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Spinal reflexive movement follows General Tau Theory

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Abstract

Background: Tau theory explains how both intrinsically and perceptually guided movements are controlled by the brain. According to general tau theory, voluntary, self-paced human movements are controlled by coupling the tau of the movement (i.e. the rate of closure of the movement gap at its current closure rate) onto an intrinsically generated tau-guide (Lee, 1998). To date there are no studies that have looked at involuntary movements, which are directly guided by innate patterns of neural energy generated at the level of the spinal cord or brain, and that can be explained by general tau theory. This study examines the guidance of an involuntary movement generated by the Patellar reflex in presence of a minimized gravitational field.

Results: The results showed that the Patellar reflexive movement is strongly coupled to an intrinsic tau-guide particularly when the limb is not moving in the direction of gravity.

Conclusion: These results suggest that the same principles of control underpin both voluntary and involuntary movements irrespective of whether they are generated in the brain or the spinal cord. Secondly, given that movements like the patellar reflex are visible from infancy, one might conclude that tau-guidance is an innate form of motor control, or neural blueprint, that has evolved over time.

Keywords: Tau theory, Involuntary movements, Gravitational field, Movement planning, Patellar reflex

1 Background

Movement, and the way it is guided or controlled by the central nervous system, has always been of great interest to researchers. To date, human movement has been studied from both perceptual and motor perspectives resulting in different theories of how it is controlled (Bernstein 1966; Gibson 1966). General tau theory is one such theory that suggests that the patterning of perceptual information, can be picked up and used by the central nervous system to temporally guide the closure of action gaps. This theory was first proposed by David N. Lee in 1976 and looked at how timing information can be directly detected through changing patterns in the optic array and to explain how the brain controls movement prospectively. Examples have included braking when driving a car or moving to intercept a ball. The theory later evolved to explain how other patterns of temporal information picked up through other sensory arrays (extrinsic control), but also generated by the central nervous system (intrinsic control), can prospectively control other forms of biological movement (Lee 1976; Lee 1998; Lee et al. 1982; Lee and Young 1985). The central tenet of this theory is that the taus of different types of action gap are closely coupled together (Lee 1998). An action gap is defined as the changing gap between a current state and the goal state. Tau (τ), an informational variable that blends space and time, specifies the time to closure of an action gap (e.g. x) at its current closure rate ($\tau_x = x/\dot{x}$; x is the magnitude of the action gap and x dot signifies its rate of change at each moment in time). Action gaps can be perceived through the patterning of information picked up through the senses (extrinsic tau) (Lee 2005) or generated intrinsically by the CNS (e.g. tau guide).

For instance, when catching a ball, the information specifying the ball's arrival position and time to arrival is specified by the tau of the ball_hand gap, specified by the pattern of information generated by the changing optic array and picked up through the eyes (Lee et al. 2001). On the other hand, when intercepting a virtually moving sound source, the position and arrival time of the sound is specified through the patterning of auditory information (tau) and is picked up by the auditory system (Komeilipoor et al. 2015). According to general tau theory, successfully intercepting a target requires that the tau of the hand-target action gap (τ_y) is tightly coupled to the tau of the hand-arrival position action gap (τ_x) ($\tau_y = K\tau_x$). The coupling coefficient k is a constant that describes how the gaps close together (Lee 1998).

For self-paced movements such as picking up a glass from a table, or putting a ball in golf, there is no dynamic information that can be picked up by the senses to guide the temporal control of these movements. In these examples, it is critically important that the movements are still controlled prospectively. In the absence of extrinsic (sensory) information to assist with the movement timing in these examples, it is hypothesized that an intrinsic pattern of information generated by the nervous system guides the control of the movement (Lee 2005). The tau equation that specifies the patterning of neural energy needed to guide these movements depends on the duration of movement and is defined as: $\tau_g = 0.5(t - T^2/t)$ (Lee 1998; Lee 2005). T is the duration of movement and t is time as the movement unfolds (from movement initiation to the end of the movement). Research has shown that in the case of moving one's hand to one's mouth and putting a ball in golf (both self-paced actions) that the movements are tightly coupled to an intrinsic tau-guide (Craig et al. 2000; Lee et al. 1999). Indeed, other research has shown that different levels of skill are manifested through different coupling coefficients, with highly skilled participants having higher coupling coefficients compared to the non-skilled (Rodger et al. 2013).

