Modality and Direction-Location Coherence of Instructions Modulate Long-Latency Reflex Amplitudes

by

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Abstract

Stable upper limb movements are essential for tasks, and the sensorimotor system utilizes the stretch reflex and voluntary control to counter unexpected mechanical perturbations, ensuring skilled motor behaviour. The stretch reflex is composed of two distinctive components, the short-latency (SLR) and long-latency (LLR) responses. Given their unique modulation and the mysterious neural circuitry underlying them, much remains to be discovered about LLRs. The task dependency of the long-latency response has been a focus of research since its discovery, though further exploration of the impact of a broader range of instruction characteristics is still needed. To tackle this gap in LLR research, this study investigated how changes in instruction modality and coherence of instruction direction and location influenced the LLR amplitude. An experimental paradigm with two identical tasks was designed, where subjects were instructed to reach a target visually or audibly. Furthermore, both logical and conflicting instructions were used. Mechanical countering perturbations were applied to the subjects, eliciting stretch reflexes. It is hypothesized that the LLR response amplitude estimate will show dependency on the varying instruction characteristics. The results revealed new insights into the relationship between LLRs and their dependence on task instructions. LLR amplitude estimations revealed differences between modalities. The effect of instruction coherence was not present in both modalities. The findings of this study suggest that changes in response time between modalities lead to discrepancies in LLR amplitudes. Also, the effect instruction logic and clarity have on subject confidence influences reaction times and intent, leading to differences in LLR strength. The differences in neural pathways that localize, recognize and then transform stimuli to perceptual information are seen as new potential contributors to the long-latency stretch component.

1

Introduction

In our everyday lives, we use our upper limbs for various tasks, such as reaching for a toothbrush or holding a cup. Many functional tasks require stable movement execution when interacting with the external world, where unexpected mechanical perturbations can jeopardize task success (Nashed et al., 2012; Pruszynski et al., 2008). The sensorimotor system is capable of countering mechanical perturbations through a sequence of muscle activities known as reflexes and voluntary control (Pruszynski et al., 2011). By compensating for unexpected external stimuli, feedback control aids in achieving skilled motor behaviour (I. Kurtzer et al., 2009).

Muscle activity, monitored through electromyography (EMG) recordings, reveals two distinct stretch reflex responses, followed by the voluntary response (VOL) (I. L. Kurtzer, 2015; Palmer & Ashby, 1992; Reschechtko & Pruszynski, 2020). The first component is the short-latency reflex (SLR) (I. L. Kurtzer, 2015). Previous research shows that SLRs occur between 20-50 ms post-perturbation onset, making them the fastest response to mechanical disturbances. Due to its latency onset and duration, this response is considered a spinal, monosynaptic response (Reschechtko & Pruszynski, 2020).

Following the SLR, the next response observed is the long latency stretch reflex (LLR) (I. L. Kurtzer, 2015; Palmer & Ashby, 1992; Reschechtko & Pruszynski, 2020). The LLR is regarded as a more enigmatic response than the SLR, due to its unique characteristics, origins, and modulation (Pruszynski et al., 2011). Occurring 50-100 ms post-perturbation onset, LLRs demonstrate simplicity and rapidity, much like SLRs. At the same time, they display goal-oriented behaviour and knowledge of limb dynamics, not only responding due to muscle stretch but rather integrating more information to reach a higher level of sophistication (I. Kurtzer et al., 2014; I. L. Kurtzer, 2015; Pruszynski & Scott, 2012). This behaviour is akin to voluntary response. Furthermore, the origins of the LLR are still not well-established (Pruszynski & Scott, 2012). Evidence shows that the primary motor cortex (M1) has been identified as one of the main contributors to the reflex but is not seen as its sole contributor (I. L. Kurtzer, 2015; Pruszynski & Scott, 2012). Other neural structures such as the cerebellum, basal ganglia, and brainstem are also considered possible contributors (I. L. Kurtzer, 2015). However, there is still no clear consensus on the origins of the response. Many authors consider it more of a collective net impact of both spinal and supraspinal circuits, which cooperate within a 50-100 ms post-perturbation window (I. L. Kurtzer, 2015).

The LLR's task dependency has been a topic of interest since its discovery in 1956 by Hammond, whose second-ever paper on the topic noticed subject LLRs responded differently when instructed to ”let go” or ”resist” (Hammond, 1956). Since then, multiple studies have consistently demonstrated that LLR modulation depends on the instructions that direct the subjects' intent (Calancie & Bawa, 1985; Lewis et al., 2006; Nashed et al., 2012; Pruszynski et al., 2008; Ravichandran et al., 2013). However, there remains a necessity to diversify the range of instructions provided to subjects, as most paradigms currently feature similar instructions, such as ”resist/let go”, and ”compensate/do not intervene” (Pruszynski & Scott, 2012).

Both visual and auditory modalities have been previously employed in protocols studying the LLR to instruct subjects (Colebatch et al., 1979; Pruszynski et al., 2008). Previous studies on both sensory pathways have shown that their structure and processing latency differ, which brings about different response times (RT). (Jain et al., 2015; Kemp, 1973; Møller, 2011). As of today, there remains a need to better understand how different sensory pathways interact with and contribute to sensorimotor control, and how these pathways differ from each other. However, no studies currently exist that directly compare the influence of the two modalities on the LLR.

Instructing stimuli can be found in many forms in our surrounding environments (Cisek & Kalaska, 2010). Many sensory and cognitive processes work together in localizing and recognizing stimuli, transforming sensory information into perceptual representations that help construct knowledge which leads to decision-making (Cisek & Kalaska, 2010; Gallivan et al., 2018; Wolpert, 1964). Finally, decisions are implemented as actions. To the best of current knowledge, all studies investigating task instruction dependency use clear and coherent instructions in their paradigms (Colebatch et al., 1979; Hammond, 1956; Pruszynski et al., 2008; Rothwell et al., 1980). That does not represent real-world situations, which contain many unclear and conflicting stimuli (Behrmann et al., 2004; Cisek & Kalaska, 2010; Kerns et al., 2004)

In this study, the goal was to test the effects of instruction modality, along with the coherence of location and direction within each modality, on the amplitude of LLR responses. Subjects performed two identical tasks, one containing visual instructions and another with auditory instructions. The instructions would alternate between presenting coherent and incoherent directions and locations in each modality task. A wrist perturbator occasionally applied rapid countering perturbations to the subjects' hands, eliciting stretch reflexes that were studied using electromyography (EMG).

It is hypothesized that LLR amplitudes are dependent on instruction modality, due to differing latencies of visual and auditory pathways, which subsequently affect limb configuration, muscle contraction, and motor planning. Faster RTs observed during auditory tasks are expected to result in lower LLR amplitudes. Furthermore, it is hypothesized that the coherence between instruction direction and location increases LLR amplitudes during both visual and auditory modality tasks. Incoherent instructions are expected to reduce the long-latency (LL) stretch component amplitude by affecting decision confidence, which in turn influences subject intent and task performance (Gallivan et al., 2018). The experimental paradigm also enables the investigation of novel neural substrates that potentially contribute to LLR modulation, leading to a better understanding of one of the most complex mechanisms underlying human motor control.

2

Methods

2.1. Apparatus

The device used is a wrist manipulator called the PoPe (Schouten et al., 2006). Fig. 2.1 shows a top view of the device, with its main parts listed. The PoPe is a system consisting of a servo-motor controlling the position, velocity or force of the handle which the participants grab a hold of. The handle (A in Fig. 2.1) can move in a range of +/- 0.436 radians (+/- 25°) and is used to apply perturbations to the subject's hand. Fig. 2.1 also shows the zero angle, located in the middle of the handle's range of motion. The PoPe also has two pads (B1 and B2 in Fig. 2.1), used to keep the participant's forearm in place during the experiment. These pads are adjustable to the needs of the participant. The platform (C in Fig. 2.1) is where subjects place their forearms when grabbing the handle. Lastly, two plastic screws (D1 and D2 in Fig. 2.1), found on each side of the device platform, are used to lock the handle in any desired position to conduct maximum voluntary contraction (MVC) tests.

Along with the PoPe, a desktop screen displayed the experiment's interactive graphical user interface (GUI), such as the targets, cursor, and visual cues. A pair of headphones were used to deliver auditory instructions to the subjects. A safety button was provided next to the PoPe for subjects to use in case they experienced any discomfort or pain.

2.2. Subject Preparation/Experiment Setup

Seventeen right-handed, healthy individuals participated in the experiment (11 male and 6 female; mean age = 26.3). Participants included mostly students, found through personal networks, who all consented through the consent form. The protocol was approved by the Human Research Ethics Committee (application number: 3952). No subjects were paid for their participation.

Before experimentation began, electrodes were placed on subjects' arms to record surface electromyography (EMG) from the main wrist muscles: flexor carpi radialis and extensor carpi radialis. The muscle bellies were located through palpation, and markers were drawn on the subjects' arms as references for electrode placement. A two-bar electrode (Delsys, Boston, MA) was affixed over the muscles using an adhesive interface. The orientation of the electrode bars was perpendicular to the muscle fibres. The reference electrode was placed on the participant's elbow. EMG data was sampled at 2500 Hz and amplified (gain = 1k), and with these settings, the Delsys main amplifier unit (Delsys Incorporated) filters the signal to bandwidth between 20 Hz and 450 Hz.

Subjects were seated in an adjustable chair and placed their dominant forearm on the PoPe's platform. The pads of the PoPe and the chair were adjusted according to the participant's preference. Subjects are given headphones only during the auditory task. During the experiment, the elbow and shoulder joint movement was not restricted, but subjects were asked to use only wrist motion to complete the task.

