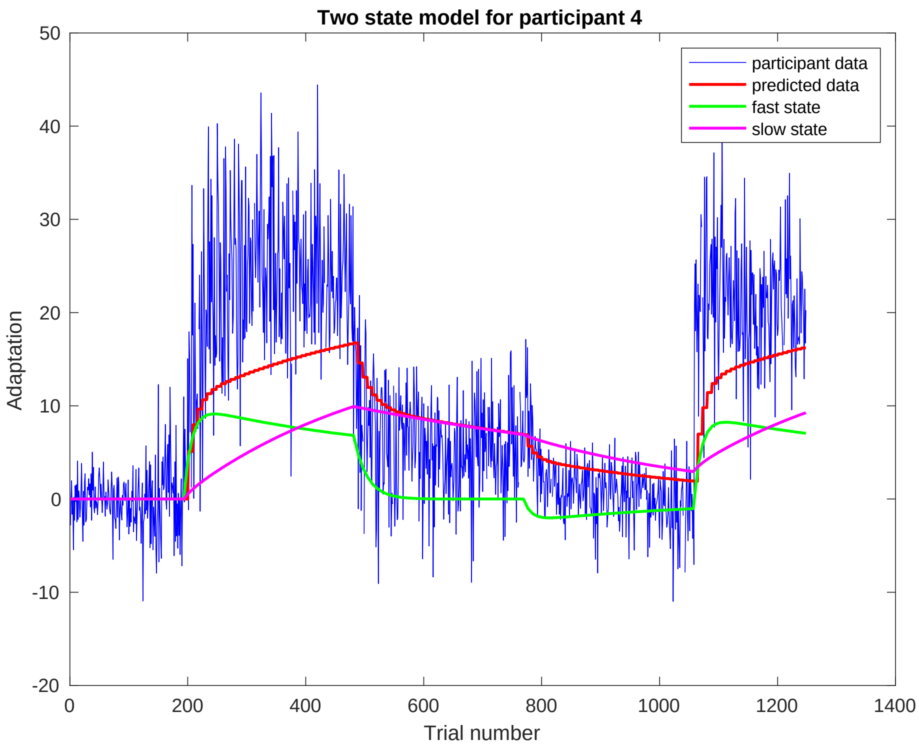
Participant 2



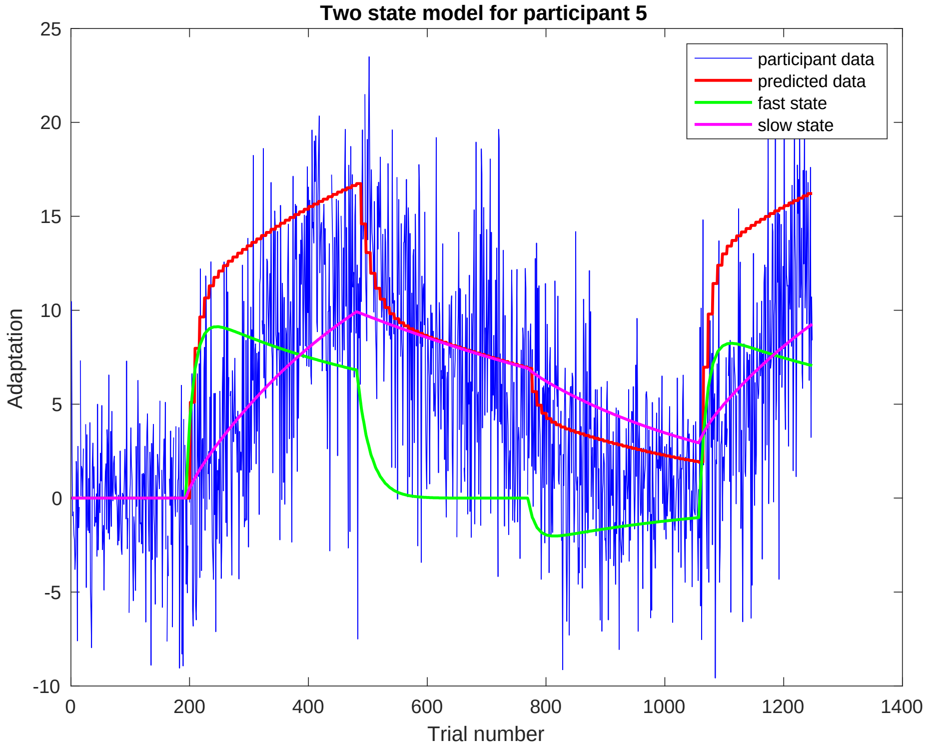
Participant 3



Participant 4

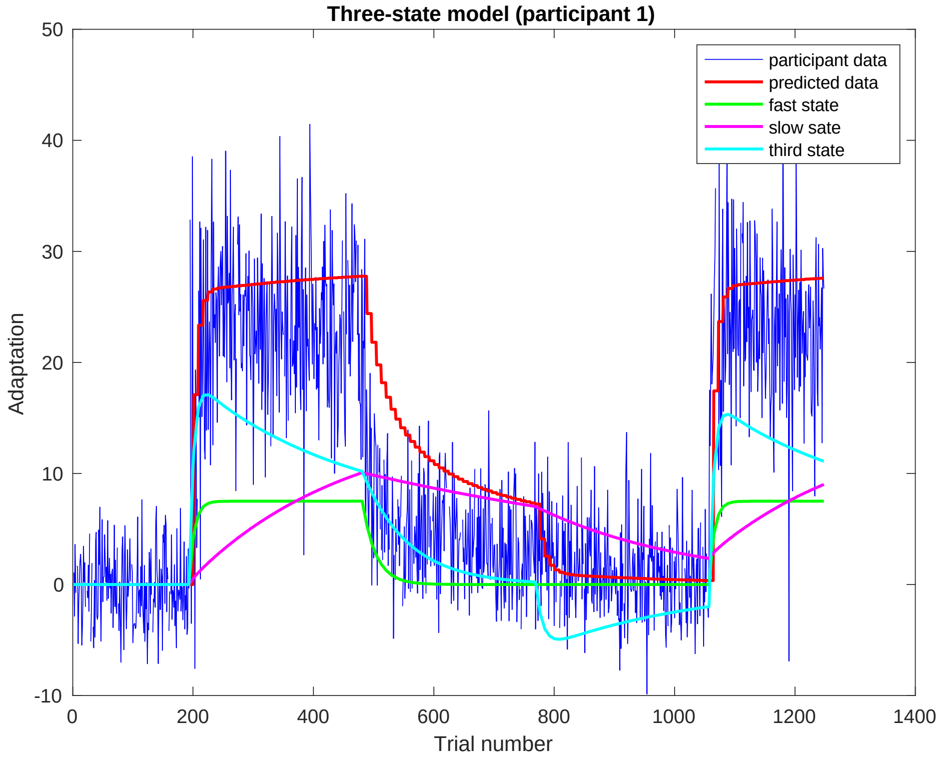


Participant 5



The above figures show the plots for the two models for each participant. As it can be seen from the plots, overall, the models appear to fit the data well with the fast state showing a faster more rapid increase and the slow state showing a slower but more steady increase in learning. The slow state however seems to fit the data less than the fast model. The predicted data fits the original data well especially for participants 2 and 5. As it can be observed by comparing the figures, the models adjust to the data of each participant even though the oscillations of the raw data vary a lot in shape and amplitude across the participants. That shows that the models have good generalizability.

6 and 7) ***Model comparison and three state model***



A third model was added with A=0.9 and B=04. It is expected that as a third state is added the model will perform better than the two state or single state one. From the figure it is observed that the third state model shows a rapid increase mimicking the raw data and compared to the other two models, it more closely follows the data.

To compare the results of the models and determine which one fits the data better, the MATLAB 'goodnessOfFit' function was used which compares two or more models. It does so by measuring the error of the models and has three available cost functions to choose from; mean squared error (MSE), normalized root mean squared error (NMRSE) and normalized mean squared error (NMSE). In the present case the NRMSE was used. The NMSE outputs a value for each model indicating the error; the closer the value is to 0 the better the model fits the data. A value of 1 or above means that the model is no better at fitting the data than a straight line, meaning that it is as good as a random prediction. The results for all three models are as follows:

NMSE single state	NMSE two state	NMSE third state
0.366	0.512	0.330

As it can be observed, when comparing the first two models the single state one performs better than the two state one. However, when a third state is added the model fit is improved and the third state fits the participant data better than the single state one as its error is closer to zero (0.330). The results indicate that adding a slow state to a single state model might make the model fit the data less. This is because in this case the participants did not exhibit slow learning. Rather, during the adaptation stage they showed rapid motor learning making a single state model more accurate than one that has a slow state. Adding a third state improved the model fit since it created more balance between the fast and slow state.