Up until now, general tau theory has only looked at voluntary movements which require temporal control and prospective guidance (Craig et al. 2000; Komeilipoor et al. 2015; Lee et al. 1999; Lee et al. 2001). To make a voluntary movement, signals generated in the primary motor cortex are first carried by the corticospinal tract to a

particular spinal cord segment, before exiting the spinal cord to reach the specific muscles required to produce that particular movement (Kandel et al. 2000).

Reflexive movements, on the other hand, are generated in an involuntary manner with some reflexes being present from birth (Marcel 2003). In the case of spinal reflexes, the brain receives the activation message from the onset of the movement (Augustine 2008). Reflexes are categorized into three types: 1) spinal reflexes e.g. patellar reflex, 2) cortex reflexes e.g. dermal reflexes, and 3) the reflexes of the posterior parts of the brain responsible for complex reflexes such as swallowing (Pasztor 2004). Considering the number of neurons engaged in the reflex, reflexes are either monosynaptic or polysynaptic.

Since there is no study that looks at the control of involuntary movements using tau theory, the main aim of this study was to see if general tau theory could explain the temporal control of reflexive type movements. We chose to examine the Patellar reflex, one of the primary reflexes that is present from early infancy (Pillitteri 2010; Schott and Rossor 2003). This reflex is classed as a monosynaptic and tendinous reflex generated by direct command from the spinal cord (Freberg 2009).

The sequence of events that make up the Patellar reflex is as follows: (i) the quadriceps tendon is suddenly and briefly stretched by the hammer blow, (ii) this briefly stretches the quadriceps muscle, (iii) this briefly stretches the spindles in the quadriceps, thereby briefly increasing their tension, (iv) this brief increase in tension causes the quadriceps muscle to briefly contract to reduce the tension in the spindles, (v) the contraction of the quadriceps muscle starts the leg on its upward course, (vi) as the leg moves upward against gravity, the length of the quadriceps muscle to decrease at a normal (non-jerked) rate, (vii) this causes the lengths of the muscle spindles within the quadriceps to decrease at a normal rate, thereby decreasing the tension in the muscle spindles at a normal rate. At this stage, when the leg, muscles and spindles are all moving within normal bounds, voluntary control of the leg kicks in, to ensure that the rate of deceleration of the leg is adequate to stop the knee at a safe angle. In this study, we will look at whether the coupling of taus of angular action gaps (τ_a) and the Cartesian action gap of the leg (τ_d) are controlled using τ_g during this type of patellar reflexive movement (see figure 1.A).

Although the mathematical formula for the tau equation is derived from a bouncing ball movement in the presence of gravity (Lee 2005), it is worth noting that the electromyographical activity of the muscles causing patellar reflex is very short (about 40ms) compared with the whole movement duration (Bevilacqua-Grossi et al. 2008; Vickery and Smith 2012), so after the offset of muscle activation, the remainder of the movement produced by the initial reflex could be partially regulated by gravity. To control for the possible influence of gravity on limb movement, we decided to elicit the patellar reflexes using two different body postures: 1) in the typical sitting position with the lower limb positioned vertically with respect to the floor so that the influence of the gravitation field would be present, and 2) in a lying side position where the lower limb was positioned horizontally with respect to the floor thereby minimizing the influence of gravity.

2 Methods and Materials/Instruments

2.1 Participants and task

Six participants (four males and two females; mean age: mean \pm standard deviation (std) = 24.2 ± 2.5 years old; mean height: 175.5 ± 8.5 m; mean weight: 74.2 ± 18.3 kg) participated in this study. The study was approved by the local ethics committee. The participants had not taken part in any similar experiment and were unaware of the aims

of the experiment. The participants gave informed consent and understood that they were free to leave at any time. The participants did not suffer from any motor or neuromuscular disease and had no history of any neurological disorder.

2.2 Procedure

2.2.1 Vertical plane

To produce the patellar reflex movement, participants were asked to sit in a chair that was sufficiently high so that their legs were able to hang freely over the edge when they were seated (Vickery and Smith 2012). An appropriate and medically approved reflex hammer was used to evoke the reflex. The hammer was attached to a pendular structure that could freely swing when held at the end. To hit the correct spot at the right speed, it was released at a 90° angle without applying any extra force. In order to maximize the chances of successfully triggering a reflex with a large magnitude, the best spot on the participant's knee for tapping was chosen through trial and error (Chandrasekhar et al. 2013). In addition, to maximize the jerk and muscle contraction when eliciting the knee jerk, the Jendrassik manoeuvre was used (Burke et al. 1996). To this end, participants were instructed to interlock their left and right hands and pull in response to an oral prompt given before the tendon was tapped. About two seconds after this manoeuvre began, the participant's patellar tendon was tapped, and the reflex was recorded. For each participant, the reflex test was performed 10 times with a 30 seconds interval between each reflex.

