



Comparative Analysis of Movement Direction Decoding: M1 vs. PMd Neural Populations in Macaque Monkeys

Jesse Lavin

Abstract

To improve the precision of neural decoding for applications like prosthetic device control, a critical need arises for more accurate decoding methods. Various brain regions have been identified as potential sources for encoding the direction of movement, presenting a fundamental question: which neural population provides superior decoding accuracy? This research addresses this question by undertaking a comparative analysis of decoding accuracy between two prominent neural populations: the primary motor cortex (M1) and the dorsal premotor cortex (PMd). While our study initially suggested a striking disparity, indicating that M1 neurons might exhibit significantly greater tuning specificity towards the direction of executed movements when contrasted with PMd neurons, our subsequent rigorous analysis found no statistically significant difference in their tuning specificity. In light of these revelations, I determined that both regions may be employed to empower individuals with motor disabilities to control external devices easily using their own neural signals.

Keywords: M1, PMd, Population Vector, MLE, DSI, Confusion Matrix, Raster Plot

Introduction

The ability to decode neural activity and translate it into meaningful information has captivated scientists and researchers in the fields of neuroscience and biomedical engineering. By understanding how the brain represents and processes information, they've unlocked new ways to improve the quality of human life. One significant area of interest is decoding the direction of movement using neural activity in the motor cortex (M1) and premotor cortex (PMd). Decoding the direction of neural activity in these areas of the brain may improve the treatment for individuals with motor impairments or disabilities [1]. Millions of people around the world are affected by conditions that limit their ability to perform everyday tasks.

This field of study holds immense potential to revolutionize various aspects of society, ranging from medical procedures to the control of advanced prosthetic devices. One of its key contributions lies in driving advancements in neuroprosthetics, where it enhances brain interfaces and empowers individuals with motor disabilities to control external devices using their own neural signals [4]. Furthermore, this research plays a vital role in informing the development of targeted rehabilitation techniques for individuals with motor impairments, such as stroke or spinal cord injury [3]. Gaining a deeper understanding of how the motor cortex represents movement direction provides



valuable insights into brain function, thereby contributing significantly to the broader field of neuroscience.

Moreover, this research's potential extends to offering novel treatments for neurological disorders that affect motor function, offering hope to patients with conditions like Parkinson's disease or cerebral palsy [1]. By unraveling the complexities of the brain's mechanisms for controlling movement, it enriches our fundamental knowledge of the brain and its inner workings. Consequently, the research conducted in this area holds undeniable and far-reaching implications, from improving lives to advancing technology and deepening our understanding of the brain.

In addition to its impact on society and healthcare, the practice of decoding directional movement using neural activity in the motor and premotor cortex holds great promise for various technological applications. This transformative technology has the potential to revolutionize the development of brain-computer interfaces (BCIs) and neuroprosthetics [3]. Through real-time decoding of neural activity, individuals with motor disabilities can now control external devices, such as robotic arms or computers, through their thoughts, ushering in newfound independence and an enhanced quality of life [3].

Beyond neuroprosthetics, this technology also finds application in enhancing virtual reality and gaming experiences. By allowing users to control characters or objects using neural signals, these interactions become more immersive and intuitive [1]. Moreover, advancements in prosthetic limb control offer amputees the ability to experience more natural and precise movements, significantly improving their daily lives [4]. Furthermore, human-machine interaction can be greatly enhanced, leading to more responsive and efficient robotic systems [1].

In neural decoding, the primary motor cortex (M1) has generally demonstrated a higher level of accuracy compared to the dorsal premotor cortex (PMd) in most experiments [5]. Much of the current understanding of neural decoding is supported by experimental research on animal models conducted by various universities and other institutions. In these experiments, researchers trained Macaque Monkeys to reach towards uncertain visual cues representing various targets [5]. Neurons in the dorsal premotor cortex encoded the chosen direction well before the monkey executed the reach [5]. In addition, they seemed to encode other movement directions that were not executed later [5]. On the other hand, neurons in the primary motor cortex only signaled the direction of the actual reach, making its neurons seemingly more accurate in predicting movement [5]. This study sheds light on the decision-making process involving the PMd and its interaction with the M1 during reaching tasks.