Lab 8 (Tactile Neurons)

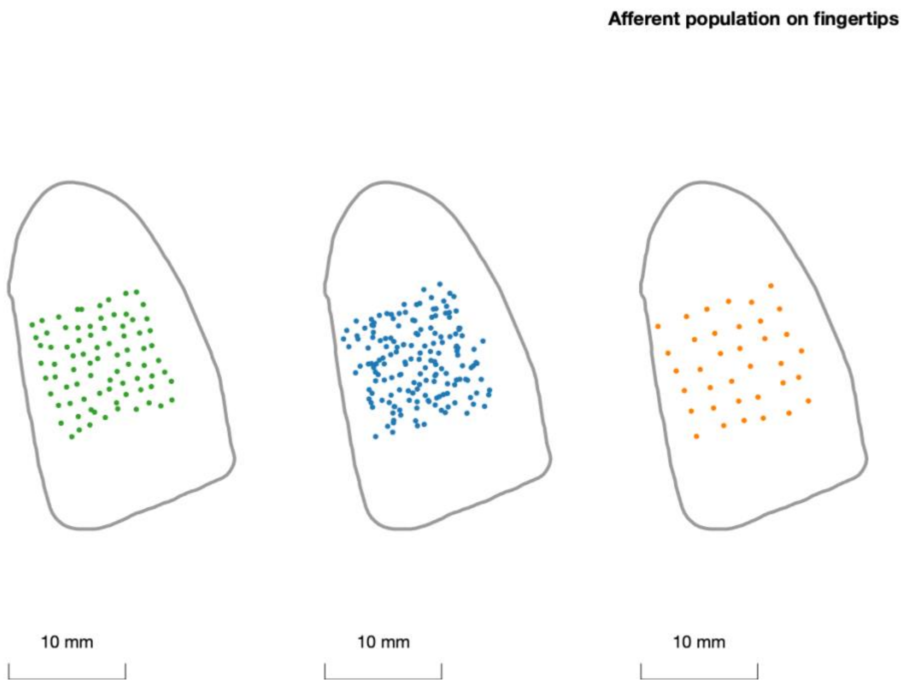
Intro/Research Question (a)

The property of the stimulus that was chosen for manipulation was the shape. More specifically, two different letters were chosen O and I to observe the differences in firing rate when it comes to spatial characteristics of objects. These two letters were chosen as they differ significantly in shape, one being a circle and the other a straight line. They also differ in complexity as O has more edges.

It is expected that since SA1s are slowly adapting afferents, they will exhibit an ongoing activation while the stimulus is present. Conversely, RAs and PCs as rapidly adapting receptors, they will respond fast during stimulus onset and then again after the stimulus is gone and will not respond continuously. As discussed in the lecture, that happens because they do not respond when the stimulus is constant. Since SA1s and RAs are known to respond to coarse features like edges, it is expected that they will have a stronger response and a higher spiking to letter O as it is a more complex geometrical shape with more edges that letter I (Saal et al., 2017). SA1s especially have been found to be important in edge detection and are expected to be more activated when letter O is present even though current research indicates that all three afferents contribute to the detection of the stimulus properties (Saal & Bensmaia, 2014).

Methods (b)

Figure 1



The above plot represents the afferent population in the virtual fingertips. Compared to the afferent population of human participants, virtual afferents lose some of the elements and complexity. That happens because during modelling it was assumed that the skin is a continuous mass and that all the skin elements have the same properties. As mentioned in the lecture, that is not the case with real skin and more accurate modelling methods, like the Finite Element Modelling (FEM) can better represent the skin mechanics. However, FEM is a more complex approach that requires long computations and for the purposes of the present experiment the continuous mass model will suffice.

The present afferent population model also differs from human afferents in the distribution of the afferents across the skin. In real, human skin, afferents are distributed more randomly across the whole finger and are not perfectly aligned inside a square. To account for that the randn function was used in MATLAB to make the afferents spread more randomly and to 'blur' the edges of the square (figure 1).

Figure 2

Pin location of the letter 'O' on the fingertip

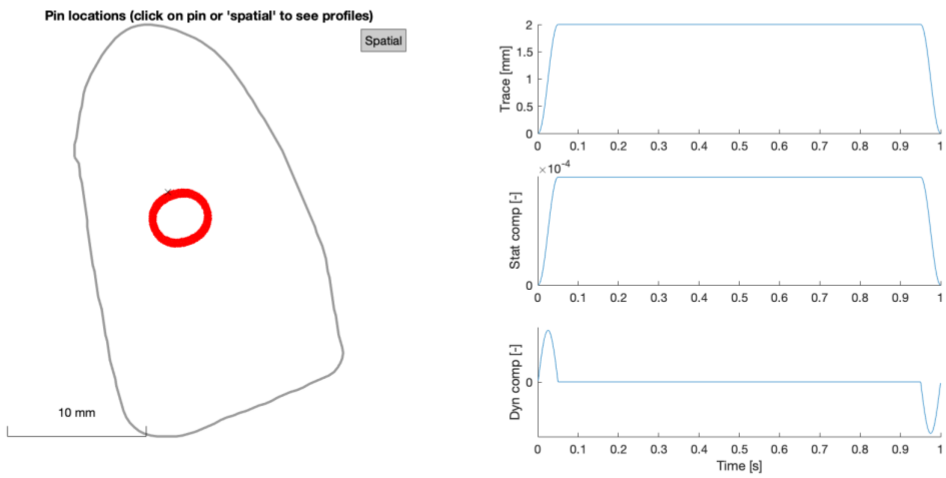
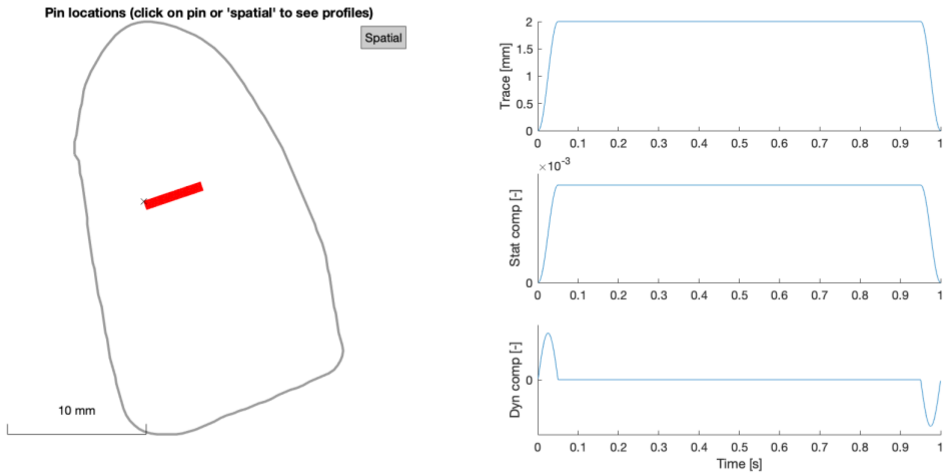


Figure 3

Pin location of the letter 'I' on the fingertip



The above figures show the two stimuli used (letter O and I), plotted on the fingertips. The subplots on the right show the ramp which was modelled using the sine option instead of the linear as it allows for a more smooth and realistic transition. The density of the pin per millimeter was chosen to be 20 which created a more dense and well-defined shape for the letters.

When creating the stimuli, it was taken into account that the present task and results would not be easily generalizable. Thus, inferences about the contribution of the afferents to different types of tasks with different stimuli are difficult to make. That is one of the limitations of computational models as there are specific stimuli and conditions modelled for each simulation. In an experiment with human participants there would be more flexibility since the participants could do more tasks of a different nature. Thus, the generalizability of the results to different tasks would be easier. Moreover, since the results are simulated they must be compared to real participant data.

Results (c)