2.2.2 Horizontal plane

Participants were asked to lie down in a comfortable position on the right-hand side of the body on a standard mattress (see figure 2). In order to ensure the body position was as similar to the one described above in the sit position, the resting leg, that was laying on the mattress, was positioned in such a way that the thigh was at a 90-degree angle to the upper body. A 2.8 m rope attached to the ceiling was loosely wrapped around the ankle so that was still free to move in the horizontal plane. For each participant, the reflex test was performed 10 times with a 30 seconds interval between each reflex.

2.3 Recording

To record the patellar reflexive movement, two circular markers were attached to the participant's knee and ankle (figure 1.A). A 120 frame per second camera recorded the markers' location. The camera was positioned 80 cm from the participant's leg and parallel to the two markers (see figure 1.A). The position of the centre of each of the two markers was extracted 120 times a second through a post-processing procedure available in MATLAB software (MathWorks Inc.). The position of marker A was considered as the origin of the Cartesian coordinates.

The raw data were filtered using a second-order Butterworth low pass 8 Hz filter type 1 and the movement action gaps were obtained using the following equation (1):

$$X_{AG}(t) = x(t) - x_{end} \quad , \quad Y_{AG}(t) = y(t) - y_{end} \quad (1)$$

where x and y represent the position of the ankle in Cartesian coordinates over time, where x_{end} and y_{end} represent the position of the ankle at the end of movement, and X_{AG} and Y_{AG} represent the action gaps of the x and y coordinates.

Ten representative action gaps for one individual are shown in figure 1.B. The angle of the leg β (see figure 1.A) was obtained by calculating the angle between the vertical coordinate and the line that connects the centres of the two markers. The angular action gap (α) was calculated as:

$$\alpha(t) = \beta(t) - \beta_{end} \quad (2)$$

(Insert Fig. 1 about here)

(Insert Fig. 2 about here)

2.4 Analysis of the Behavioral data

The mean and standard deviations of the amplitude, peak velocity and time to reach peak velocity of the ankle displacement and angular movement for all participants for vertical and horizontal conditions are reported in Table 1. All the variables were not significantly different in the Vertical and Horizontal conditions (paired sample t-test; for all comparisons: $p > 0.324$)

Table 1. The amplitude, peak velocity, and time to reach peak velocity for both ankle displacement and angular movement for all participants. Standard deviations are in brackets.

Condition	ANKLE DISPLACEMENT			ANGULAR MOVEMENT		
	Amplitude (cm)	Peak velocity (cm/s)	Time to peak velocity (ms)	Amplitude (rad)	Peak velocity (rad/s)	Time to peak (ms)
Vertical	8.8 (± 3.2)	39.1 (± 17)	158.3 (± 18)	16.5 (± 5.1)	73.8 (± 31)	160.2 (± 19)
Horizontal	7.8 (± 1.2)	46.9 (± 15)	158.1 (± 20)	15.1 (± 2.7)	89.7 (± 31)	158.1 (± 20)

From the displacement data the ankle movement action gaps (d_{AG}) were calculated using equation (3).

$$d_{AG}(t) = \sqrt{X_{AG}^2(t) + Y_{AG}^2(t)} \quad (3)$$

The tau of the ankle displacement (τ_d) and the tau of the angular movement (τ_α) were calculated using equations (4) and (5).

$$\tau_d = d_{AG}(t)/\dot{d}_{AG}(t) \quad (4)$$

$$\tau_\alpha = \alpha(t)/\dot{\alpha}(t) \quad (5)$$

In keeping with other studies, only the part of the movement in each trial that was greater than 10% of the trial's peak velocity was analysed (Lee et al. 1999).

Using the time series in which the movement was generated, τ_g was calculated using equation (6) below.

$$\tau_g = 0.5(t - T^2/t) \quad (6)$$

where, T is the duration of the movement and t is time as the movement evolves.