The alleged superiority of M1 in accuracy can be attributed to several factors. First, M1 neurons exhibit a strong directional tuning, responding vigorously and selectively to movements in particular directions [7]. This pronounced directional selectivity allows for a more precise decoding of movement direction from the neural signals. Additionally, M1 is primarily responsible for the execution of voluntary movements [7]. When a movement command is initiated, M1 becomes active and directly influences muscle activity, leading to the precise execution of the intended

movement [6]. As a result, its neural activity provides a clear representation of the actual executed movement direction, enhancing the accuracy of neural decoding [6]. Moreover, M1 neurons display a strong contralateral bias, meaning they are more active when movements are executed on the side opposite to the neuron's location [7]. This lateralization of neural activity can further augment the accuracy of neural decoding, as it corresponds to the actual movements performed by the individual [7]. Furthermore, M1 neurons enable decoding at a higher signal-to-noise ratio (SNR), making their neural responses more reliable and less susceptible to noise [7]. This improved signal quality contributes to the accuracy of decoding movement direction from the neural activity [7]. Additionally, M1 typically possesses a larger population of neurons compared to PMd, providing more cortical area for recording hardware and decoding algorithms to extract movement-related information accurately [6]. However, it is essential to recognize that the accuracy of neural decoding can vary based on several factors, including the specific task, the brain region being studied, and the decoding algorithms employed [2]. While M1 excels in certain contexts, PMd may still be valuable for decoding other aspects of movement planning or motor control [2]. Both M1 and PMd play pivotal roles in the complex process of motor control and movement representation, but M1's unique features make it apparently more accurate in certain neural decoding tasks [2].

A few studies were performed to investigate the superiority of using neurons from the M1 region to decode movement direction. This work intends to validate this claim using data recording from monkeys while executing a motor task.

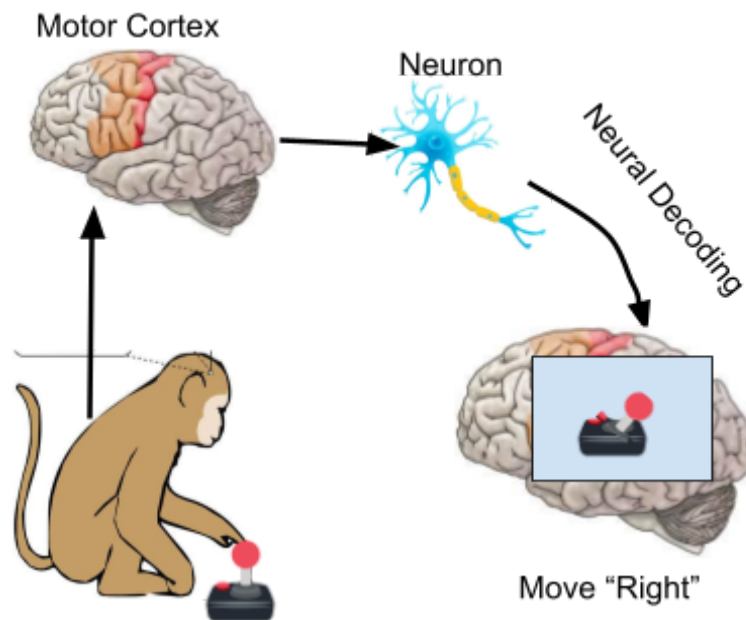


Figure 1. Macaque monkey performs reaching tasks while neural activity is recorded from the motor cortex to decode movement directions.

Methods

In these decoding studies, the Maximum Likelihood Estimation (MLE) and the Population Vector (PV) method, were used to infer the intended movement direction based on neural activity. The MLE method approaches decoding as a statistical problem, aiming to find the most likely movement direction by calculating the probability of observing neural activity patterns for each potential direction and selecting the one with the highest probability [9]. It assumes a probabilistic model relating neural activity to movement direction [9]. On the other hand, the Population Vector method involves summing the preferred direction vectors of individual neurons to obtain a resultant vector representing the decoded movement direction [8]. Each neuron's firing rate is treated as a vector, and the resultant vector points towards the decoded direction [8].