2.3. Protocol

At the beginning of each experiment, the MVC was collected. Subjects applied their maximum effort to the PoPe handle locked at the zero angle (Fig. 2.1) for 8 seconds in the direction instructed. First,

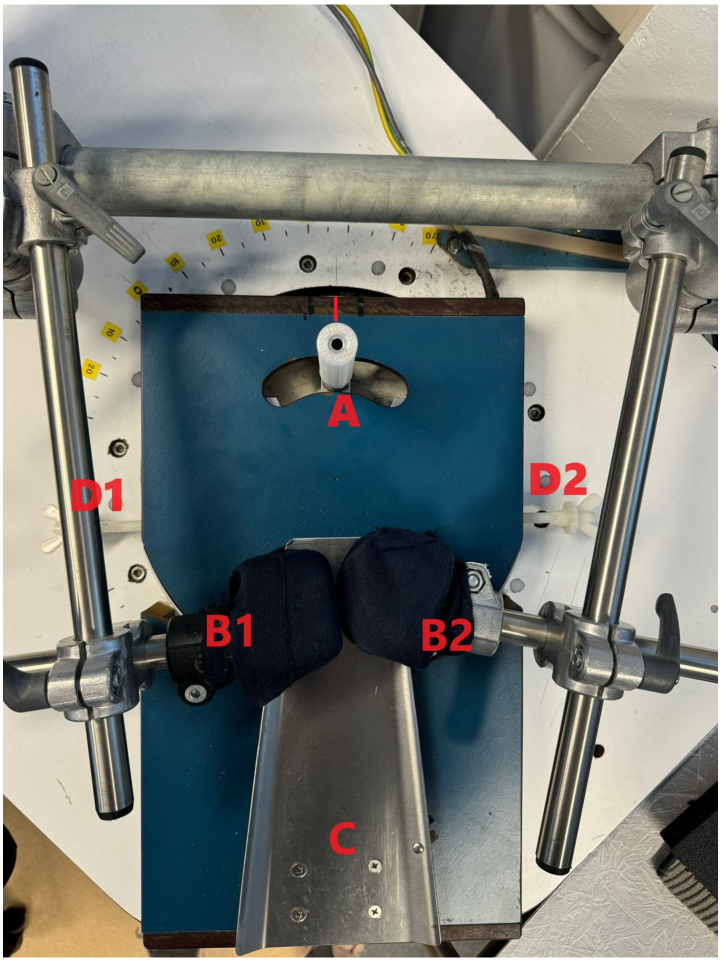

Figure 2.1: A top view of the PoPe, with each key component labelled: A) Handle; B1 and B2) Pad cushions; C) Platform; D1 and D2) Plastic screws. The red line on the top of the device refers to the zero angle.

the MVC of the wrist flexor was recorded, followed by that of the extensor. The MVC was collected to normalize the EMGs of each muscle in subsequent analyses. The flexion torque was also collected, as it was used to set the background load applied during the length of the experiment, which was 1% of the maximum value.

The experimental paradigm consisted of two identical tasks designed to elicit LLRs in wrist flexors and extensors during trials while subjects were instructed to move towards a designated target. As the trial began, an interactive GUI was shown to the participants. Fig. 2.2 displays the subject seated before the trial GUI. Two targets were presented to them as two red circles at each edge of the screen, along with the starting position, a smaller red circle (base target) found in the centre. An x-shaped cursor is also present, which subjects could control using the handle to reach the targets.

As the trial starts, the subject is asked to move the cursor to the designated position, the base target. A 3-second countdown then begins, during which subjects must hold the cursor in place. Once the countdown ends, the participant is instructed to move to either the left or right target, responding as quickly as possible to the instruction. To reach the left or right target, flexion or extension of the wrist is required, respectively. Once subjects reach the target, they must hold the cursor on the designated target until ”Trial Completed!” is displayed, which signifies the end of the trial. The whole trial lasts 8 seconds in total.

Instructions were given visually (VIS) in one task and auditorily (AUD) in the other. The order of modalities was counterbalanced so that approximately equal numbers of participants started with each type of instruction, with 8 out of 17 subjects beginning with VIS. Each task contained 120 trials in total. During the visual task, instructions consisted of arrows pointing left or right, displayed on the desktop screen. Auditory instructions were delivered through headphones, with subjects hearing the words ”left”

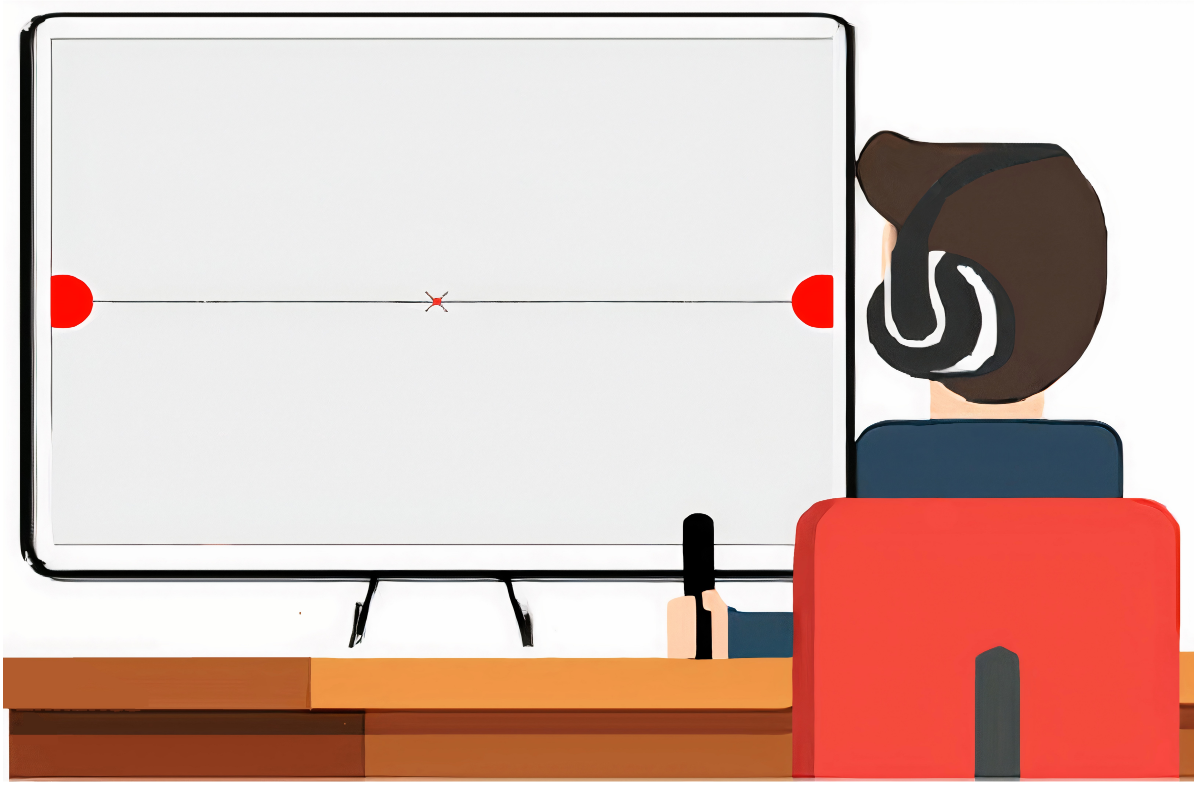

Figure 2.2: A graphical representation of the experimental setup depicts the subject seated in front of the user interface, grasping the handle. In the image, the subject is using headphones, indicating an auditory task. The interactive user interface depicted in the figure is presented to the subjects at the beginning of each trial. One of the two targets, represented by red circles on each edge of the screen, is to be reached by the subjects when instructed. The smaller red circle in the middle of the screen is the base target, where subjects must begin the trial. The x-shaped cursor is controlled by subjects to reach the targets.

or ”right”, with no other visual cues related to it. Fig. 2.3 visually represents both instruction modalities and types.

Subjects were presented with two types of instructions, ”normal” and ”misdirecting”. The coherence of the instructed direction and location varied between the two instruction types. Normal instructions consisted of a coherent direction and location, e.g., an arrow pointing right on the right side of the screen, or hearing the word ”left” on the left ear of the headphone. Normal instructions for the visual and auditory modalities are denoted VIS-N and AUD-N in the study, respectively. Fig. 2.3 (top) shows examples of normal instructions. Misdirecting instructions included incoherent directions and locations, e.g., an arrow pointing right on the left side of the screen, or the word ”left” heard in the right ear of the headphones. Misdirecting instructions for the visual and auditory modalities are denoted VIS-M and AUD-M, respectively. Fig. 2.3 (bottom) shows examples of misdirecting instructions. In the 120 trials of both tasks, there was an equal amount of left and right instructions. Misdirecting instructions constituted one-third of the total instructions per modality and were equally distributed between the left and right sides.

During each modality task trial, there was a 1 in 4 chance that the subject would experience a perturbation. The applied disturbances always opposed the instructed movement during the trial, inducing extensions when the left target was specified, and flexions when the right target was specified. Perturbations in the extension direction elicited flexion stretch reflexes, whereas those in the flexion direction elicited extension reflexes. These perturbation specifications applied to all subjects, who were all right-handed. Equal numbers of perturbations inducing flexion and extension were used during the experiment. Fig. 2.4 shows the subject's hand installed in the PoPe and the directions of the applied perturbations. The PoPe handle is first set to Force mode to allow free movement. During perturbed trials, the MATLAB Simulink controller switches to Velocity mode to apply 5.4 rad/s, 100 ms long velocity perturbations to the hand and then switches back to Force mode after the perturbation is applied.