After calculating the different taus, τ_d , τ_α and τ_g for each trial, the strength and duration of the coupling between the relative taus ($\tau_d - \tau_g$ and $\tau_\alpha - \tau_g$) was calculated in the following way (Lee et al. 1999). When τ_g is plotted against τ_d the total number of samples equals N (Figure 3); where the start of the movement is equal to $n = N$ and the end is where $n = 1$. The first step is to fit a line to the last $m = 10$ data points ($n = 1:m$). The strength (r^2) of the linear regression (r_{10}^2) for those 10 points along with the standard deviation ($S10$) was then calculated. Provided that $r_{10}^2 > 0.97$, the sample number (m) was increased by one sample ($m = 11$) at a time and a new regression line was fitted to samples $n = 1:m$. To calculate the straightness of the raw data, the parameter $d_m = Sm/S10$ was also calculated; where Sm is the standard deviation of the m points. By increasing m , if d_m reaches 4, the samples $n = 1:m-1$ were considered as the part of movement where coupling occurred. The percentage of movement (MP) where a strong linear coupling was found was calculated using the equation below (7).

$$MP = \frac{m - 1}{N} * 100 \quad (7)$$

(Fig. 3 about here)

After analysis of the MP between $\tau_d - \tau_g$ and $\tau_\alpha - \tau_g$ in both conditions, the data were then analysed by defining a 2 (Plane: vertical and horizontal) \times 2 (Coupling type: $\tau_d - \tau_g$ or $\tau_\alpha - \tau_g$) repeated measures ANOVA (rmANOVA) to study the effect of each plane on MP within different action gaps and taug. Bonferroni corrections were applied where necessary and the significance level as set at $p < 0.05$.

3 Results

The rmANOVA results revealed a significant effect of Plane (Fig. 4; $F_{(1,5)} = 25.8$, $p = 0.004$, $\eta_p^2 = 0.838$), presenting higher values of MP in the Horizontal plane ($89.4\% \pm 2.2\%$) compared to the Vertical plane ($76.6\% \pm 0.6\%$). On the other hand, the difference in the Coupling type was not significant ($p = 0.573$). Furthermore, the results showed a significant Plane \times Coupling type interaction ($F_{(1,5)} = 63.45$, $p = 0.001$, $\eta_p^2 = 0.927$). Post-hoc comparisons revealed higher MP values in the horizontal plane for both displacements ($89.0\% \pm 2.4\%$) and angular ($89.8\% \pm 2.1\%$) action gaps compared to the vertical plane (displacement: $77.6\% \pm 0.9\%$; angular: $75.6\% \pm 0.7\%$; for both comparisons: $p < 0.008$).

(Fig. 4 about here)

4 Discussion and Conclusion

According to general tau theory, voluntary self-paced movements, such as reaching for a static object, are guided by coupling the tau of the action gap with a tau guide (τ_g) generated intrinsically by the central nervous system (Lee 1998). It is known from the literature, that the production and guidance of reflexive movements are very different from voluntary movements. Reflexive movements are classed as innate, simple, ballistic patterns of movement that originate in the spinal cord or in the brain (Augustine 2008).

The main aim of this study was to investigate if the control of the trajectory of a movement generated by a reflex can also be explained by general tau theory. To this end, this study looked at a simple spinal reflex, the patellar reflex, which was initiated under two different conditions (horizontal and vertical) to control for the possible influence of gravity on limb movement. In the vertical condition the potential influence of gravity was high, whilst in the horizontal condition the influence of gravity was seen as being negligible. Having the two different conditions allowed us to conclude if the amount of coupling was due to acceleration under the influence of gravity or some kind of prospective control (Lee 2006).

For the vertical condition where the subject sat in a chair with the limb positioned vertically with respect to the floor, the results showed that both τ_a and τ_d were tightly coupled to an intrinsic tau guide τ_g ($r^2 > 0.97$). A possible interpretation could be that the formula for tau g (derived from the form of movement of a bouncing ball) could be due to the effects of gravity and not any type of prospective control as hypothesised by the tau g theory.

To counteract this, the second horizontal condition was designed to see if the strong coupling still existed when any effects of gravity were minimised. In this case the reflexive movement produced showed that the τ_a and τ_d couplings to the intrinsic τ_g were still present and were even stronger than those found in the vertical condition. Both results reinforce the idea that the temporal control of involuntary movements, such as the patellar reflex, are intrinsically guided in a way that is similar to voluntary movements.

Our results suggest that even though voluntary and involuntary movements are generated in different levels of the brain and spinal cord, they are both still coupled to a more universal tau neural imprint that is adapted to gravity. Taking this into consideration, one could suggest that the scope of tau theory should be extended so it becomes a more general theory for describing the neural control of both voluntary and involuntary movements. Secondly, given that the patellar reflex is present from infancy, one can conclude that there are innate patterns of neural activity that correlate with tau to help plan and guide movement. Most probably, the innate patterns of neural activity were gradually generated during evolution through the interaction of the organism with gravity, one of earth's most important environmental factors.