The equation for the MLE method can be represented as follows:

$$P(R|d) = \Pi \prod_{i=1}^n P(r_i|d)$$

- The left side of the equation is the probability of the movement direction given the observed neural activity [9].
- The right side is the probability of observing the neural activity for the given movement direction. This is often modeled using a probability distribution that relates neural activity to movement direction [9].
- The equation includes the prior probability of the movement direction - our prior knowledge or belief about the likelihood of different movement directions before observing the neural activity. The prior probability can also be incorporated into the calculation to further refine the estimate [9].

The equation for the Population Vector method can be represented as follows:

$$\vec{P} = \sum_{i=1}^n w_i \vec{C}_i$$

- The left side refers to the Population Vector, which is a vector representing the estimated movement direction [8].
- The right side includes the response of the i th neuron, which indicates the firing rate or activity level of that neuron [8]. It also contains the preferred direction of the i th neuron, representing the direction of movement to which the neuron is most sensitive [8].

To illustrate comparisons of the M1 and PMd neurons, I chose to compare their average firing rates. Initially, I developed a code to calculate the firing rate for each neuron in response to various movement directions. This involved organizing the recorded spike times in correspondence with the specific trial directions. By segmenting

and aligning the spike times to the onset of the respective movement directions, accurate firing rates were computed for each neuron across different trials.

To quantitatively evaluate the extent of direction selectivity, the Direction Selectivity Index (DSI) was employed. The DSI is a well-established metric that quantifies the preference of neurons for specific movement directions [9]. By calculating the DSI for each neuron, the degree of direction selectivity was quantified as a single value. This was achieved by determining the difference between the average firing rate for the preferred direction and the average firing rate for the anti-preferred direction, divided by their sum.

The equation for the DSI can be represented as follows:

$$DSI = \frac{R_p - R_o}{R_p + R_o}$$

- The variable with subscript p represents the preferred firing rate [9].
- The variable with subscript o represents the firing rate orthogonal to the preferred firing rate [9].

In order to assess the statistical significance of the observed differences in direction selectivity between M1 and PMd neurons, a T-test was implemented. The DSI values calculated for the M1 and PMd neurons were subjected to this statistical test to ascertain if the observed variation in firing rates was statistically meaningful. The resulting p-value served as a critical indicator, providing insight into whether the differences in direction selectivity between the two neuron populations were likely to have occurred due to random chance.

By employing this systematic methodology involving DSI calculation and subsequent statistical analysis through T-testing, the study was able to rigorously compare the firing rates of M1 and PMd neurons. This approach enabled a data-driven assessment of the neural populations' directional preferences and provided valuable insights into the differential contributions of these regions to motor control and execution.

Results

In the macaque monkey neural decoding experiment, the data from neural recordings were collected separately from M1 and PMd [7]. The goal was to compare the decoding accuracy of movement direction between these two brain areas [7]. To begin, the monkeys were trained to perform reaching tasks towards targets represented by fuzzy, uncertain visual cues [7]. During these tasks, neural activity was recorded from both M1 and PMd [7]. The recorded data consisted of the firing rates of individual neurons in response to different movement directions [7]. The data were then split into

two separate datasets, one for M1 and the other for PMd [7]. These datasets contained the neural responses from the respective brain areas during the reaching tasks [7].

To assess the decoding accuracy of each method, a confusion matrix was created for both MLE and Population Vector [7]. The confusion matrix is a table that compares the decoded movement directions with the actual movement directions that the monkeys performed during the reaching tasks [7]. The rows of the confusion matrix represent the actual movement directions, while the columns represent the decoded movement directions. Confusion matrices were also used for each brain area (M1 and PMd) to provide insights into how well the decoding methods correctly predicted the movement directions [7]. The diagonal elements of the confusion matrix represented the correct predictions, and off-diagonal elements represented misclassifications or errors in decoding [7].

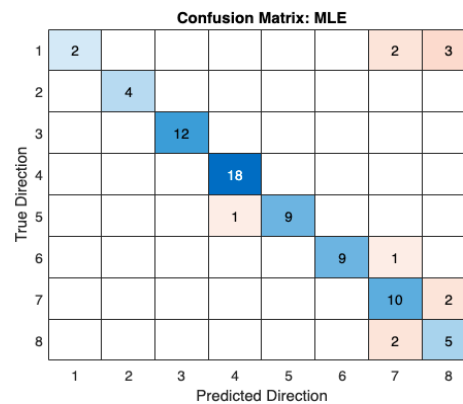


Figure 2. This is the confusion matrix for the MLE method. The decoding accuracy using MLE was 80.00%.