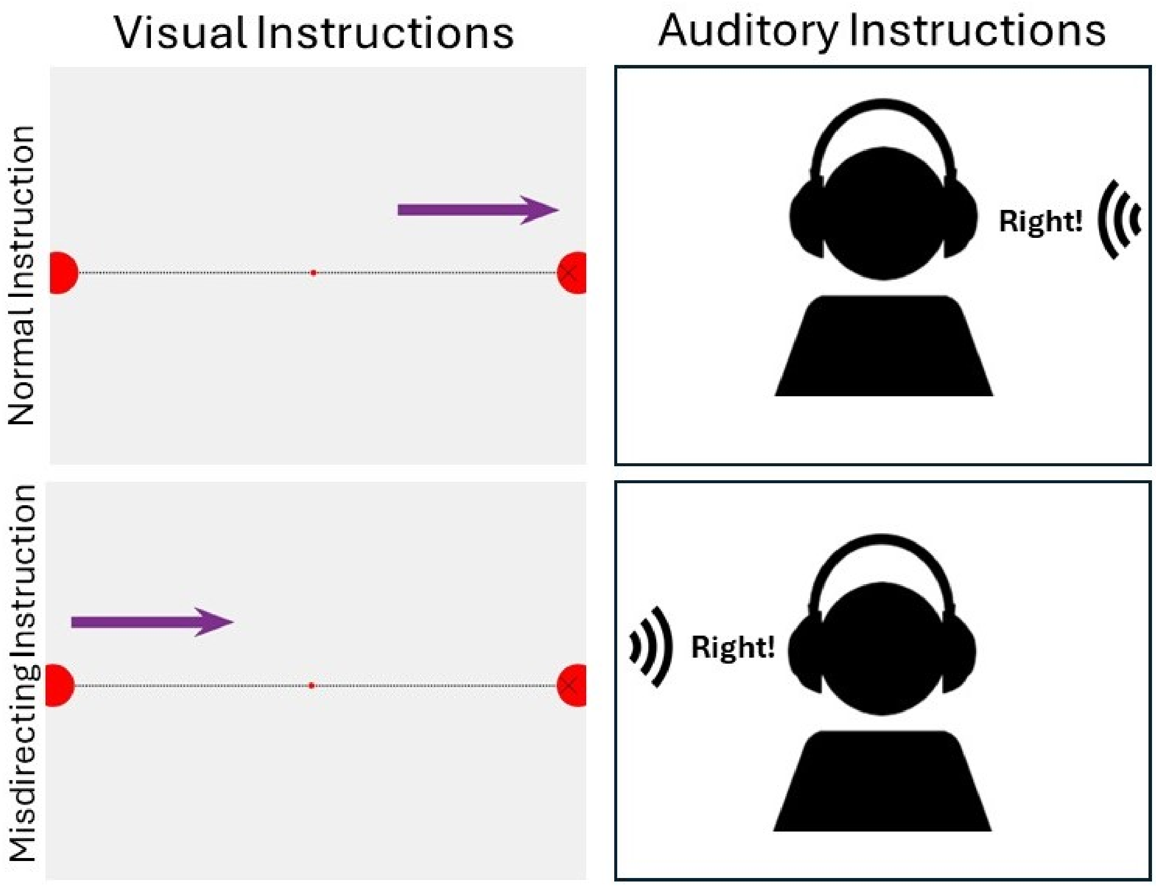

Figure 2.3: Graphical representation visual (left) and auditory (right) instructions. Visual instructions, in the form of arrows, appear as they would in the user interface. Auditory instructions are represented by a participant, with their back facing the reader, hearing the instruction through headphones. Normal instructions are found in the top row, with the location of the instruction coinciding with the direction instructed. Misdirecting instructions are found on the bottom row, with the location of the instruction conflicting with the direction instructed.

The perturbation onset for both modalities was pre-determined based on my average RT across 20 unperturbed trials. The onset was to match the RT to the instruction. For the visual task, the perturbation onset was set at 3.25 s post-trial onset in the visual task. For the auditory task, a perturbation onset of 3.85 s was used. The difference in perturbation timings between modalities was due to software issues resulting in a lag in the sound output relative to the intended timing. This led to a slight shift in auditory instruction after the countdown ended. Thus, the perturbation timing was shifted to match the delayed RT. Fig. 2.5 shows a step-by-step graphical representation of the experimental paradigm.

Both experiment parts were split into five blocks of 24 trials. Each block included perturbations in 1/4th of the trials. Of the 24 trials, 1/3rd of them contained misdirecting instructions. Each block contained an equal number of flexion and extension-inducing perturbations. Similarly, all blocks had the same amount of ”left” and ”right” directing instructions. The instruction conditions and perturbations were randomly allocated throughout each block to achieve a fair and counterbalanced distribution.

2.4. Post-Experiment Questionnaire

After the experiment concluded, a short questionnaire was given to the subjects, containing multiple-choice questions about their experience during the experiment. Subjects were asked to express their preference between the two instruction modalities based on the clarity of the instruction (Q1). They were also asked about the perceived difficulty of misdirecting instructions compared to normal ones (Q2), with an additional prompt to explain their preference. Additionally, subjects were asked whether they perceived the task increasingly challenging as the experiment progressed (Q3). The impact of

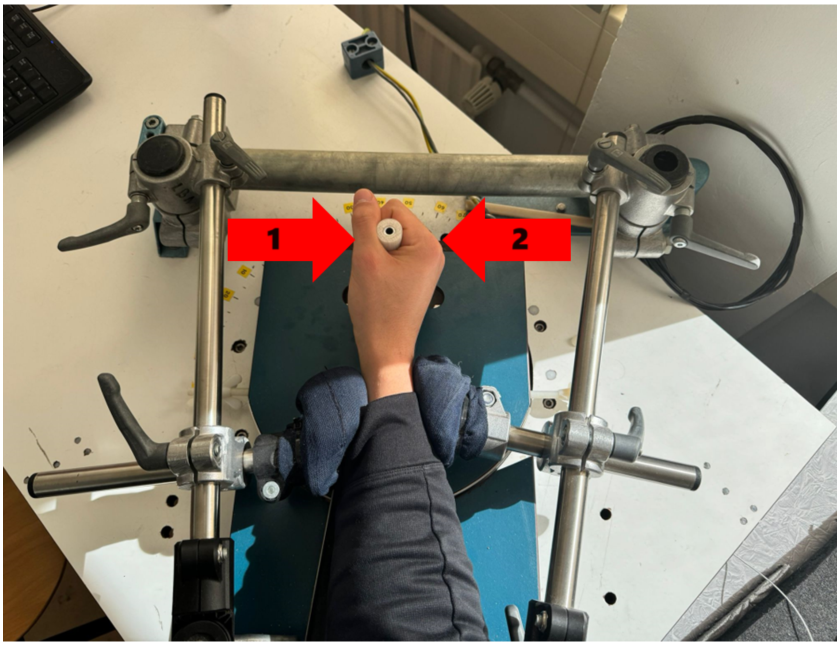

Figure 2.4: A top view of the PoPe, with a participant's hand already set up. The red arrows represent the perturbations which are applied to the subject's hand through the PoPe's handle. Arrow 1 represents an extension-inducing perturbation, whereas arrow 2 represents a flexion-inducing one.

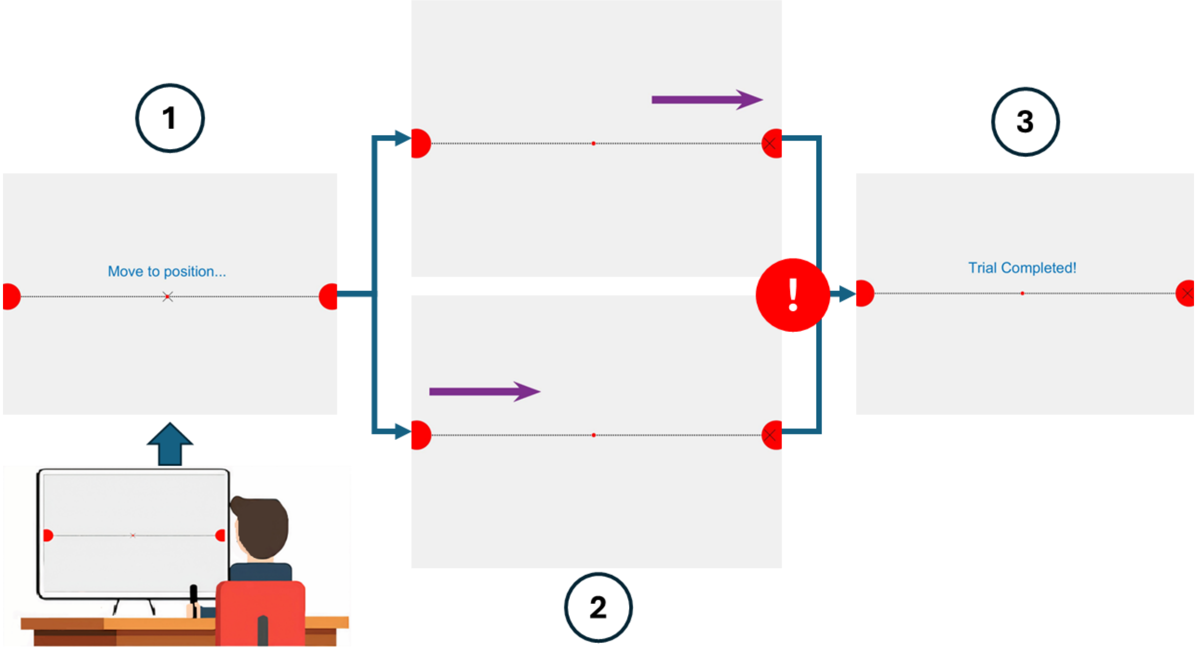

Figure 2.5: A step-by-step graphical representation of the experimental trial. In the bottom left corner, the subject is set up in front of the screen, holding the PoPe handle. After trial onset, the subject is shown the text ”Move to position”, and must first move to the base target (Step 1), in the middle of the screen. After a countdown, the subject is instructed to go to one of the two directions (Step 2). In this example, the visual task is underway, so arrows are used. The instruction could either be a normal type (top of step 2) or a misdirecting type (bottom of step 2). Immediately after the subject is instructed, there is a chance a perturbation occurs, which is represented by the red circle with an exclamation point. After the subject reaches the designated target, the trial is completed (Step 3).

encountering a misdirecting instruction on their performance in subsequent trials was also assessed (Q4). The subjects' age and gender were also inquired.

Besides the questionnaire, other additional, more personalized questions were asked of the subjects when novel behaviours were seen. Subjects were asked if they took upon any strategies during any of the experiment parts. If subjects had time, they elaborated on the choices made in their questionnaires. Subjects were also asked to explain why they preferred one of the modalities.

2.5. Data Analysis

Muscle activity and handle position were recorded for each subject. Wrist flexor and extensor EMG data were collected exclusively during perturbed trials to investigate the LLR response. To quantify muscle activity, EMG data was mean-corrected and rectified. After rectification, the maximum EMG signal of the MVC trials was collected and used to normalize the perturbed EMG signals. The final unit of the data was in % MVC. The resulting signals were then low-pass filtered using a 4th-order Butterworth filter with a cut-off frequency of 150 Hz. All EMG data was aligned to perturbation onset. The filtered EMG was averaged across all perturbed trials, which accounted for 30 of the 120 trials per task.

The instruction conditions resulted in four EMG variables per modality. For visual instructions, the data variables included flexor EMG after normal VIS ($FLEX_V - N$), extensor EMG after normal VIS ($EXT_V - N$), flexor EMG after misdirected VIS ($FLEX_V - M$), and extensor EMG after misdirected VIS ($EXT_V - M$). The equivalent data was collected for AUD, resulting in the variables ($FLEX_A - N$), ($EXT_A - N$), ($FLEX_A - M$), and ($EXT_A - M$).

To estimate the LLR amplitude from each average EMG, the area under the curve (AUC) was calculated using Simpson's method (Tallarida & Murray, 1987). The integration was done over the LLR epoch, 50-100 ms post-perturbation onset. The LLR interval was chosen from previous findings in existing literature (I. L. Kurtzer, 2015; Pruszynski & Scott, 2012).

Handle position data was collected during non-perturbed trials to estimate participants' error tendencies, aiming to investigate the effectiveness of misdirecting instructions on subject behaviour, and if their effect changed with the modality of the instructions. Furthermore, it would be used as complementary data to support behaviour observations and reports from the questionnaires.