Figure 4

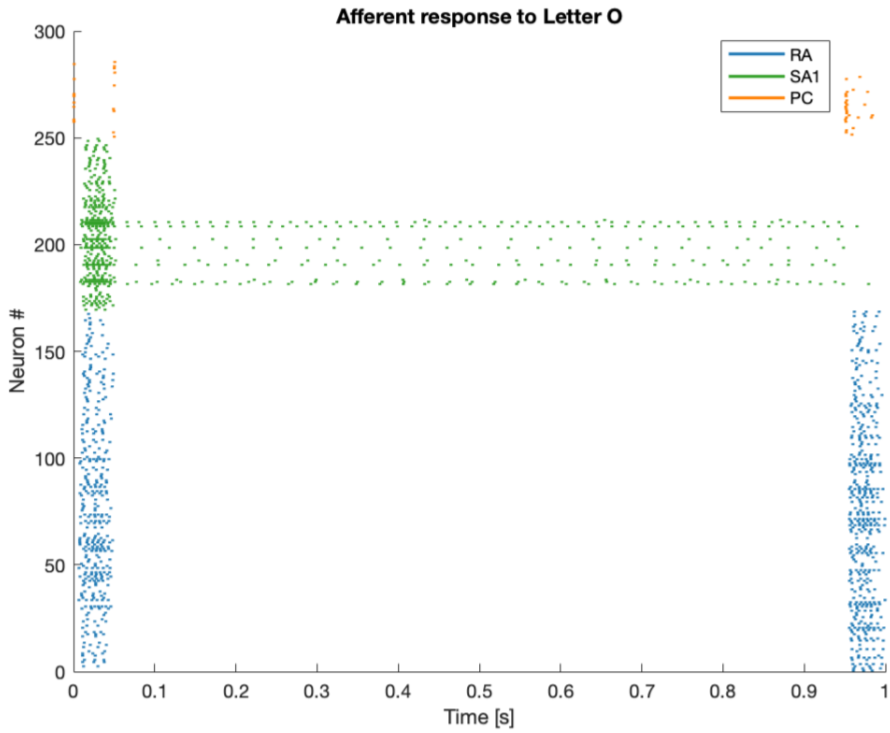
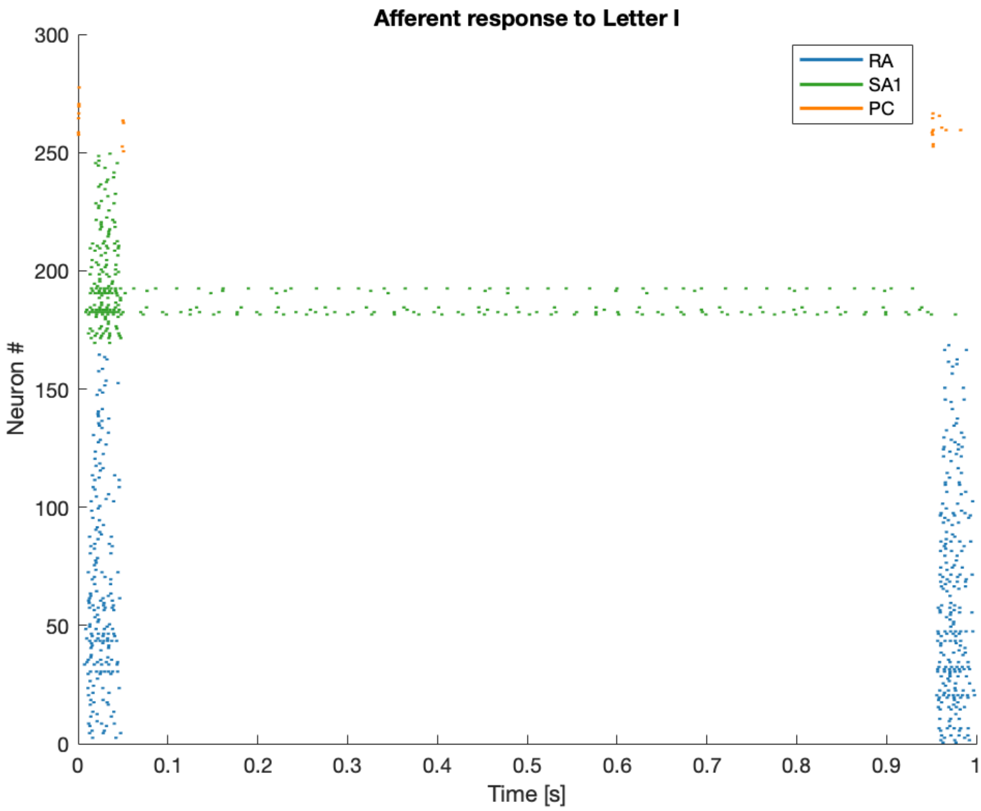


Figure 5



The above raster plots illustrate the firing of the afferents in response to the two letters. The dots represent the spikes of the neurons while the y axis shows the number of neurons and the x axis the time in seconds. As discussed in the introduction, the SA1 is active throughout the whole duration of the stimulus while the RA and PC only respond during stimulus onset and stimulus offset. When comparing the responses for both stimuli it is observed that the RA afferent is more activated during the letter O condition releasing more spikes. The SA1 is also activated more when the letter O is presented providing more evidence to the contribution of SA1 in edge detection. Lastly, the PC afferent also shows a slightly higher response to letter O when compared to letter I.

Figure 6

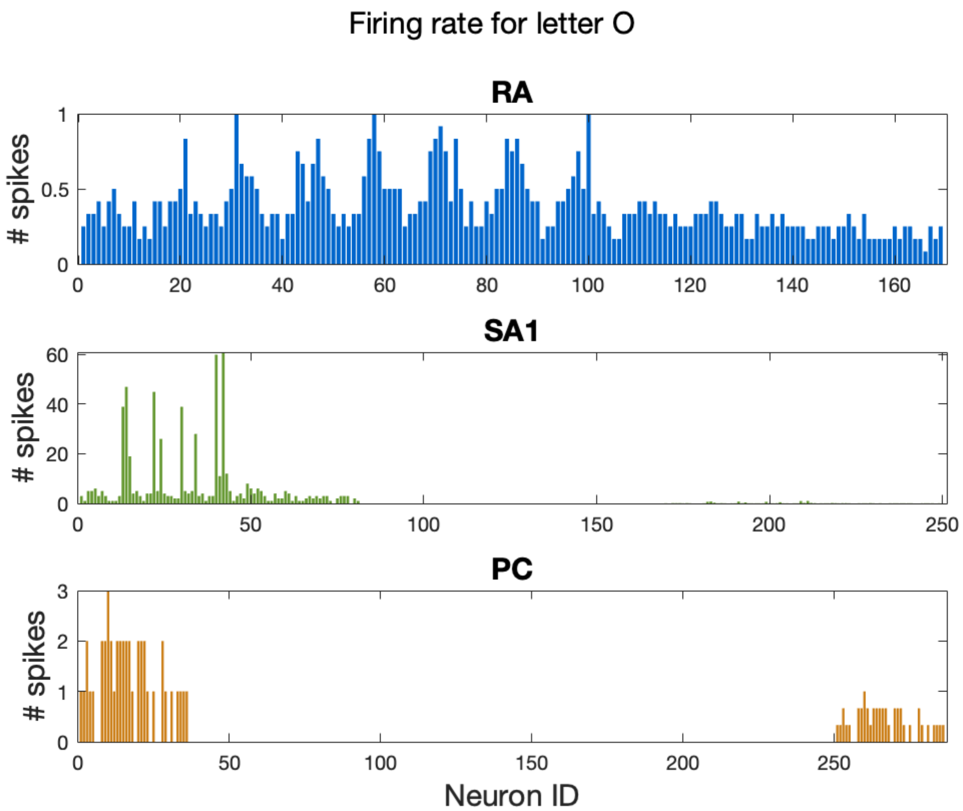
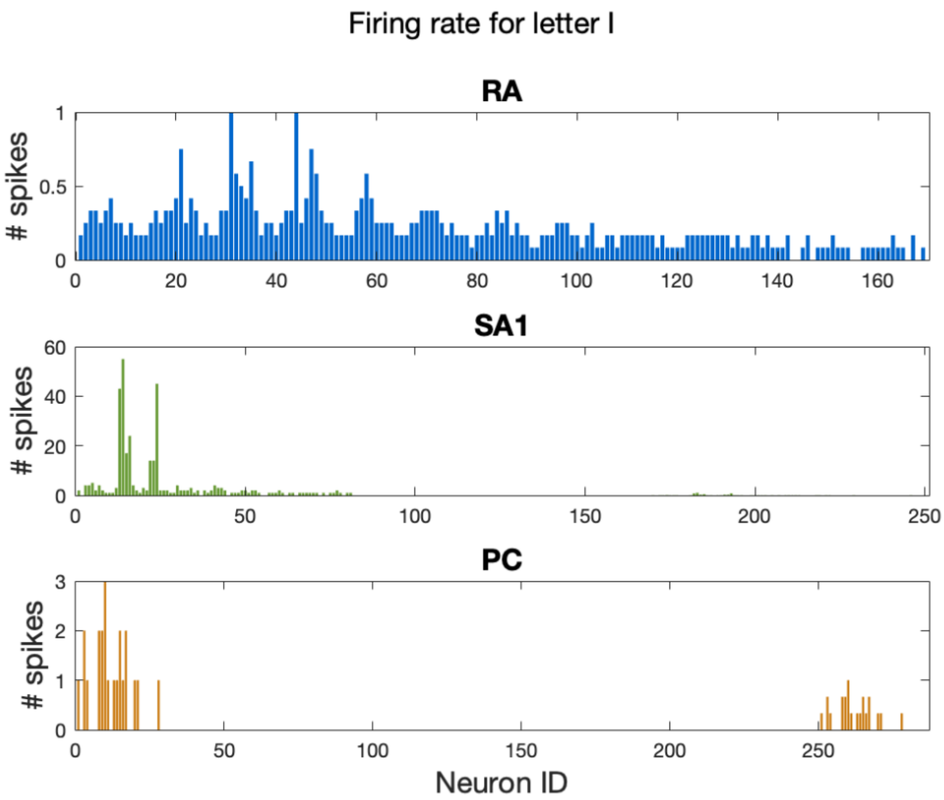


Figure 7



In order to visualize the firing rate in a clearer way box plots for each afferent were also obtained. The y axis shows the spike amplitude while the x axis shows the neurons. Looking at the box plots the firing rate of RA afferents is especially apparent here and is illustrated more clearly than when looking at the raster plots.

Conclusion (d)

Overall, the results show that SA1s exhibit a higher activation when presented with letter O (that has more edges) which indicates that SA1 contribute more to edge detection (Phillips et al., 1988). However, all three afferents respond stronger to letter O which supports the theory of submodality convergence as all three afferents contribute collectively to the detection of the letter shape. Regarding the model used, it managed to successfully replicate the findings of previous studies regarding the role of afferents in the different stimulus properties (in this case shape) which provides more evidence for the usefulness of computational models in the study of the sensory system. More specifically, it provides support for the use of less complex models for examining tactile perception as despite its simplicity it was still able to give accurate results.