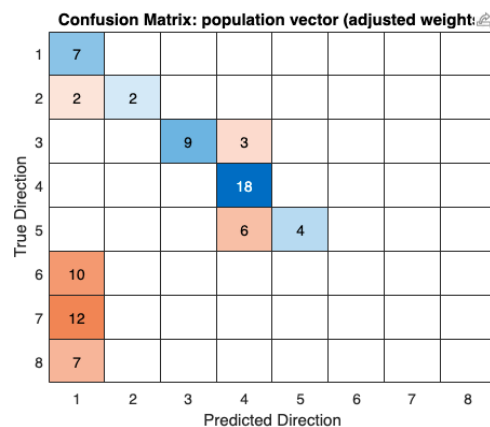


Figure 3. This is the confusion matrix for the Population Vector method. The decoding accuracy using Population Vector was 50.00%.

The diagonal element of the matrix corresponds to instances where the predicted movement direction matched the movement direction performed by the monkey during the reaching tasks [7]. Since the numbers are higher toward the center, these decoding methods correctly classified a significant portion of the neurons. The more diagonal matrix, which used the MLE method, is clearly more accurate as the diagonal elements represent the number of points for which the predicted label is equal to the true label, while off-diagonal elements are those that are mislabeled by the monkey.

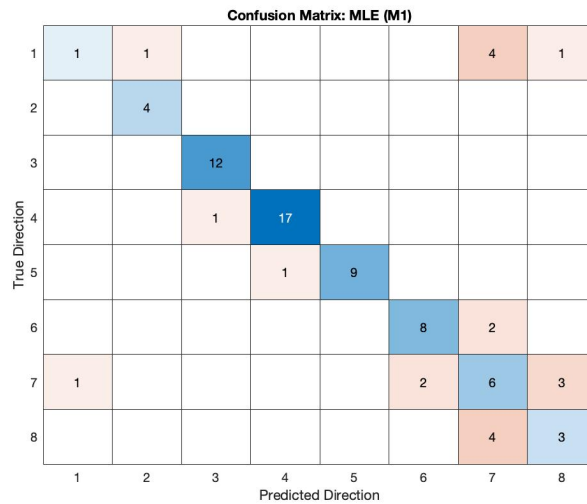


Figure 4. This is the MLE confusion matrix using M1 neurons.

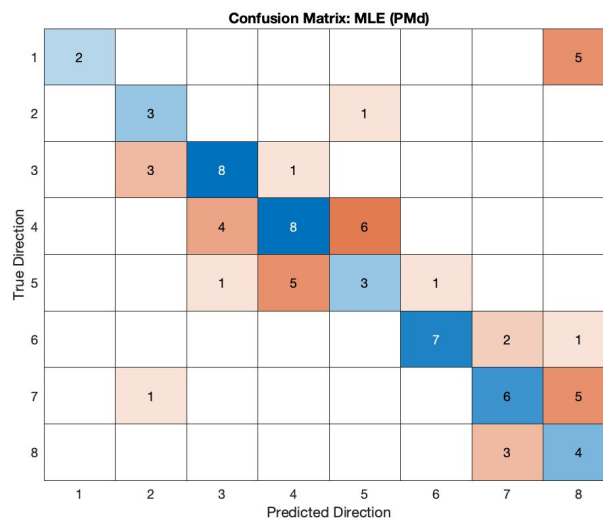


Figure 5. This is the MLE confusion matrix using PMd neurons.