A neutral zone must first be established to evaluate if an error occurs during a trial, defined as an angle range in which subject movements are considered undecided or uncertain. Fig. 2.6 illustrates the chosen error zone. In the experiment protocol, subjects must bring the cursor to the base target and hold it there until being instructed. Thus, the neutral zone limits were set just outside the base target, corresponding to a handle position of +/- 0.02 rad (or +/- 1.15 °). Any movement beyond the neutral zone was considered an error if they were in the opposite direction to that instructed. Only unperturbed trials were chosen to be studied to avoid perturbations influencing the results, as they would force the hand to move in the same direction as the error limit. The unperturbed trials accounted for 90 out of the 120 trials per task.

Subject error tendencies were estimated by calculating the mistakes and the proportion of trials with mistakes for each modality (error rates). The percentage of errors observed after a misdirecting instruction and the mean error amplitudes, defined as the maximum angle in the wrong direction, across all unperturbed trials were also calculated. Lastly, the total mistakes and mean amplitudes across all 17 subjects were assessed.

2.6. Statistical Analysis

Two statistical comparisons were performed to address the hypotheses posed. The first comparison assessed the impact of the instruction modality on the LLR amplitude estimate. Flexor and extensor LLR AUCs elicited after only normal visual stimuli were compared to those evoked after normal auditory cues, e.g., ($FLEX_V - N$) vs ($FLEX_A - N$). The second comparison evaluated the difference of LLR AUCs following normal and misdirecting instructions to examine the impact of the direction-location coherence within the same modality, e.g., ($FLEX_V - N$) vs ($FLEX_V - M$).

The Shapiro-Wilk normality test decided the statistical test used in the study. If the test indicated normally distributed data, paired t-tests would be used to test the significance of the results. In the case of non-normally distributed data, a Wilcoxon signed-rank non-parametric test would be utilized. For this scenario, medians and the distribution of differences would evaluate the highest data value. While Wilcoxon signed-rank tests do not directly compare medians, they are a good way to infer differences in central tendency between paired samples. Regarding the distribution of differences, if the majority

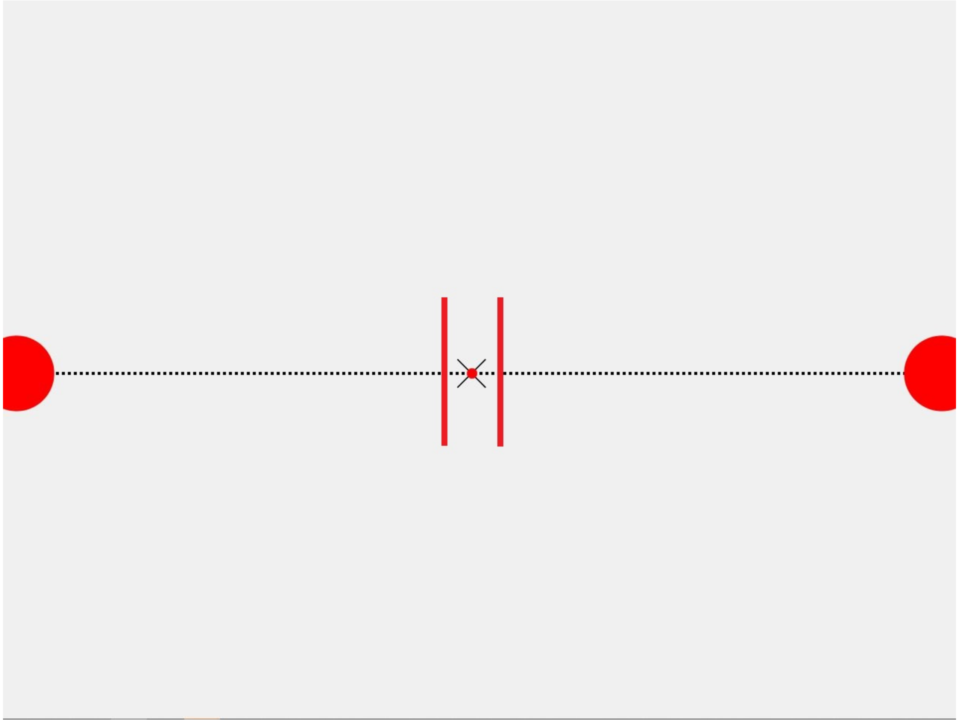

Figure 2.6: The GUI featuring the neutral zone, represented by the area within the two red lines. Any movement where the cursor crosses either of the two lines is considered an error.

of the differences are positive, it indicates that the second measurements are generally larger than the first. On the other hand, if most of the differences are negative, it suggests that the first data group is larger than the second. The number of positive and negative differences are represented by the variables n_{pos} and n_{neg}, respectively.

A statistical analysis was also conducted to compare the mean error amplitudes. Similar to the previous statistical study, a Shapiro-Wilk test was used to determine the normality of the data. If the test indicated that the data followed a normal distribution, paired t-tests would be conducted to evaluate the significance of the results. Alternatively, if the data did not meet the normality assumption, the Wilcoxon signed-rank test, a non-parametric method, would be applied.

3

Results

3.1. Muscle activity evoked by perturbations

Hand displacements caused by countering velocity perturbations consistently resulted in stretch reflex activity in both the flexor and extensor carpi radialis. The post-perturbation activity resulted in higher EMG values than the baseline, defined here as the EMG activity during unperturbed trials.

Specifically, flexion-inducing perturbations resulted in extensor stretch reflexes, whereas extension-inducing ones led to stretch reflex activity in the flexor muscle. Three distinct epochs were recognized post-perturbation onset: SLR (20-50 ms), LLR (50-100 ms), and VOL (100 ms - end). In all three epochs, the mean EMG post-perturbation resulted in higher EMG peak values in both muscle groups. Fig. 3.1 shows an example of the average EMG signals of a subject with all three epochs shown.

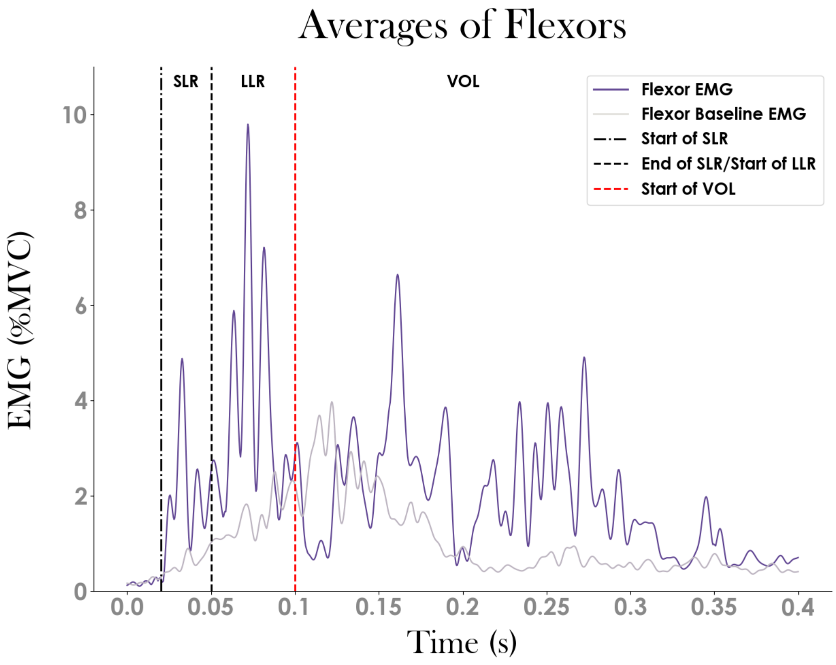

Figure 3.1: Mean EMG data of wrist flexor muscles (flexor carpi radialis) after normal instructions and an extension-inducing perturbation. The short-latency reflex (SLR), long-latency reflex (LLR), and voluntary contraction (VOL) are visible in their respective epochs, 20-50ms, 50-100 ms, and after 100 ms, respectively. The epochs are denoted by vertical dashed lines. The baseline EMG is also displayed, representing the flexor muscle activity in the same instruction conditions while unperturbed. The y-axis shows the mean LLR EMG area under the curve (AUC), in units of maximum voluntary contraction percentage (%MVC).

In some subjects, the latency of their stretch responses appeared to be delayed compared to the rest. The first observed stretch reflex activity was in the LLR epoch, with no SLR activity present. While three peaks of LLR activity were still present, they were recorded at a later latency. Fig. 3.2 illustrates the delayed stretch response behaviour. The delayed responses did not affect the determination of stretch component time windows throughout the study.

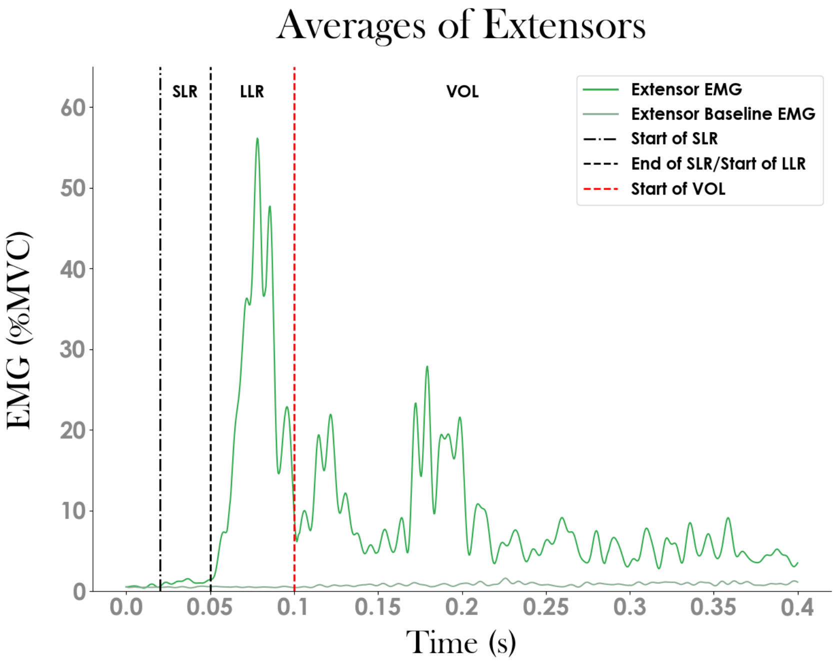

Figure 3.2: A delayed mean EMG data of wrist extensor muscles (extensor carpi radialis) after normal instructions and a flexion-inducing perturbation. No reflex activity is found in the short-latency reflex (SLR) epoch (20-50 ms). The long-latency reflex (LLR) and voluntary contraction (VOL) are visible in their respective epochs, 50-100 ms and after 100 ms, respectively. The epochs are denoted by vertical dashed lines. The baseline EMG is also displayed, representing the extensor muscle activity in the same instruction conditions while unperturbed. In this example, due to the subject consistently responding late during unperturbed trials, the response is not in the given time window. The y-axis shows the mean LLR EMG area under the curve (AUC) in units of maximum voluntary contraction percentage (%MVC).