References

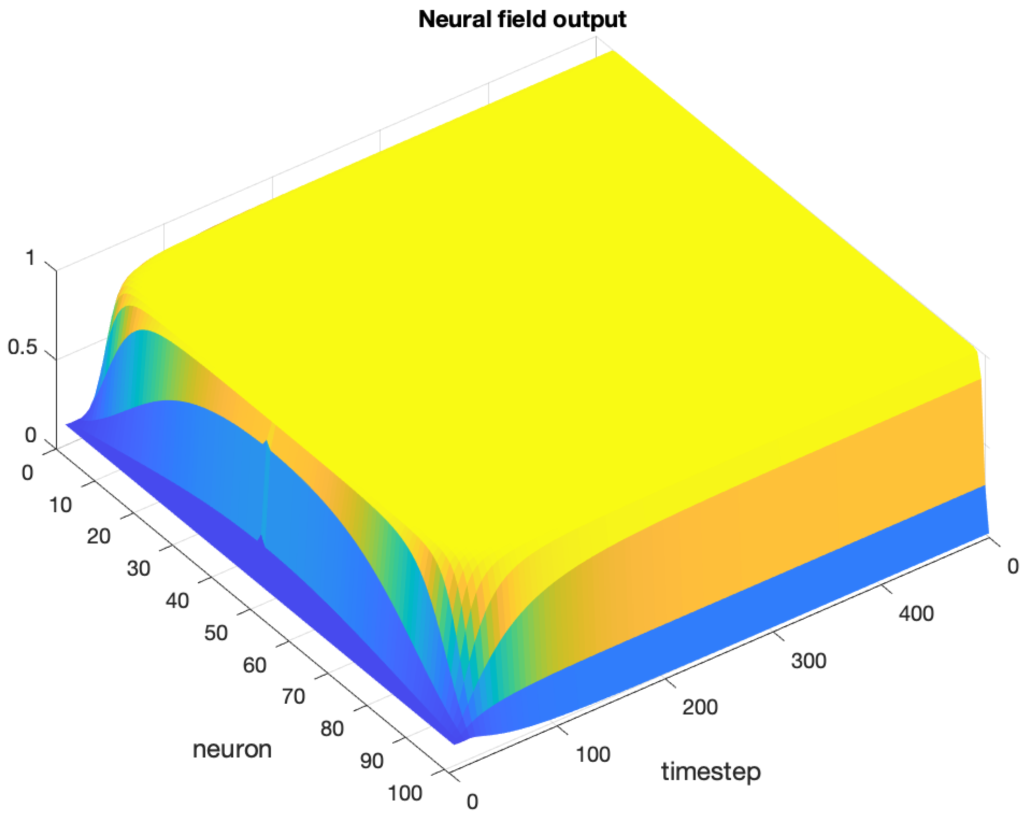
Phillips, J. R., Johnson, K. O., & Hsiao, S. S. (1988). Spatial pattern representation and transformation in monkey somatosensory cortex. *Proceedings of the National Academy of Sciences*, *85*(4), 1317–1321. https://doi.org/10.1073/pnas.85.4.1317

Saal, H. P., & Bensmaia, S. J. (2014). Touch is a team effort: interplay of submodalities in cutaneous sensibility. *Trends in Neurosciences*, *37*(12), 689–697. https://doi.org/10.1016/j.tins.2014.08.012

Saal, H. P., Delhaye, B. P., Rayhaun, B. C., & Bensmaia, S. J. (2017). Simulating tactile signals from the whole hand with millisecond precision. *Proceedings of the National Academy of Sciences*, *114*(28), E5693–E5702. https://doi.org/10.1073/pnas.1704856114

Lab 9 (Neural Field)

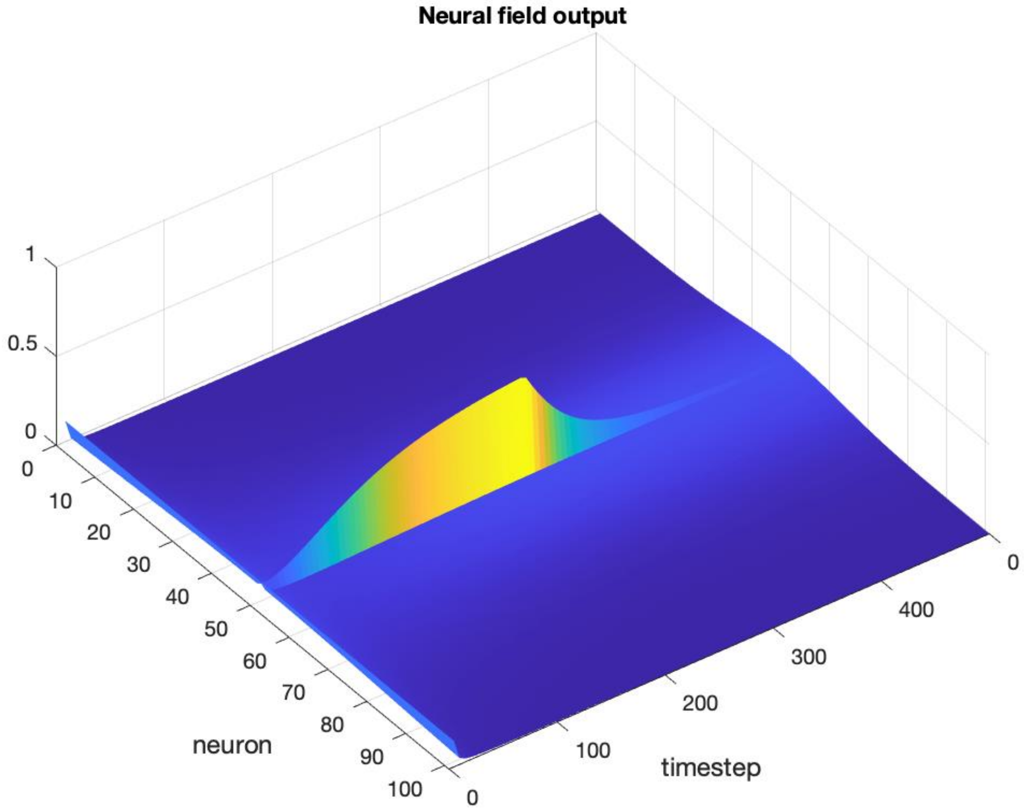
Growing activity plot:



Parameter values chosen: sigma = 1.62, A = 1.3, C = 0.8.

Sigma is the spread of the excitation and when it is a high value more neurons are activated laterally. When it is small the excitation spreads less. A is the strength of excitation and when it is a high value there is more activation. When it is small the activation goes down, and the units are inhibited. Lastly when C (constant inhibition) is bigger the activation goes down and when it is smaller excitation increases. The above figure shows growing activity which means that the whole dynamic filed becomes activated even when the external input is removed. That is evident in the figure as there is overall excitation that spreads out uniformly throughout the whole field and does not decrease after the input is gone. Hence, the sigma is large, and the C is small.

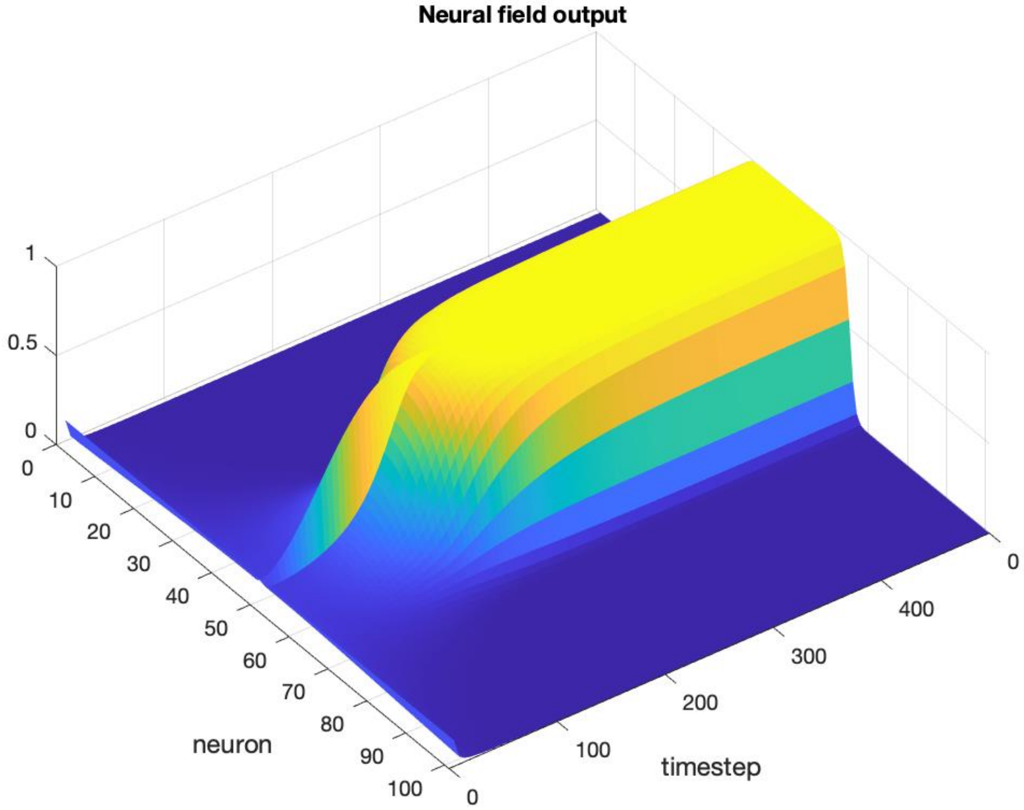
Decaying activity plot:



Parameter values chosen: sigma = 1, A = 1.2, C = 1.2.