The M1 matrix is significantly more centered on the diagonal, indicating that its neurons were more accurate in predicting movement. Raster plots are a common visualization technique used in neuroscience to represent the timing of neuronal activity during specific tasks or events. In the context of the macaque monkey neural decoding experiment, the raster plots provide valuable insights into how individual neurons in the motor cortex respond to different reaching directions [7]. Each raster plot corresponds to a specific reaching direction, and it shows the firing times of a single neuron during multiple trials of that particular direction [7]. In the plots, time is represented along the x-axis, and each vertical line represents the occurrence of a single action potential (spike) from the neuron [7]. The y-axis represents individual trials of the reaching task for the given direction [7]. When examining the raster plots, certain patterns emerge. Neurons in the motor cortex typically display increased firing rates when the monkey performs reaching movements in specific directions [7]. This is reflected in the raster plots by clusters of vertical lines occurring at particular time intervals during the reaching trials. It is common for different neurons to exhibit diverse patterns of firing activity in response to different reaching directions [7]. Some neurons may show stronger responses to certain directions, indicating a preference for those directions, while others may be less selective and show similar firing rates across multiple directions [7]. With the macaque monkey, the most drastic differences in firing activity are evident when comparing the raster plots of M1 and PMd neurons [7].

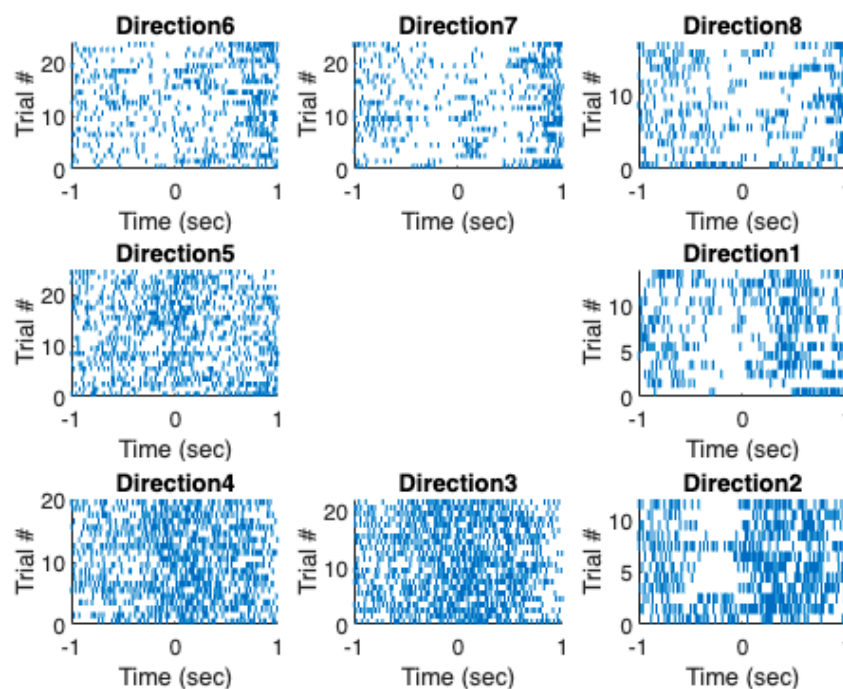


Figure 6. This is the raster plot for neuron #140, an M1 neuron.

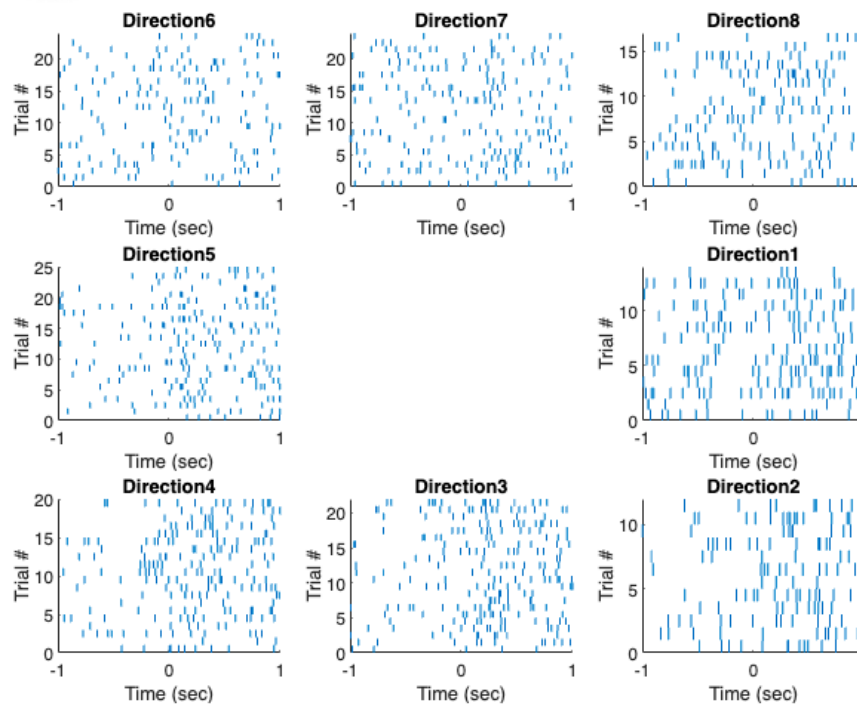


Figure 7. This is the raster plot for neuron #30, a PMd neuron.