3.2. Comparison between Visual and Auditory instructions

Normality test results concluded that all the average LLR AUC data points followed a non-normal distribution. Therefore, Wilcoxon signed-rank tests assessed the significance of the comparisons.

LLR responses in wrist flexors exhibited significantly different AUCs when elicited after visual or auditory instructions $[FLEX : (VIS - N)\ vs\ (AUD - N) : W = 27; p = 0.0174]$. Fig. 3.3 (right) shows the median comparison, which revealed that the estimated flexor LLR amplitude post-VIS-N was higher than that after AUD-N $[FLEX : 0.16\ (AUD - N) < 0.34\ (VIS - N)]$. The direction of differences tended to favour the estimated amplitude of LLRs post-VIS-N as well $[FLEX : (AUD - N) - (VIS - N) : n_{\text{pos}} = 5; n_{\text{neg}} = 12]$. Fig. 3.4 (right) depicts the distribution of tendencies for results in flexor muscles.

The Wilcoxon signed-rank test revealed a significant difference in LLR signal AUCs between subjects instructed visually versus auditorily in wrist extensors $[EXT : (VIS - N)\ vs\ (AUD - N) : W = 19; p = 0.00463]$. When comparing the LLR amplitude estimates of the data groups, the median comparison showed that signals post-VIS displayed larger values than LLRs post-AUD during normal-type instructions $[EXT : 0.26\ (AUD - N) < 0.36\ (VIS - N)]$. Fig. 3.3 (left) shows the median comparison for extensor muscles. The direction of the differences also determined that VIS-N led to larger LLR signals $[EXT : (AUD - N) - (VIS - N) : n_{\text{pos}} = 4; n_{\text{neg}} = 13]$. Fig. 3.4 (left) visually represents the difference distribution. Thus, we can conclude that LLR AUCs after VIS-N are significantly larger than those post-AUD-N in both wrist flexors and extensors.

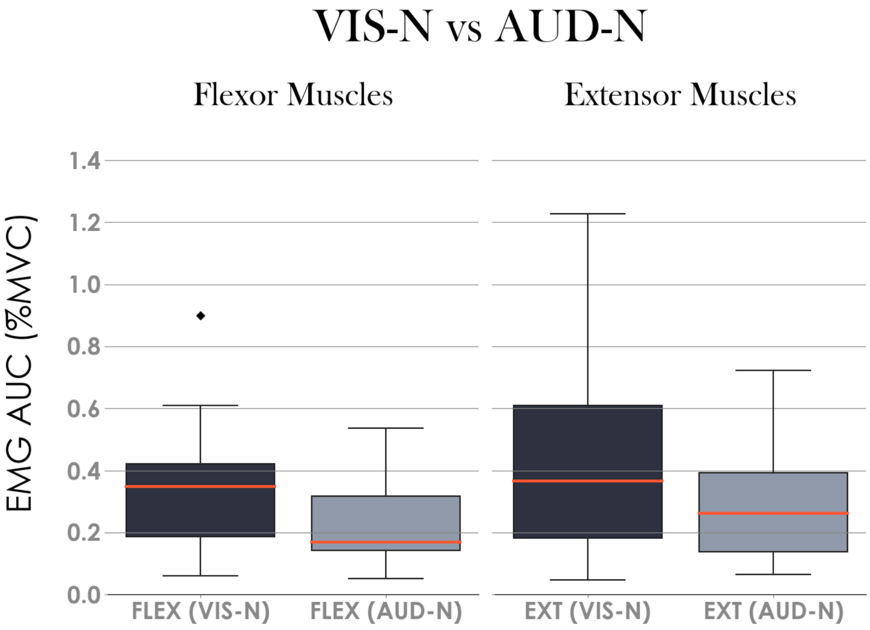

Figure 3.3: Comparison of the data distribution of mean long-latency reflex (LLR) amplitude estimates (area under the curve across the LLR epoch) in wrist flexors (left) and extensors (right) after normal visual (VIS-N) and normal auditory (AUD-N) instructions. On the y-axis, LLR AUC in units of percentage of maximum voluntary contraction (MVC). The median is highlighted by the orange line. It estimates whether the LLR AUCs of one group are significantly larger than those of the other group. The outliers are denoted by the diamond-shaped markers.

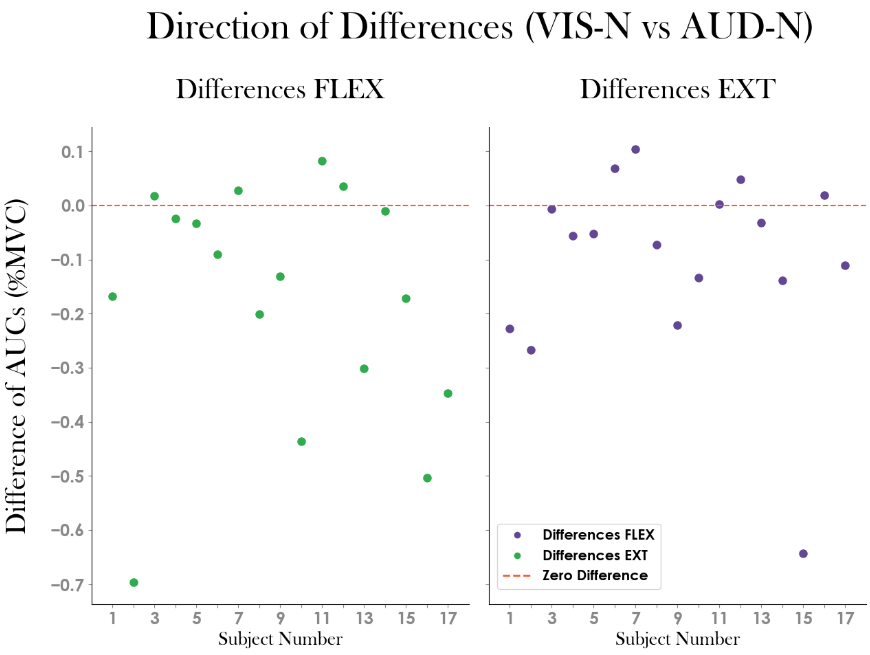

Figure 3.4: Scatter plots displaying each subject's direction of differences between long-latency reflex (LLR) amplitude estimates (area under the curve across the LLR epoch) in wrist flexors (left) and extensors (right) after normal auditory (AUD-N) and normal visual (VIS-N) instructions. If most differences are positive, measurements after AUD-N are generally larger than those after VIS-N. The y-axis shows the difference between mean LLR AUCs after AUD-N and VIS-N in units of percentage of maximum voluntary contraction (MVC). The orange dashed line signifies where a difference of zero would be located.

3.3. Comparison between Normal and Misdirected instructions

Marginally significant differences were observed in the long-latency component of flexors after normal and misdirecting visual instructions [$FLEX : (VIS - N)\ vs\ (VIS - M) : W = 39; p = 0.0797$]. When evaluating the comparison in wrist flexors, the medians showed that post-VIS-M LLR AUCs were smaller than the results post-VIS-N [$FLEX : 0.238\ (VIS - M) < 0.348\ (VIS - N)$]. Fig. 3.5 (right) shows the median distribution for flexor muscles. Displayed in Fig. 3.6 (right), the difference distribution showed the same LLR tendencies [[$FLEX : (VIS - M) - (VIS - N) : n_{\text{pos}} = 6; n_{\text{neg}} = 11$]. Therefore, both tests found that misdirecting instructions again resulted in lower LLR responses post-perturbation in wrist flexors compared to normal ones. This demonstrates a consistent trend in the impact of misdirecting instructions during visual tasks.

A significant difference was found in LLR signal estimated amplitudes between normal and misdirected visual instructions in wrist extensors [$EXT : (VIS - N)\ vs\ (VIS - M) : W = 0.0; p = 0.000015$]. Reflexes following misdirecting instructions were lower than those after normal instructions, exhibited by the results of the median comparison [$EXT : 0.184\ (VIS - M) < 3.65\ (VIS - N)$], Fig. 3.5 (left), and difference directions [$EXT : (VIS - M) - (VIS - N) : n_{\text{pos}} = 0; n_{\text{neg}} = 17$], Fig. 3.6 (left).

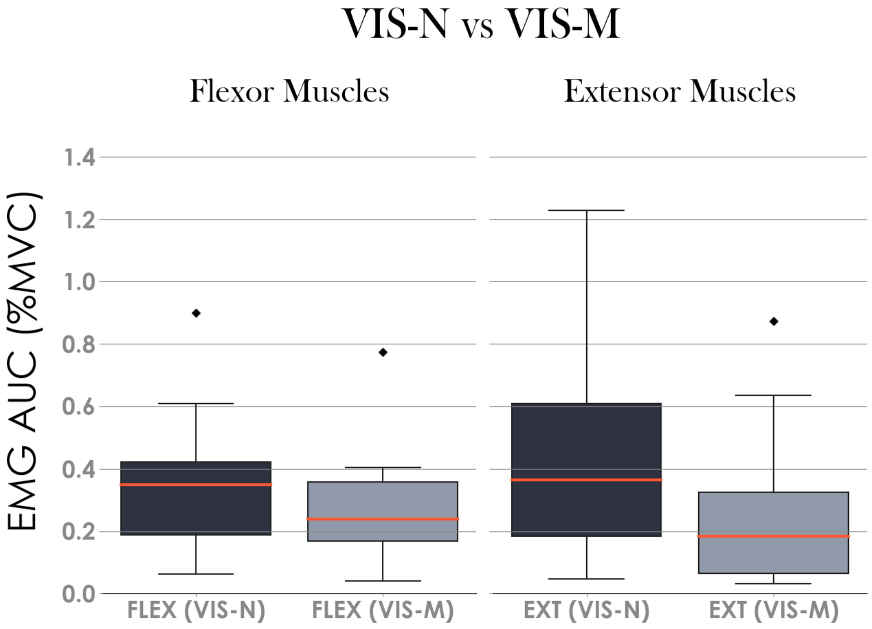

Figure 3.5: Comparison of the data distribution of mean long-latency reflex (LLR) amplitude estimates (area under the curve across the LLR epoch) in wrist flexors (left) and extensors (right) after normal visual (VIS-N) and normal auditory (VIS -M) instructions. On the y-axis, LLR AUC in units of percentage of maximum voluntary contraction (%MVC). The median is highlighted by the orange line. It estimates whether the LLR AUCs of one group are significantly larger than those of the other group. The outliers are denoted by the diamond-shaped markers.