Decaying activity occurs when the excitation of the neurons decays after the input is removed. As it can be seen in the figure, neural activation is observed around the 50^{th} neuron that reaches its peak (bright yellow) and then decays close to the 300^{th} timestep after the external input is removed. In this case sigma is reduced meaning the spread is smaller and not many neurons are activated laterally. A and C have the same value to balance out the excitation.

Memory activity plot:



Parameter values chosen: sigma = 0.8, A = 1.2, C = 1.

Memory activity is when the active area in the neural field stays active even when the input is removed. That can be seen here since the activation spreads in the nearby neurons and continues throughout all subsequent timesteps. Compared to the decaying plot form earlier, it does not decay after the stimulus is removed but also does not spread towards the whole neural filed as in the growing figure that indicated very high excitation.

Lab 11 (Vision)

Task 1

Figure 1

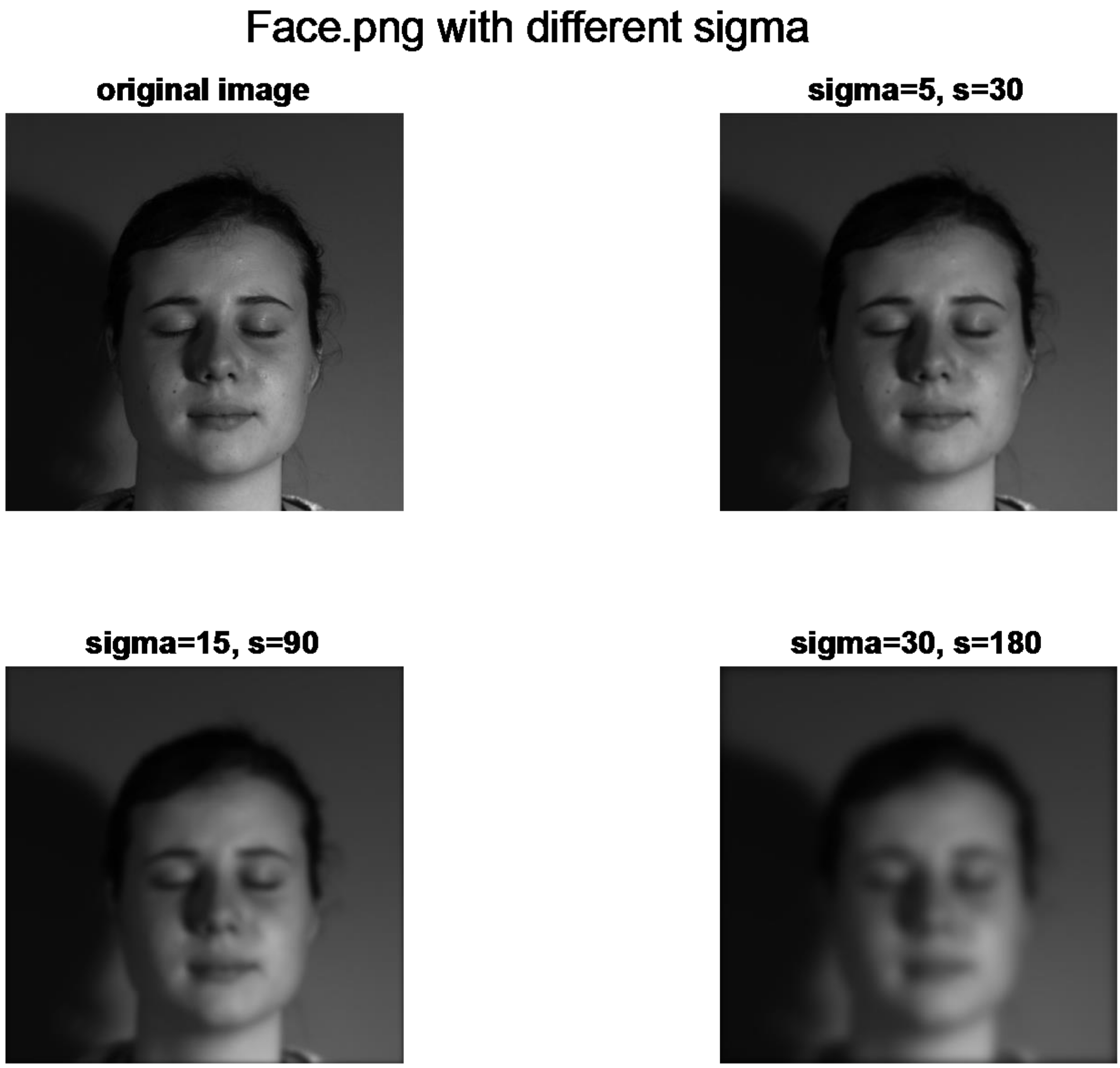
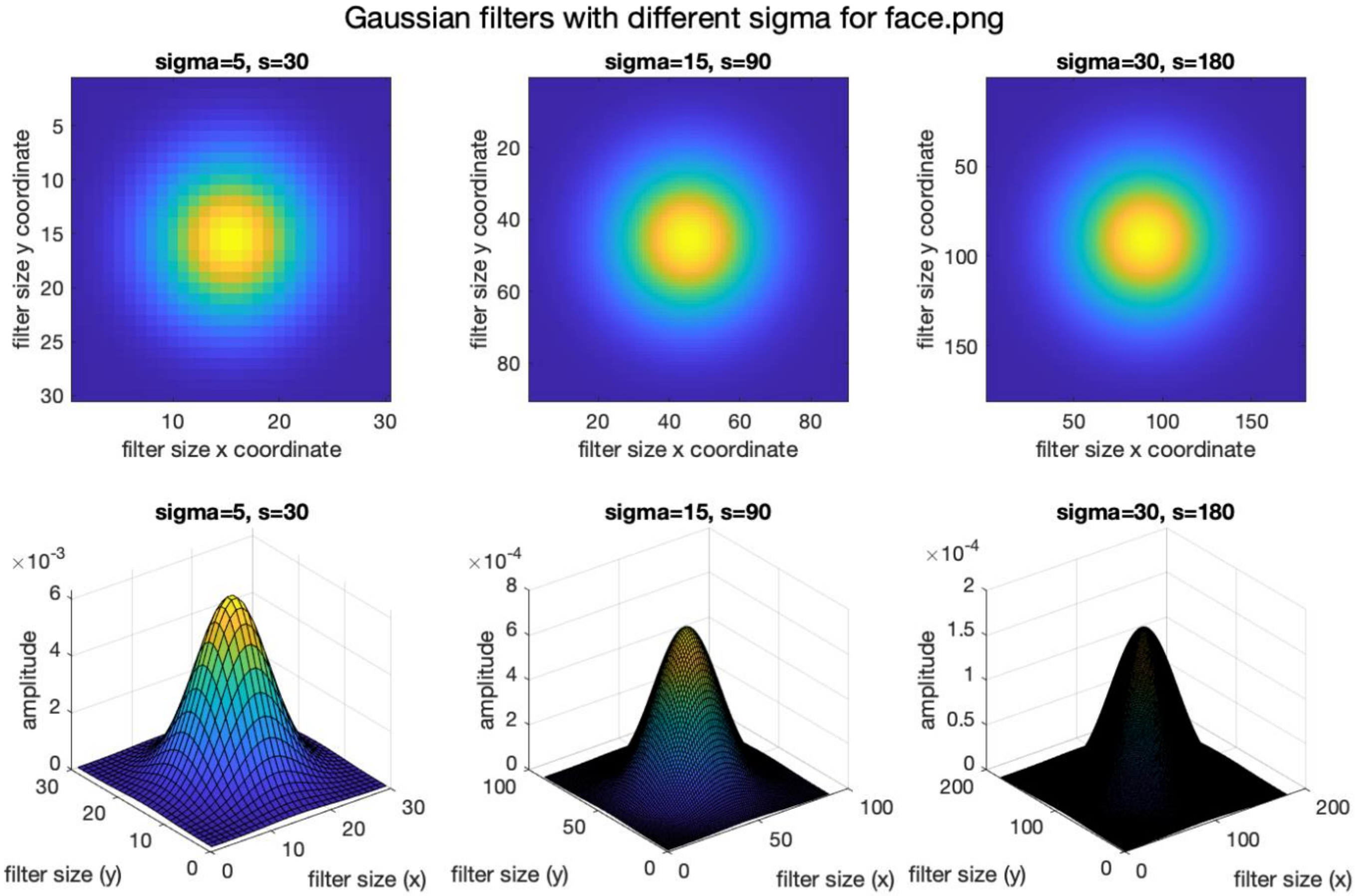


Figure 2



**Report the results and describe the effects of filtering with increased sigma. What do you notice about the time taken for each filtering operation and what impact might this have on a complex filter-based model: especially one where filter parameters are optimised by a cost function? Look at the filters using imshow() write how do they compare to retinal ganglion cells receptive fields?*

The image shows face.png with sigma = 30 and size (s) = 180. As it can be seen when sigma increases the image is smoother and more blurred whereas when sigma decreases the image is less blurred. That is because sigma controls how wide the Gaussian is, representing the standard deviation. As the Gaussian becomes wider (with a larger sigma) the details of the image become blurrier. Regarding the time taken for each filtering operation the larger the size was the more time it took for the computation to be complete in MATLAB. When the size is the largest (s=2048) the operation took significantly longer than when size was just 30. That is because the matrix dimensions of the filter increased (2048x2048 compared to 30x30) and operations needed to be done in more points when applying the gaussian kernel during convolution.