The raster plot for neuron #140 exhibited a relatively high level of activity, showing numerous spikes occurring at different time points, suggesting this neuron is highly tuned to movement. This heightened activity indicates strong responsiveness to cognitive processes, which in this case, is the movement direction of the monkey. On the other hand, the raster plot with little activity for neuron #30 displays fewer spikes, implying less responsiveness and engagement of the neurons. In this context of the PMd, which is involved in motor planning, the low activity signifies that neurons are less active during execution and more so during preparatory phases. These contrasting patterns offer valuable insights into the neural functions of these specific brain regions during different tasks or conditions. The raster plot for M1 shows a lot of activity, while the raster plot for PMd has little activity, suggesting that the neurons in M1 are more active and responsive during the execution of the movement, whereas the neurons in PMd are relatively less involved in the actual movement execution. In other words, M1 neurons are more fit to predict the actual movement direction.

However, the small sample size and non-randomness used to determine these results are not enough to indicate statistical significance. This is where employing the systematic methodology involving DSI calculation and subsequent statistical analysis through t-testing to rigorously compare the firing rates of M1 and PMd neurons is necessary.



Neuron (PMd)	DSI Value
16	0.221109023
7	0.252631148
11	0.326708462
12	0.378486801
16	0.132811023
17	0.178200417
18	0.301202311
23	0.106855577
27	0.198733024
28	0.256629134

Figure 8. This is the table containing the randomly selected sample of PMd neurons and their corresponding DSI values.

Neuron (M1)	DSI Value
67	0.411107463
69	0.164490862
132	0.28297922
86	0.127573258
124	0.195923519
135	0.177500273
140	0.445545078
105	0.302091942
122	0.103315088

127	0.189288078
-----	-------------

Figure 9. This is the table containing the randomly selected sample of M1 neurons and their corresponding DSI values.

	A	B	C	D	E
1					
2					
3	Neuron #	PMd	M1		
4	16	0.221109023			
5	7	0.252631148			
6	11	0.326708462			
7	12	0.378486801			
8	16	0.132811023			
9	17	0.178200417			
10	18	0.301202311			
11	23	0.106855577			
12	27	0.198733024			
13	28	0.256629134			
14	67		0.411107463		
15	69		0.164490862		
16	132		0.28297922		
17	86		0.127573258		
18	124		0.195923519		
19	135		0.177500273		
20	140		0.445545078		
21	105		0.302091942		
22	122		0.103315088		
23	127		0.189288078		
24					
25					0.460334

Figure 9. This is an image of the Microsoft Excel setup used to calculate the p-value regarding the difference DSIs.

After calculating the DSI values using the equation explained above, I logged them onto a Microsoft Excel spreadsheet for comparison. To ensure statistical rigor, I randomly selected ten neurons from the M1 and the PMd populations. I utilized the “TTEST” function on excel, setting my first array as B4:B13, the second array as C14:C23, the tails as 1, and the type as 1. The calculated p-value, which amounted to 0.460334, emerged as a pivotal outcome. This p-value, being greater than the conventional significance level of 0.05, signified that there was no statistically significant difference between the firing rates of neurons recorded from the M1 and PMd regions. In other words, our results indicated that, in this specific context, the choice of brain region did not yield significantly different outcomes in terms of directional selectivity.