Comparisons between AUCs of LLR signals evoked in wrist flexors did not lead to any significant differences [$FLEX : (AUD - N)\ vs\ (AUD - M) : W = 74; p = 0.9265$]. Likewise, the LLR response amplitude estimates in the extensor muscles, following normal and misdirecting auditory instructions, showed no significant differences [$EXT : (AUD - N)\ vs\ (AUD - M) : W = 68; p = 0.7119$]. Thus, no significant effect of misdirecting auditory instructions on LLR AUC was observed in either wrist flexors or extensors.

3.4. Post-experiment questionnaire and interview

Fig. 3.9 summarizes the results of the post-experiment questionnaire multiple-choice questions, filled in by all 17 subjects. The majority of subjects (65%) preferred the auditory instructions to the visual ones. Most participants (82%) answered Q2 by saying misdirecting instructions were harder to follow than normal ones. Next, most participants (53%) found that dealing with misdirecting instructions did

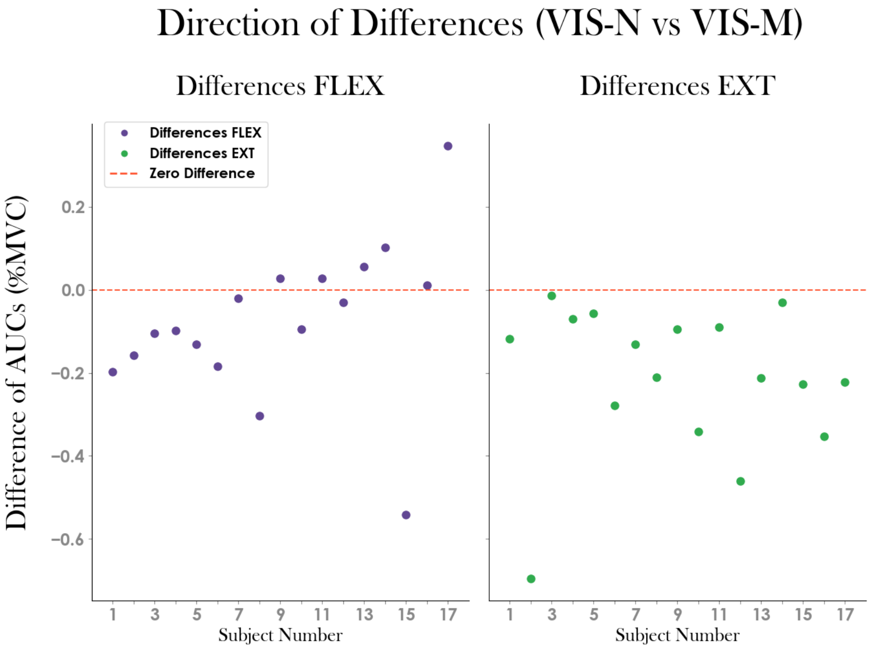

Figure 3.6: Scatter plots displaying each subject's direction of differences between long-latency reflex (LLR) amplitude estimates (area under the curve across the LLR epoch) in wrist flexors (left) and extensors (right) after normal visual (VIS-N) and misdirecting visual (VIS-M) instructions. If the majority of the differences are positive, it indicates that measurements after VIS-M are generally larger than those after VIS-N. The y-axis shows the difference between mean LLR AUCs after VIS-M and VIS-N, in units of percentage of maximum voluntary contraction (MVC). The orange dashed line signifies where a difference of zero would be located.

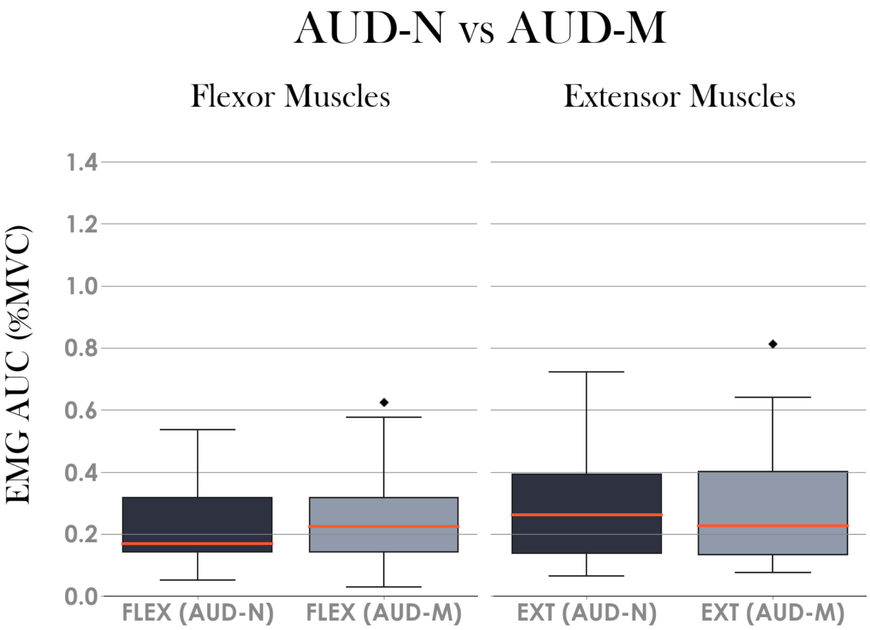

Figure 3.7: Comparison of the data distribution of mean long-latency reflex (LLR) amplitude estimates (area under the curve across the LLR epoch) in wrist flexors (left) and extensors (right) after normal visual (AUD-N) and normal auditory (AUD-M) instructions. On the y-axis, LLR AUC in units of percentage of maximum voluntary contraction (%MVC). The median is highlighted by the orange line. It estimates whether the LLR AUCs of one group are significantly larger than those of the other group. The outliers are denoted by the diamond-shaped markers.

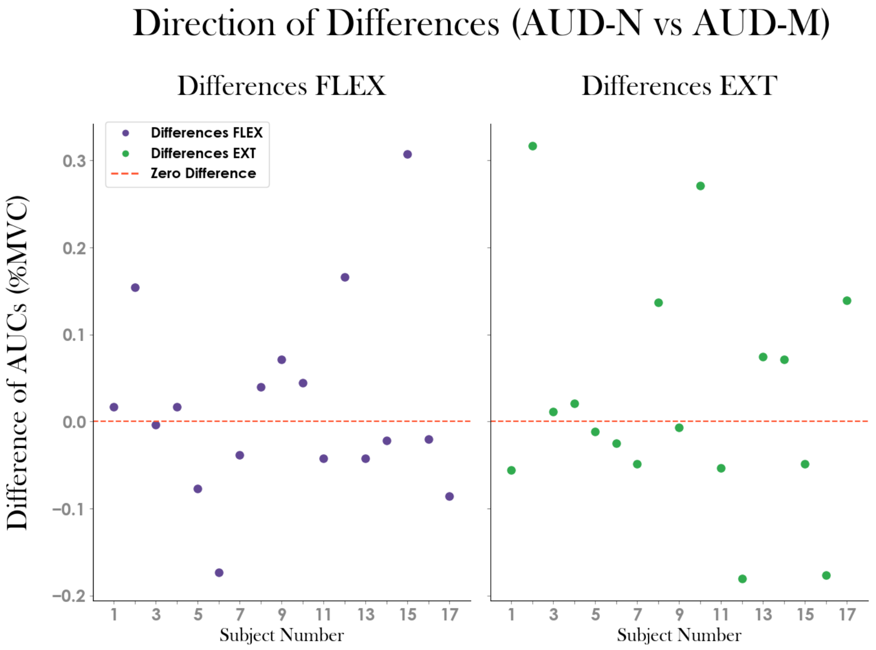

Figure 3.8: Scatter plots displaying each subject's direction of differences between long-latency reflex (LLR) amplitude estimates (area under the curve across the LLR epoch) in wrist flexors (left) and extensors (right) after normal visual (AUD-N) and misdirecting visual (AUD -M) instructions. If the majority of the differences are positive, it indicates that measurements after AUD -M are generally larger than those after AUD -N. The y-axis shows the difference between mean LLR AUCs after AUD -M and AUD -N, in units of percentage of maximum voluntary contraction (MVC). The orange dashed line signifies where a difference of zero would be located.

not become more difficult as the experiment progressed. Finally, a significant portion of subjects (70%) reported that responding to a trial immediately after experiencing misdirecting instructions was not more difficult than responding to a trial after normal instructions.

All but one subject was asked supplementary questions after the post-experiment questionnaire. All subjects elaborated on their challenges related to the task and the instruction modalities. They then described how they approached the experiment and devised strategies to overcome their difficulties. The opposite was also true, as subjects described why they did not experience any difficulties completing the task, even if they had one preferred modality. The supplementary questions shed light on many discrepancies in how subjects viewed and conducted themselves during the experiment.

People who preferred AUD found that keeping track of the arrows' direction and location was challenging. Some reported that the shapes of the two arrow types (normal and misdirecting) were too hard to distinguish at times, which led to either wrong or delayed responses. They mentioned that it would have helped if the colours of the arrows were different. The need to shift their gaze across the different locations of the screen was also considered a challenge. Some subjects reported that the constant gaze shifting combined with the meticulous observation needed to discern the misdirecting arrows from the normal ones led to a faster loss of concentration during the visual trials.

Several participants reported employing strategies to handle VIS. For most subjects, the primary approach was to distance themselves from the screen to reduce their gaze-shifting as much as possible. Others mentioned attempting to focus on only specific areas of the screen, e.g., where the arrow's main body would appear. Another subject directed their attention to the centre of the screen, focusing on the arrow base rather than its tips. Similar to before, the strategy aimed to reduce attention shifting as much as possible.