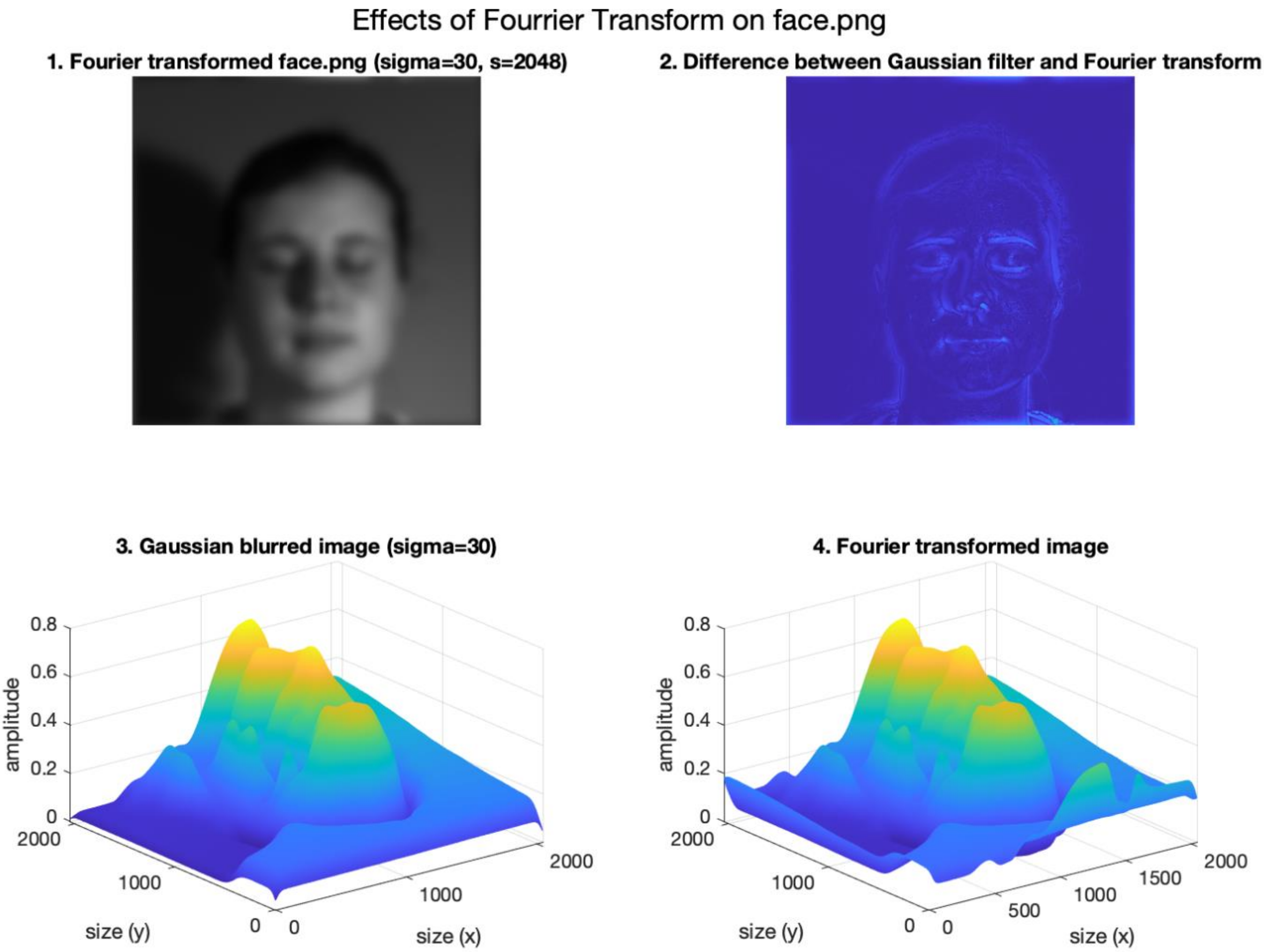
Complex filters are used in many domains for example in vision-guided robotic systems where detecting the environment and especially edges are important. When it comes to edge detection specifically, applying a gaussian filter helps to achieve better detection of edges as it gets rid of the noise in the image. In this case an increased sigma would minimize the cost function of complex filters. The cost function is the amount of error in the model and how far away the model's output is from the desired results. The model would benefit from a larger sigma since more smoothing results in better edge detection and hence the cost function is minimized. Mathematically, in the gaussian function $G=\exp(-(x^2+y^2)/2\sigma^2)/2\pi\sigma^2$, both the exponent and the coefficient are dependent on $1/\sigma^2$ so a larger sigma will result in a smaller value of the gaussian function. And if the cost function is dependent on the gaussian function it will decrease as well.

Ganglion cells in the retina have receptive fields similar to Gaussian filters. Their receptive fields have either an 'ON' center and 'OFF' surround or an 'OFF' center and an 'ON' surround (Snowden et al., 2012). Light that is hit directly to the center of the ON-center cells makes them activate and their activation takes the form of a Gaussian. That is because there is very high activation in the center of the cell and not on the sides resulting in a peak in the center that diminishes the further away from the center. When sigma is increased the gaussian becomes more spread out meaning that the light passing through is wider, so it does not hit only the center directly resulting in a more blurred out image as there is less focus on the central point.

The similarity between the receptive fields and the Gaussian filters is more apparent when looking at figure 2 that shows the Gaussian filters plotted using imagesc and serf in MATLAB. Looking at the first row the yellow circle in the middle represents the ON center/ receptive field of the ganglion cells. Row 2 which is the Gaussian plotted in 3D, represents the activation of the receptive field with a high activation in the center where the light is absorbed and a lower activation in the OFF center. Moreover, it is observed that the larger the sigma and the size of the filter the less noise (pixels) exists in the filter. That enables a more accurate detection of the edges. Thus, Gaussian filters are used for edge detection by the ganglion cells as they get rid of the noise and edges are processed better.

Task 2

Figure 3



**Compare the image produced this way with one produced using conv2(). What differences are there between the filtered images? What are the implications of this for modelling visual processes? What is the possible drawback of the Fourier method?*

The first subplot shows the effect of Fourier transform (FT) on face.png while the second subplot shows the difference between the image when using conv2 and when transforming the image to the frequency domain and then back to the spatial domain. The last two (3 and 4) show the gaussian filter and the Fourier transform using the surf plot in MATLAB. The 'parula' colormap was used to make the differences more apparent. The difference when comparing the two methods are in the borders with the gaussian blurred image having black borders. That happens because during convolution when the kernel is passing through the image matrix the calculations that happen at the edges of the kernel involve much smaller numbers as they are away from the center. At the center the numbers are higher as it is the peak of the gaussian. An example of such a kernel:

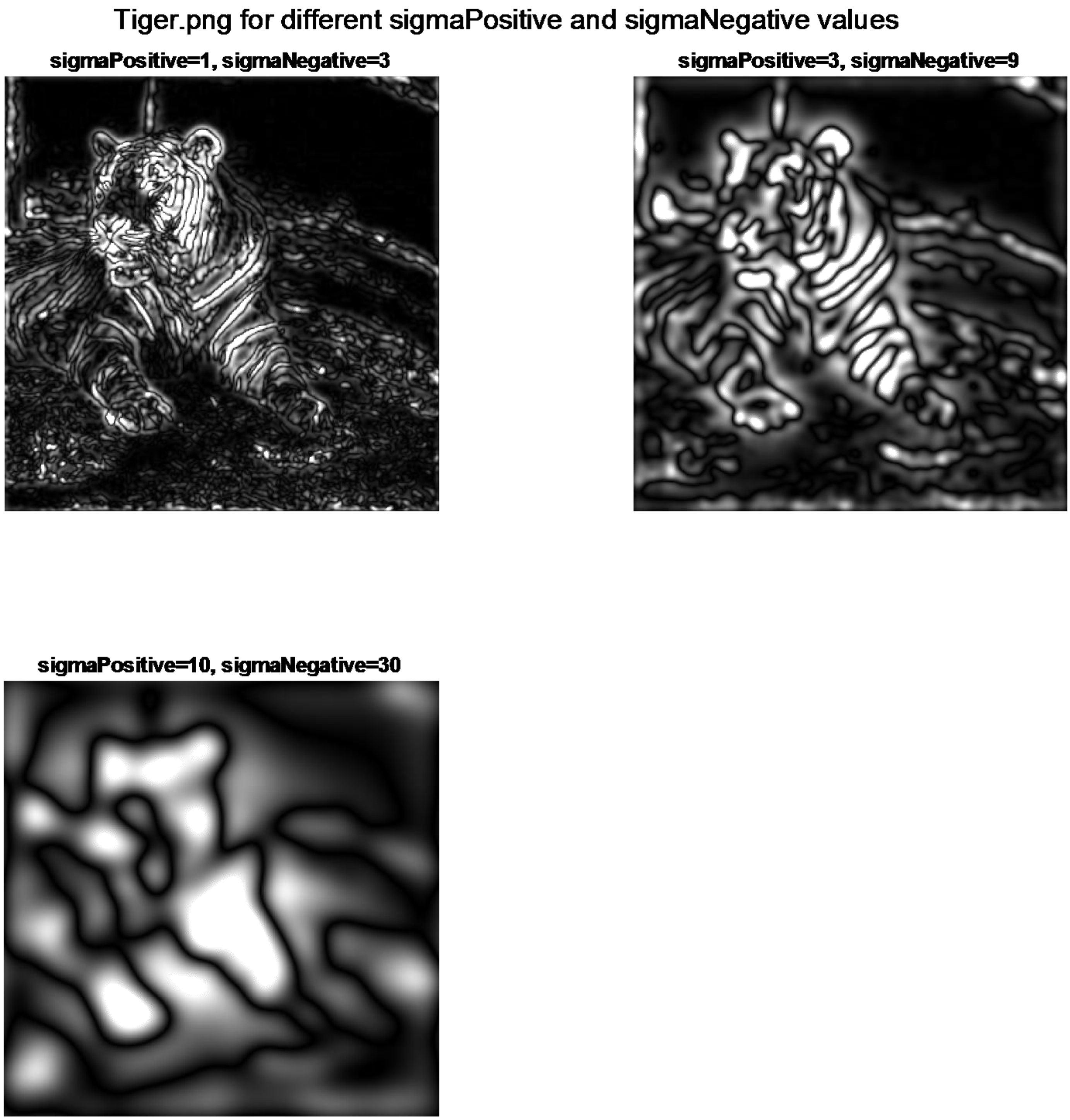
1	2	1
2	4	2
1	2	1

That results in darker borders in the image (see figure 1). When applying Fourier transform in a gaussian function the result is another gaussian which explains why the difference in the borders is still there. However, after FT is performed, the borders become less dark than before since the information is transferred in the frequency domain. That can be seen looking at the 3D plots 3 and 4 where the edges increase in the Fourier domain.

Research has shown that the visual system might use Fourier analysis to process visual information by transforming the light passing through the retina into spatial frequencies with variations in light described as sinusoidal waves. Amplitude of the wave would represent the contrast in brightness. Using the face.png image as an example it could explain how the brightness of the image is encoded into high and low frequencies in the primary visual cortex (V1) to detect the edges. A limitation of the FT is the fact that spatial information is not taken into account as the image is processed in the frequency domain making some of the information lost. Another limitation is that the FT is a periodization of the original image in the frequency domain which means that it considers the signal to be periodic/repeating through time. This is understood when thinking of a sinusoidal wave that repeats in the frequency spectrum. However, images and in this case the real environment that is processed by the visual field is nonperiodic (Bonnet & Vautrot, 1997).

Task 3

Figure 4



**What sorts of features are picked out by the filter. That is, what features remain, and which are removed? What would the brain do to use filters at different scales? Discuss the utility of DoG and Gabor filters as models of spatial vision in humans using images from this workshop as examples. Discuss ways in which DoG filters mimic retinal processing.*

Difference of Gaussian (DoG) is the subtraction of one Gaussian blurred version of an original image from another less blurred version of the image. The features picked up by the filter is the edges. Edges can be defined as the contrast between different levels of brightness or the areas in the image where light intensity is changing. When applying the filter, especially when the sigmas increase, the image is getting blurrier and only the more prominent edges remain. In the first picture when the two sigmas have lower values more edges are detected (noted by the black lines) whereas as the sigmas increase less and less edges are detected with only a rough outline of the tiger remaining.

The Gabor filter is used to provide information about directionality and edges as well as texture and is a combination of a Gaussian and a sinusoidal wave. Applying Gabor filters to images allows us to keep only specific orientations and filter out others. Taking the tiger image as an example, the tiger has stripes going vertically from right to left. Applying a Gabor filter following the same direction of the tiger's stripes, filters out the rest of the information making the stripes stand out more. Using the filter in the opposite direction minimizes the appearance of those stripes.

Gabor filtering can be thought of as mimicking the simple cells in the V1 area. The V1 area is a specialized area for processing information about orientation and has simple simple cells that are orientation selective and responding only to specific orientations. When the tiger image is analyzed by V1, specific cells get activated only for the stripes going vertically from right to left. Other cells get activated only for the stripes in the head of the tiger that go from top to bottom. In that regard orientation processing in the V1 is very similar to Gabor filters.

Regarding DoG, the visual system processes spatial information using the DoG filter to detect edges by smoothing the image using the Gaussians. It then extracts only the edges filtering out other information. Ganglion cells are particularly important in edge detection as they only respond to differences in light intensity and not when there are overall changes in light in the image. That is because they have a small ON center and when a lot of light is projected it cancels out by the OFF surround resulting in a low response. However, when edges fall on the receptive field of the ganglion cells they are activated since there is a contrast between the light intensity going from low to a high frequency in the edges.

The brain can use filters on different scales due to its cortical layers (hypercolumns) in the V1 area. The layers have orientation columns with each column containing cells that respond only to a specific orientation (e.g., vertically from left to right). The preferred orientations for each column can be represented as Gaussian tuning functions of different shapes (wider or with a higher peak) and hence of different sigma values. Different scales are also used in different areas of the visual cortex (e.g., V1, V2, V3) and when visual information processing moves from low level to high level vision with more complex computations happening on higher levels.

References

Bonnet, N., & Vautrot, P. (1997). Image Analysis: Is the Fourier Transform Becoming Obsolete? *Microscopy Microanalysis Microstructures*, *8*(1), 59–75. https://doi.org/10.1051/mmm:1997106

Snowden, R., Thompson, P., & Troscianko, T. (2012). *Basic Vision: An Introduction to Visual Perception* (Revised ed.). Oxford University Press.

Lab 12 (Individual lab: Essay (word count:1099))

Analysis of two theories to explain low-level visual processes

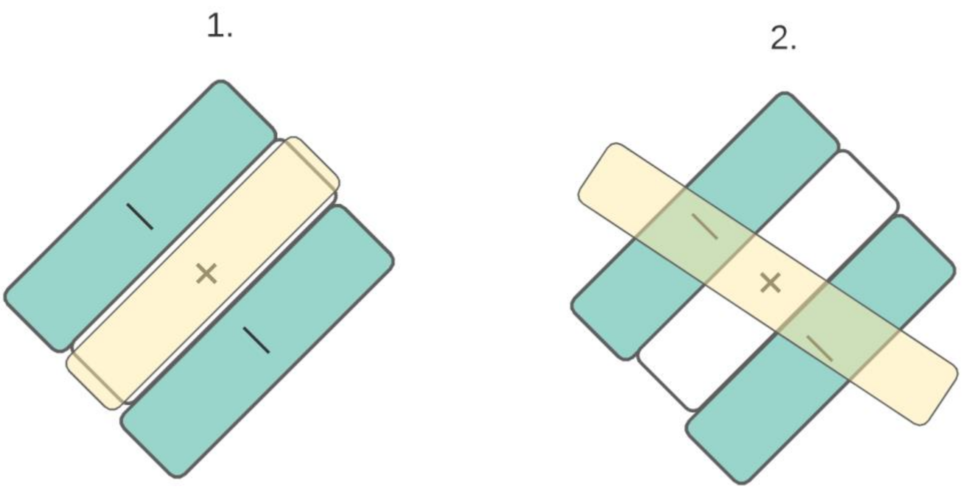
Vision can be divided into low and high-level; low-level vision ranges from detecting edges to detecting motion (Hood, 1998). High-level vision processes the shape of objects in 3D as well as information about the identity of objects, where memory is also involved (Herzog et al., 2016). The present report will focus on low-level vision and will discuss two theories of visual processing: the Hubel and Wiesel (1959) theory and the spatial frequency theory (SFT).

In 1959, Hubel and Wiesel found that the visual cortex and specifically the V1 area that is associated with orientation, had simple and complex cortical cells that responded to different orientations of light. Those cortical cells had a rectangular shaped receptive field. The receptive field is the area where, if light shines there, it influences the cell's activity; it either makes it decrease or increase its firing. The area surrounding the receptive field can be thought of as an 'OFF' surround where light does not produce a response.

Hubel and Wiesel (1959) observed that simple cells responded to bars of light of specific orientation and did not respond to light of a different orientation (figure 1). Conversely, complex cells were not as selective and could respond to light of slightly different orientations. The Hubel and Wiesel model has important implications for the arrangement of cortical cells in the V1 area (Snowden et al., 2012). The V1 area has cortical layers that encode and transmit information to different brain areas for further stimuli processing. According to their model, the layers have 'orientation columns' containing cortical cells that activate in the presence of specific orientations while they remain deactivated for others.