Conclusion

In conclusion, this research aimed to compare the decoding accuracy of movement direction between the M1 and the PMd neural populations. Initial experimentation suggested that M1 might provide better decoding accuracy, given its role in executing voluntary movements and its strong directional tuning. However, the systematic analysis of Direction Selectivity Index (DSI) values and subsequent statistical testing using t-tests challenged this notion. Contrary to my initial hypothesis, the calculated p-value of 0.460334 indicated that there was no statistically significant difference in the firing rates of neurons between the M1 and PMd regions regarding directional selectivity. This result highlights the importance of empirical testing and statistical rigor in drawing conclusions about neural decoding accuracy. My study sheds light on the complexity of neural processing in different brain regions and highlights that decoding accuracy can be context-dependent. While M1 excels in certain contexts, such as predicting actual movement directions, PMd may have its unique contributions in other aspects of motor control and planning. Overall, this research underscores the potential of neural decoding in transforming society, offering hope to individuals with motor impairments, advancing our understanding of the brain, and driving technological innovations in neuroprosthetics. It also emphasizes the importance of rigorous statistical analysis and empirical testing in neuroscience research to draw reliable conclusions about neural function and decoding accuracy.

References

- [1] Bouton, C. Neural Decoding and Applications in Bioelectronic Medicine. *Bioelectron Med* 2, 20–24 (2015). <https://doi.org/10.15424/bioelectronmed.2014.00012>
- [2] Brian M Dekleva, Pavan Ramkumar, Paul A Wanda, Konrad P Kording, Lee E Miller (2016) Uncertainty leads to persistent effects on reach representations in dorsal premotor cortex [eLife 5:e14316](https://doi.org/10.1371/journal.pone.0143166)
- [3] Chandler JA, Van der Loos KI, Boehnke S, Beaudry JS, Buchman DZ, Illes J. Brain Computer Interfaces and Communication Disabilities: Ethical, Legal, and Social Aspects of Decoding Speech From the Brain. *Front Hum Neurosci*. 2022 Apr 21;16:841035. doi: [10.3389/fnhum.2022.841035](https://doi.org/10.3389/fnhum.2022.841035). PMID: 35529778; PMCID: PMC9069963.
- [4] Dong Y, Wang S, Huang Q, Berg RW, Li G, He J. Neural Decoding for Intracortical Brain–Computer Interfaces. *Cyborg Bionic Syst*. 2023;4:Article 0044. <https://doi.org/10.34133/cbsystems.0044>

- [5] Ince NF, Gupta R, Arica S, Tewfik AH, Ashe J, Pellizzer G. High accuracy decoding of movement target direction in non-human primates based on common spatial patterns of local field potentials. PLoS One. 2010 Dec 21;5(12):e14384. [doi: 10.1371/journal.pone.0014384](https://doi.org/10.1371/journal.pone.0014384). PMID: 21200434; PMCID: PMC3006173.
- [6] Kim T, Freeman RD. Direction selectivity of neurons in visual cortex is non-linear and laminar dependent. [Eur J Neurosci. 2016 May;43\(10\):1389–99](https://doi.org/10.1523/JNEUROSCI.4310-15.2016).
- [7] M. Filippini, D. Borra, M. Ursino, E. Magosso, P. Fattori Decoding sensorimotor information from superior parietal lobule of macaque via Convolutional Neural Networks Neural Network., [151 \(2022\)](https://doi.org/10.1016/j.neunet.2022.03.011)
- [8] Mahan, M.Y., Georgopoulos, A.P. (2014). Neuronal Population Vector. In: Jaeger, D., Jung, R. (eds) Encyclopedia of Computational Neuroscience. Springer, New York, NY. https://doi.org/10.1007/978-1-4614-7320-6_401-1
- [9] Wywił, J.L. On the Maximum Likelihood Estimation of Population and Domain Means. *J Stat Theory Pract* **17**, 40 (2023). <https://doi.org/10.1007/s42519-023-00337-4>

Acknowledgments

I would like to express my gratitude to all those who contributed to the successful completion of this research paper. First and foremost, I extend my appreciation to the subjects, the Macaque monkeys, who participated in the neural recording experiments. Their invaluable contributions provided the foundation upon which my study rests. I am deeply indebted to my associate, Omar Tawakol whose guidance, insights, and expertise were instrumental throughout this research endeavor. His unwavering support and mentorship enriched the quality and depth of my work. I also extend my thanks to the academic community for their contributions to the field of neuroscience and neural decoding. Their prior research and insights provided the necessary context and foundation for my study. This work stands as a collective effort, and I am grateful to all those who contributed directly or indirectly to its completion.