Some of the challenges associated with AUD arose from difficulties in distinguishing between the sound's source and the word's intended meaning. Participants who struggled with this modality reported that the sound caught their attention first, moving towards its direction before comprehending it, leading to erroneous movement. Even when subjects understood the word, many reported difficulties in accurately interpreting the intended direction. They stated that this task demanded greater cognitive

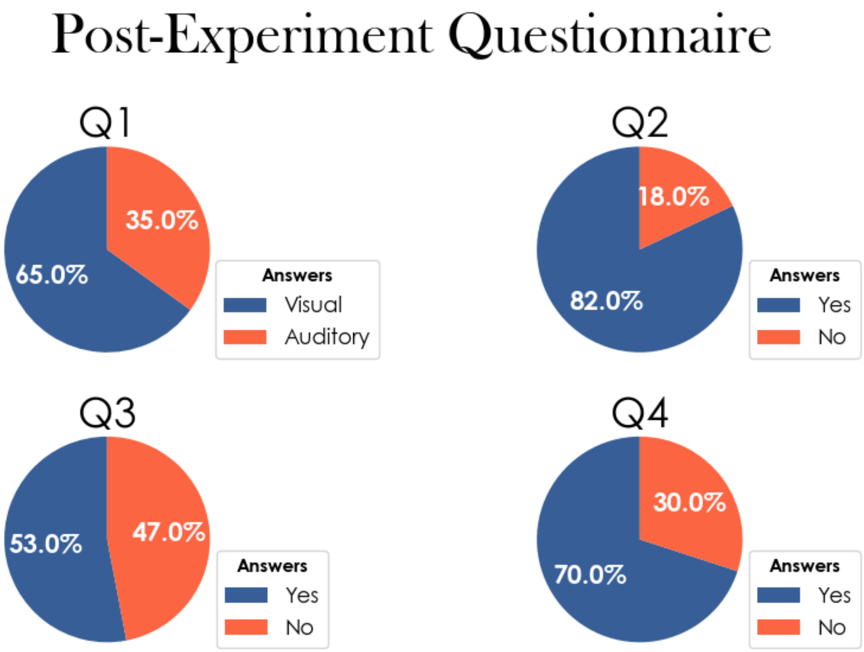

Figure 3.9: A summary of the responses to the four questions in the post-experiment questionnaire. All questions were multiple choice (two options). The questions were Q1: "Which modality do you prefer?"; Q2: "Were misdirecting instructions more challenging than normal ones?"; Q3: "Did dealing with misdirections become more difficult as the experiment continued?"; Q4: "Did misdirecting instructions influence the response of the subsequent trial?".

effort than the visual task, which, for them, clearly indicated the target subjects had to reach. These subjects also found integrating information from multiple senses to be challenging, as they had to focus on the cursor and target location while also listening to the instruction.

Many subjects devised strategies to effectively perform the auditory task. Most people removed their attention from the screen or closed their eyes once they reached the base target. This strategy reportedly helped them focus solely on instruction comprehension. Others stated they attempted to disregard the change in location side and focus on the word itself, as the words were sufficiently distinct to differentiate between them. This tactic was challenging to implement during visual instructions due to the arrows resembling each other. One subject attempted to leverage the speed of sound detection to their advantage. Once they identified its source, they would promptly respond and move towards the corresponding target before fully understanding the instruction. They then made corrections on the fly if they realized they had errored.

Some subjects did not find the tasks hard to execute, stating they could consistently succeed in completing the task with minimal errors. When asked to explain why the tasks were easy, visual instructions were described to clearly indicate the corresponding target, even in cases of incoherent instructions. Three subjects reported being unaware of any difference in sound source side during the auditory task. Instead, they recognized the word and followed it accordingly. However, one subject noted that after making an initial mistake, subsequent errors became more likely due to increased awareness of the instruction's confusing aspects.

3.5. Error estimation

Tables 3.1 and 3.2 summarize the study's findings regarding subjects' error tendencies during VIS and AUD, respectively. Each table includes data on total errors, error rate, error rate following misdirection, and mean error amplitude for each subject in both tasks. Additionally, the mean of each variable across all subjects was calculated along with the total mistakes of each task.

In 11 out of 17 subjects, the preferred modality choice reflected the lowest error rates. Two subjects which did not display this behaviour made an equal number of errors in both tasks. Four subjects

Subject Number	Modality Preference	Mis-takes	Overall Error Rate (%)	Error Rate post-misdirection (%)	Mean Error Amplitude (rad)
1	AUD	13	28.89	84.62	0.22
2	AUD	15	16.67	100	0.13
3	AUD	1	1.11	100	0.02
4	AUD	8	8.89	87.5	0.14
5	AUD	4	4.44	50	0.23
6	VIS	7	7.78	100	0.09
7	AUD	2	2.22	100	0.15
8	AUD	12	13.33	91.67	0.15
9	VIS	21	23.33	85.71	0.09
10	AUD	3	3.33	66.67	0.04
11	VIS	3	3.33	100	0.08
12	AUD	11	12.22	100	0.11
13	AUD	11	12.22	81.82	0.08
14	VIS	5	5.56	100	0.12
15	VIS	7	7.78	100	0.09
16	VIS	2	2.22	50	0.03
17	AUD	27	30	70.37	0.15
Means	-	8.94	10.78	86.37	0.11
Totals	-	152	-	-	-

Table 3.1: A summary of the error estimation results for the Visual Task. This estimation was done by investigating the errors during unperturbed trials. Each subject's preferred modality, mistakes made, percentage of trials with errors (Error Rate), overall percentage of errors after a misdirecting instruction (Error Rate post-misdirection), and mean error amplitude during the task were collected. The means of each variable were calculated across all subjects. The total number of mistakes during the visual task from all subjects was also calculated.

showed higher error rates within their preferred modality. The mean amplitude of errors was not consistently higher in the least preferred modality, with only 9 out of 17 subjects exhibiting the trend.

Behaviour after experiencing VIS resulted in a higher total number of mistakes in all subjects (152) compared to post-AUD (124). The average error rate across subjects after visual cues (4.78%) was higher than error rates after AUD (2.53%). Paired t-tests revealed that subjects exhibited significantly higher mean amplitudes following AUD compared to VIS [t = -2.99; p = 0.0087].

Most errors after VIS and AUD occurred after misdirecting instructions, 86.4 % and 75.4 %, respectively. Subjects also demonstrated errors after normal instructions, a behaviour found in all but two participants. Despite a lower overall mistake rate after AUD, subjects exhibited higher error rates for normal instructions with speech cues (24.6 %) compared to visual cues (13.6 %).

Subject Number	Modality Preference	Total Mistakes	Overall Error Rate (%)	Error Rate post-misdirection (%)	Mean Error Amplitude (rad)
1	AUD	9	10	77.78	0.25
2	AUD	13	14.44	84.62	0.19
3	AUD	1	1.11	0	0.14
4	AUD	4	4.44	100	0.12
5	AUD	3	3.33	100	0.16
6	VIS	5	5.56	100	0.17
7	AUD	3	3.33	100	0.23
8	AUD	7	7.78	71.43	0.21
9	VIS	21	23.33	80.95	0.16
10	AUD	0	0	0	0
11	VIS	10	11.11	50	0.16
12	AUD	6	6.67	83.33	0.25
13	AUD	3	3.33	100	0.21
14	VIS	4	4.44	50	0.15
15	VIS	6	6.67	50	0.06
16	VIS	3	3.33	100	0.1
17	AUD	26	28.89	57.69	0.14
Means	-	7.29	8.10	75.36	0.16
Totals	-	124	-	-	-

Table 3.2: A summary of the error estimation results for the Auditory Task. This estimation was done by investigating the errors during unperturbed trials. Each subject's preferred modality, mistakes made, percentage of trials with errors (Error Rate), overall percentage of errors after a misdirecting instruction (Error Rate post-misdirection), and mean error amplitude during the task were collected. The means of each variable were calculated across all subjects. The total number of mistakes during the visual task from all subjects was also calculated.

4

Discussion and Conclusion

4.1. Discussion

The Effect of Visual and Auditory Instructions

The hypothesis predicted that LLR amplitudes will vary depending on the modality of the instruction, specifically between auditory and visual modalities. The results support the hypothesis, showing that LLR amplitude estimates, calculated as AUC over the LLR epoch, were significantly larger after being instructed visually than in the auditory modality in both wrist flexors and extensors.

The difference in stretch reflexes due to the modality can be explained by the difference in RT between the two modalities. RTs post-AUD are faster than those post-VIS, as seen in studies by Jain et al. and Kemp et al. (Jain et al., 2015; Kemp, 1973). Different modality processing times bring about physical changes in limb configuration and state of motion, which have been shown to influence LLR amplitude (Bawa & Sinkjaer, 1999; I. L. Kurtzer et al., 2008). During the current study, subjects responded faster during AUD, with multiple subjects managing to react before the perturbation onset. Bawa et al.'s results showed that perturbations applied during movement resulted in lower LLR amplitudes than those seen during static tasks (Bawa & Sinkjaer, 1999). Another study by Kizuka et al. concluded that a faster response onset inhibits LLRs to help the effectiveness of voluntary reactions, as subjects could construct a more appropriate motor set (Kizuka et al., 1997). Furthermore, the variation in LLR results is likely influenced by modality preference. In addition to the inherent neural delay differences affecting RT, subjects responded faster and more accurately in their preferred modality, which for most was auditory. Thus, faster RTs during the auditory trials led to lower LLR AUCs.

The handle inheriting the user's velocity before applying the perturbation may also contribute to the lower LLR AUCs observed. The controller settings caused the handle to inherit its previous velocity when switching from Force mode to Velocity mode to apply the perturbation. If subjects responded before perturbation onset, their velocity counteracted the perturbation, leading to a lower experienced disturbance. Studies by Akazawa et al. and Smeets and Erkelens have previously confirmed that the LLR produces a response that corresponds to the amplitude of the evoking perturbation (Akazawa et al., 1983; Smeets & Erkelens, 1991). Lower LLR amplitudes would be expected during the auditory task, where weaker perturbations were experienced more frequently.

The Effect of Normal and Misdirection Instructions

In line with the second hypothesis, wrist LLRs demonstrated a dependency on the coherence of instruction direction and location, marking this the first study to reveal such behaviour. Wrist extensor LLR response AUCs after VIS-M were significantly lower than those after VIS-N. The differences in LLR amplitude estimates of wrist flexors were marginally significant while still displaying the same tendencies.

It is believed that the main reason behind the LLR amplitude tendency is subject confidence, defined as the subjective level of certainty regarding the accuracy of a decision (Fetsch et al., 2014; Kiani & Shadlen, 2009). When presented with incoherent instructions that contained conflicting evidence, subjects had to follow the correct information to complete the task accurately. Based on the interviews with subjects and behaviour observations, two possible responses to the misdirecting instructions were seen. First, hesitation due to a lack of confidence, leading to a lack of intent to move promptly respond. Second, showing overconfidence could lead to erroneous execution, as the subject's original intention was to move in the opposite direction. Previous studies have shown that both intent and confidence result in changes in LLR amplitude. Gallivan et al. showed in their research that lack of the subject's confidence in their decision-making resulted in lower LLR amplitude post-perturbation (Gallivan et al., 2018), and Colebatch et al. and Rothwell et al. demonstrated that participants' intent to ”yield” or ”resist” perturbations correspondingly changed response amplitudes to lower and higher values, respectively (Colebatch et al., 1979; Rothwell et al., 1980). In the current study, subjects were more prone to make errors during the visual modality task and reported that it was less clear for them when compared to auditory instructions. These findings align with existing literature and provide a novel explanation of the LLR amplitude behaviour when being instructed visually.