Figure 1

Example of cells described by Hubel and Wiesel



Note. 1. Shows a cell with a receptive field in the center (+) and an 'OFF' surround (-). The yellow bar represents the light. It hits the receptive field directly in the middle, so the cell gets activated and the response is a Gaussian. 2. The light hits the cell with a different orientation and the cell does not fire.

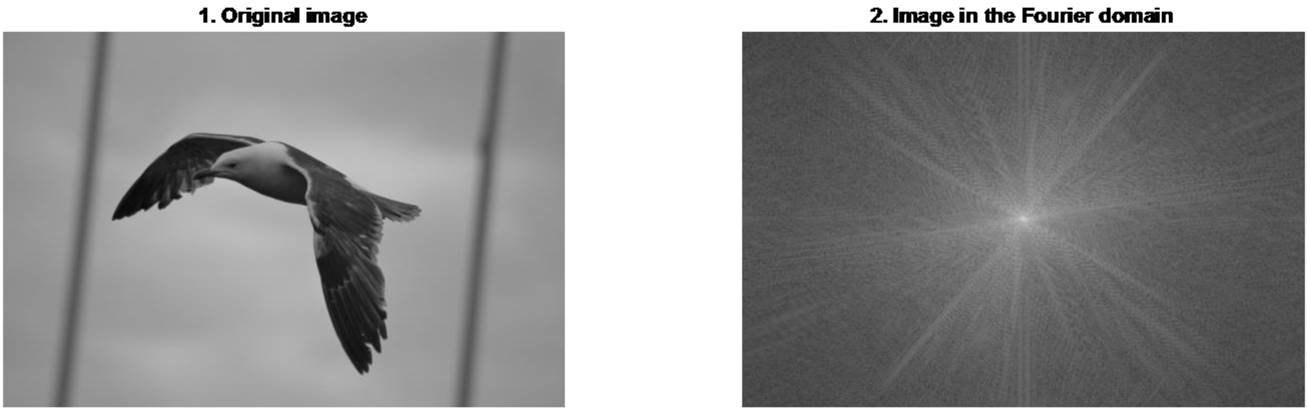
Subsequent research supported the Hubel and Wiesel (1959) findings and the existence and mechanisms of the cortical cells described in the model (see Heydt et al., 1992). Evidence for the model can also be provided by the way the visual system detects edges and orientation, which are processes that closely resemble Gaussian and Gabor filtering. When shining a light on the receptive field, the center activates whereas the surround remains inhibited. That process when plotted, resembles a Gaussian distribution with the receptive field being the center of the Gaussian (Snowden et al., 2012). When the light falls either directly on the receptive field or half on it and half on the surround, the cells produce a response. In the latter case they produce the derivative of the Gaussian by dropping to zero (zero-crossing) in the ‘OFF’ surround. That way, the cortical cells can detect the edges of objects since edges are simply a contrast between high and low brightness.

Further evidence supporting the Hubel and Wiesel model is the use of Gabor filters for orientation processing. Gabor filters just like the cortical cells described in the model, process only a specific orientation and filter out any other orientations present in the image (Kamarainen et al., 2007). However, the Hubel and Wiesel model also has some limitations, one of them being that the brain’s computations are non-linear (Korn & Faure, 2003). By describing linear processes with edge detection of lines of different orientations, the model might over-simplify visual processing. Another limitation is the fact that their theory has not been extended to explain different parts of an image like texture or shape (Garrett, 2008).

SFT can address this limitation as it is based on the idea that the brain decomposes images from the environment in the frequency domain. It does so by representing changes in luminance with a combination of sinusoidal waves using a technique called Fourier transform (FT). High spatial frequencies (more sinusoidal cycles) represent sharp features such as edges and high contrast between light and dark, while low spatial frequencies (few sinusoidal cycles) represent more coarse features (Kauffmann et al., 2014). An example of FT used in an image can be seen in figure 1.

Figure 1

Example of an image in the in the original form and in the frequency domain



Note. 1. Shows the original image of a bird in black and white colours (grayscale). 2. Shows the same image in the frequency domain. The calculation of the FT was done using MATLAB.

Subplot 2, figure 1 shows the image in the Fourier domain. The white center is the origin of the frequency component and represents the average value of the image. As the original image is quite bright, the center and most of the image when Fourier transformed is light in color. The darker areas of subplot 2 represent the darker areas of the original image. The directions of the lines in the original image are flipped in the opposite direction in the Fourier domain, so the bird's direction that extends from left to right is reversed in the Fourier domain.

The spatial frequency theory has been supported by psychophysical experiments with some studies also indicating that it may contribute to high-level visual processing (Kauffmann et al., 2014). Moreover, experiments have shown that some types of ganglion cells are sensitive to high spatial frequencies while others are sensitive to low spatial frequencies (Mahon et al., 2013; Tootell et al., 1988). However, the SFT also comes with some limitations. One of them is that there is no direct evidence or observations that could clearly demonstrate the existence of Fourier transform processing in the brain. Thus, the direct measurement by Hubel and Wiesel (using electrodes in a cat's brain) appears more robust. However, considering the popularity of Hubel and Wiesel's experiment there has not been a very large number of studies replicating these results (Garrett, 2008).

Even though both theories seem to be lacking in that regard, the SFT also has another limitation: Fourier transform considers the input image to be infinite and continuous going from minus infinity to infinity (Bonnet & Vautrot, 1997; figure 2).

Figure 2

Representation of how an image is perceived in the Fourier domain

Note. The Fourier transform considers the image to repeat to infinity which is represented in the image here.

As shown in the above image, the part of the environment processed at one time by the visual field would be represented as an infinite collection of sinusoidal waves. This deviates from detection of the environment in real life and would not benefit the visual system since more complex computations would be needed to process information represented as infinite. However, considering this complexity it could also mean that FTs take place later in visual processing, in high-level vision. It can then be concluded that the Hubel and Wiesel model can explain low-level, primal visual processing while SFT can be used by the visual system later or in different parts of the brain. That is supported by the filter-rectify-filter (FRF) model that states that filters are used by the brain in different stages of visual processing (Kingdom et al., 2003).

References

Bonnet, N., & Vautrot, P. (1997). Image Analysis: Is the Fourier Transform Becoming Obsolete? *Microscopy Microanalysis Microstructures*, *8*(1), 59–75. https://doi.org/10.1051/mmm:1997106

Garrett, J., B. (2008). *Brain & Behavior*. (2nd edition). Sage Publications, Inc.

Herzog, M. H., Thunell, E., & Ögmen, H. (2016). Putting low-level vision into global context: Why vision cannot be reduced to basic circuits. *Vision Research*, *126*, 9–18. https://doi.org/10.1016/j.visres.2015.09.009

Heydt, R., Peterhans, E., & Dursteler, M. (1992). Periodic-pattern-selective cells in monkey visual cortex. *The Journal of Neuroscience*, *12*(4), 1416–1434. https://doi.org/10.1523/jneurosci.12-04-01416.1992

Hood, D. C. (1998). LOWER-LEVEL VISUAL PROCESSING AND MODELS OF LIGHT ADAPTATION. *Annual Review of Psychology*, *49*(1), 503–535. https://doi.org/10.1146/annurev.psych.49.1.503

Hubel, D. H., & Wiesel, T. N. (1959). Receptive fields of single neurones in the cat's striate cortex. *The Journal of Physiology*, *148*(3), 574–591. https://doi.org/10.1113/jphysiol.1959.sp006308

Kauffmann, L., Ramanoal, S., & Peyrin, C. (2014). The neural bases of spatial frequency processing during scene perception. *Frontiers in Integrative Neuroscience*, *8*. https://doi.org/10.3389/fnint.2014.00037

Kamarainen, J. K., Kyrki, V., & Kälviäinen, H. (2007). Local and global Gabor features for object recognition. *Pattern Recognition and Image Analysis*, *17*(1), 93–105. https://doi.org/10.1134/s1054661807010117

Snowden, R., Thompson, P., & Troscianko, T. (2012). *Basic Vision: An Introduction to Visual Perception* (Revised ed.). Oxford University Press.

Kingdom, F. A., Prins, N., & Hayes, A. (2003). Mechanism independence for texture-modulation detection is consistent with a filter-rectify-filter mechanism. *Visual Neuroscience*, *20*(1), 65–76. https://doi.org/10.1017/s0952523803201073

Korn, H., & Faure, P. (2003). Is there chaos in the brain? II. Experimental evidence and related models. *Comptes Rendus Biologies*, *326*(9), 787–840. https://doi.org/10.1016/j.crvi.2003.09.011

Mahon, B. Z., Kumar, N., & Almeida, J. (2013). Spatial Frequency Tuning Reveals Interactions between the Dorsal and Ventral Visual Systems. *Journal of Cognitive Neuroscience*, *25*(6), 862–871. https://doi.org/10.1162/jocn_a_00370

Tootell, R., Silverman, M., Hamilton, S., Switkes, E., & De Valois, R. (1988). Functional anatomy of macaque striate cortex. V. Spatial frequency. *The Journal of Neuroscience*, *8*(5), 1610–1624. https://doi.org/10.1523/jneurosci.08-05-01610.1988