Contrary to the expectations of the second hypothesis and the behaviour after VIS, LLR amplitude estimates after AUD-M did not exhibit a difference from those after AUD-N in either flexor or extensor muscles. Unlike the modulation observed during visual instructions, the behaviour during the auditory task is fundamentally different, suggesting that the impact of instruction coherence on LLR amplitudes varies between modalities.

The LLR's modulation after auditory cues corresponded with what subjects reported experiencing during the experiment. Most subjects found auditory instructions easier to follow. Overall, participants showed higher proficiency in successfully distinguishing the word from the sound source, leading to fewer errors. Many even reported not noticing changes in the location of the instructions and were capable of accurately following the instructions, something that was only reported once during the visual task. Both factors resulted in similar LLR behaviours and reduced error rates during auditory instructions.

The preference for auditory instructions and the ability to effectively comprehend the word led to increased confidence, resulting in a similar behaviour between normal and misdirecting instructions. However, the participants' high confidence in the modality sometimes backfired. More errors occurred during normal auditory instructions compared to normal visual ones. Furthermore, the mean error amplitude was larger in the auditory modality. So, while overall performance improved after auditory instructions, instances of overconfidence occasionally led to larger mistakes and increased error susceptibility during normal instructions.

Task behavior

The post-experiment questionnaire and error estimate study complemented each other and described subject behaviour during the experiment. The reports of preferred modality were reflected in the error estimate, with 11 out of the 17 subjects exhibiting lower error rates in their preferred modality. The majority reported misdirections being more challenging than normal instructions in both modalities. Indeed, most errors were seen as a result of misdirecting instructions in both visual (86.4%) and auditory (75.4%). Furthermore, subjects who reported no difficulties with the task displayed behaviour consistent with their reports, all exhibiting lower means than the group average.

The error analysis confirmed the effectiveness of the strategies employed by participants. Only seven participants (VIS: Sub. 9, 11, 14, 15; AUD: Sub. 4, 8, 9, 14, 16) reported following a specific approach. Almost all strategies led to an improvement in performance for participants, with their error rates all being under the group mean rate. Two strategies implemented by the same subject (Subject 9) for each modality were unsuccessful, leading to higher error rates. The ineffective strategies included focusing on the base of the arrows for visual instructions and basing your initial movement on the sound source for auditory instructions.

Neural Mechanisms

The neural mechanisms contributing to LLRs are still a large part of the unknowns surrounding the feedback response. Thanks to the findings of this study, novel neural substrates that govern these responses have been considered.

The visual and auditory sensory organs first receive the instruction and then interpret it in their respective primary cortices.(Møller, 2011). For both modalities, the information is then transmitted and integrated into the prefrontal cortex for higher-order processing to finalize a decision (Miller & Cohen, 2001; Møller, 2011). After a decision has been made, motor planning and execution follow, with the latter being controlled by the primary motor cortex (M1), which engages limb musculature

(Bhattacharjee et al., 2021; Cheney & Fetz, 1980; Park et al., 2004). The disparity in processing speed between the auditory and visual pathways resulted in lower LLR AUCs after auditory instructions. Faster RTs can lead to earlier movement onset and, thus, earlier contraction. A study by Bawa et al. concluded that perturbations during movement can lead to smaller angular displacements, diminishing the LLR response. Furthermore, they showed that contracted muscles show lower LLR EMG signals (Bawa & Sinkjaer, 1999).

M1 is the main structure that projects the generated motor commands via the corticospinal track to engage limb muscles (I. L. Kurtzer, 2015). Thanks to its tight association with voluntary action, many researchers have viewed it as one of the LLR's primary contributors, attributing its task dependency to M1's involvement (Nashed et al., 2012). Experimental evidence also supports the contribution of M1 to the LLR, as temporary silencing of the M1 activity lowered the amplitude of the LLR response (Meziane et al., 2009). However, it did not eliminate the response, supporting the idea of the M1 being one of multiple neural pathways that contribute to the LLR's modulation (I. L. Kurtzer, 2015; Pruszynski et al., 2011). In the current study, the LLR's task dependency was observed when comparing normal and misdirecting instructions. When subjects displayed wavering or erroneous intent in the case of misdirecting instructions, lower LLR amplitude estimates followed.

The experiment's results suggest that the parietal cortex contributes to LLR modulation. This brain region is situated at the intersection of visual, auditory, and tactile cortices, integrating sensory information from different modalities and transforming it into motor output (Behrmann et al., 2004). The parietal cortex plays a role in several cognitive operations, including spatial representation and recognition in visual and auditory modalities, updating, attention, and abstract motor planning (At et al., 2011; Culham & Valyear, 2006). Its role in selective attention displayed across both modalities is key to interpreting the study's results (Bisley & Goldberg, 2010; Konen et al., 2007; Lewald et al., 2002).

To successfully reach the designated target during the varying instruction types, subjects needed to discern and select a subset of the input, the instructed direction. The parietal lobe's structures contribute to the task's success as they specialize in spatial recognition. Specifically, Behrmann et al. and Ikkaku and Curtis have shown that the parietal posterior cortex (PPC) plays a crucial role in visual attention, creating organized maps of objects and their locations, guiding attention allocation and eye movements towards objects important to their goals (Behrmann et al., 2004; Bisley & Goldberg, 2010; Ikkai & Curtis, 2011). Having maps of organized space is particularly relevant during the visual task, which used arrows as cues. Subjects occasionally struggled to distinguish between normal and misdirecting arrows, resulting in differing LLR behaviours.

The parietal lobe has a similar role in auditory recognition, where At et al.'s findings show that the right parietal cortex has a critical role in the build-up of spatial auditory representation, determining the position of sound sources and recognizing their relevance (At et al., 2011). Maeder et al. also show that the middle temporal gyrus and precuneus contribute to sound recognition.

As the results demonstrated no significant differences between LLR AUCs after either auditory instruction type, subjects appear to display higher proficiency at the localization and recognition during the auditory task. Participants also reported lower difficulty in distinguishing verbal directions from one another, often being unfazed by their change in location. This conduct was observed only once during the visual task, with most subjects saying it was more challenging to follow.

Managing conflicting information was an intricate aspect of this experiment, and previous studies have demonstrated that the anterior cingulate cortex (ACC) plays a crucial role in monitoring conflicts and making necessary adjustments (Kerns et al., 2004; Yeung, 2013). One example of the ACC's influence during conflicting tasks is the Stroop colour-naming task, which consists of subjects being presented with colour words printed in a certain ink colour, e.g., the word “blue” printed in orange. The task included congruent trials, where the words and colours matched, and incongruent trials, containing mismatched words and colours. During the task, subjects must only name the ink colour, not the word. Results from Kerns et al.'s study confirmed that higher ACC activity was observed during incongruent trials, and the rise in ACC activity predicted increased PFC activity in the following trial, suggesting the need for enhanced control (Kerns et al., 2004). Yeung et al. discerned that ACC activation occurs to override automatic responses in favour of controlled responses, such as naming the ink colour instead of reading a word (Yeung, 2013). My experimental paradigm was similar to a Stroop test, requiring subjects to comprehend the instructed direction despite mismatched direction and location. This similarity indicates that the ACC plays a comparable role in the task's execution, and thus, it is suggested that the ACC also influences LLR behaviour. Furthermore, the integration of information by the ACC with the PFC may differ between visual and auditory modalities, as evidenced by differing LLR modulation and behavioural outcomes.

Future Prospects

This study and its findings pave the way for numerous possibilities for future research. Modifications to the instruction settings could improve the interpretation of the results. The visual instructions can be modified by giving each direction a specific colour. Subjects often struggled to discern a normal arrow from a misdirecting one, whereas they reported that the auditory instructions were easy to distinguish. Changing each arrow to a different colour would help determine if the participants' difficulties stemmed from the visual sensory system's inefficacy in recognizing the instructions or that the visual task's design was inherently more challenging than the auditory one. Combining auditory and visual instructions is also an option, as the interaction of both senses and contributing pathways is relevant in human sensorimotor control (Pruszynski & Scott, 2012). Also, observing the impact of modality combinations on participant confidence could yield interesting findings. Indeed, people who struggled with auditory instructions stated that focusing on both the screen and their instruction was challenging. Instructing through a different modality, such as proprioceptive or tactile, can also give a different view of multisensory integration and how it interacts with LLR behaviour.

One potential avenue for enhancing future iterations of this study involves examining the latency of the stretch reflex post-perturbation onset, specifically in wrist extensors. Fig. 3.2 shows a type of EMG signal seen only in subject extensor muscles, which first peaks in the LLR epoch (50-100 ms), thus not showing any SLR response. While the lack of an SLR could be attributed to a mistake in EMG placement, the signals displayed multiple peaks, suggesting that the expected behaviour was present but slightly shifted. Thus, further studying this phenomenon and perhaps adjusting the epochs of both stretch reflexes could lead to better and more extensive results.

Exploring the interaction between neural pathways involved in LLRs could enhance our understanding of relevant motor dysfunctions. Many motor dysfunctions exist that are closely tied to possible contributors to the LLR. The existing literature shows that damage to these contributors affects the modulation and presence of the response. Some of them include stroke (Trumbower et al., 2013), Parkinson's disease (Bloem et al., 1992; Hunter et al., 1988; Romero & Stelmach, 2003; Rothwell et al., 1983), and Huntington's disease (Abbruzzese et al., 1990), and they affect the LLRs amplitude, modulation, and even overall presence. Thus, extending the study to include individuals with motor impairments can enhance our understanding of neural pathways that influence motor dysfunctions and how these structures contribute to the LLR response.

4.2. Conclusions

- Novel findings about LLR and their dependency on the modality and direction-location coherence of instructions were established.
- Instruction modality modified the LLR characteristics, with both wrist flexors and extensors LLR responses showing significantly larger amplitude estimates when instructed visually as opposed to aurally.
- In both muscle groups, visual instructions with incoherent directions and locations, or misdirecting instructions, led to lower LLR amplitude estimates compared to responses after normal instructions.
- Direction-location coherence in auditory instructions did not influence LLR amplitudes, as no significant differences were found in the LLR amplitudes between normal and misdirecting stimuli.
- Participants exhibited a higher tendency for errors in the visual modality, identified as their least preferred mode of processing information. Subjects displayed larger mean error amplitudes during the auditory task

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