Future work should look to extend data capture and analysis to include the movement of other animals but also less evolved biological organisms. The ideal scenario would be to study two types of similar animal, where one is considered an evolutionarily older version of the other one. If the presence of tau coupling is indeed related to evolution, one would predict that the percentage of movement that is tau guided is significantly less for the older, less evolved animal compared to the newer species.

5 Declarations

Ethics approval and consent to participate: The study was approved by the local ethics committee and all the participants have signed the letter of consent.

Consent for publication: The manuscript has been read and approved for the submission by all the authors.

Availability of data and materials: The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Competing interests: The Authors declare that they have no conflict of interests.

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Authors' contributions: Mehrdad Bahadori and Mehran Emadi Andani designed and planned the experiment. Mehrdad Bahadori prepared the software, collected, exported, and prepared the data. Mehrdad Bahadori and Mehran Emadi Andani analyzed the data and drafted the manuscript and created the figures and tables. Paola Cesari and Cathy Craig revised the manuscript. All authors read and approved the final version of the manuscript.

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FIGURE CAPTIONS

Fig. 1. A) A and B markers placed on the knee and ankle (yellow circles) and used to calculate the angle β (i.e. the angle of the leg with respect to the vertical axis). B) Ten representative ankle movement action gaps from one individual participant in vertical condition.

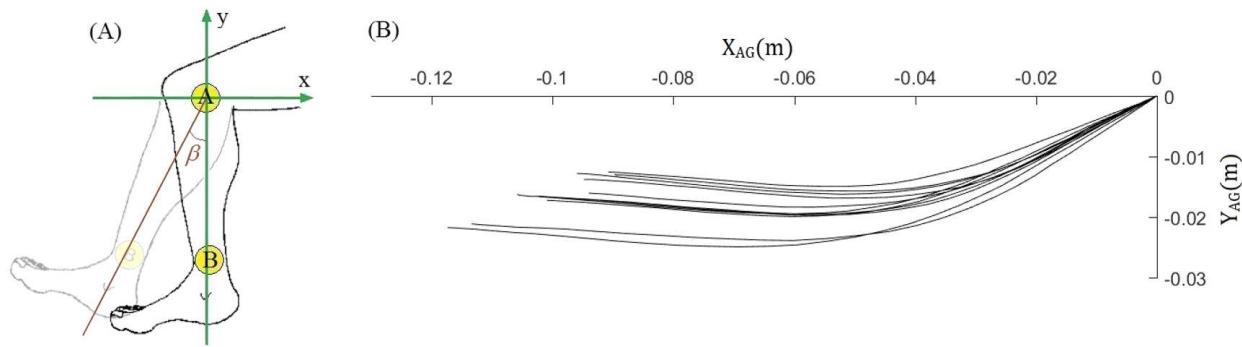


Fig. 2. The top view of participant's positioning in horizontal condition. Markers A and B are placed as the vertical condition. The green spots indicate the places where the rope was supporting the leg.

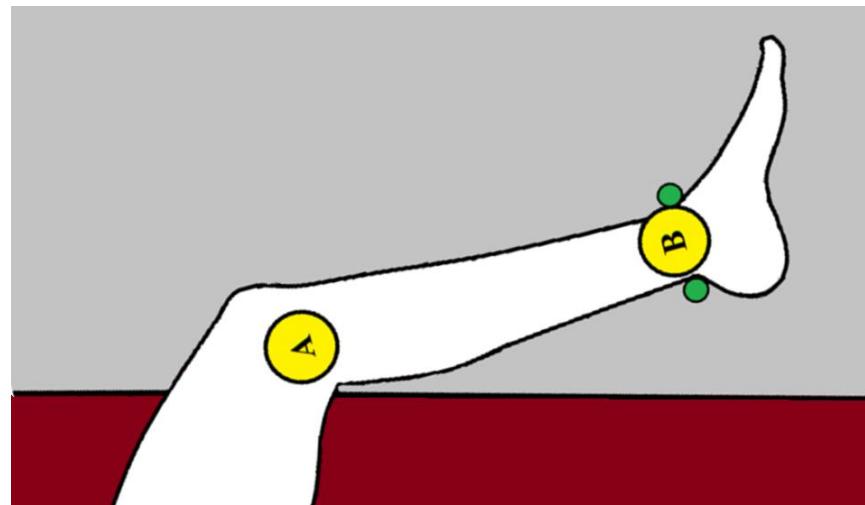


Fig. 3. τ_g plotted against τ_d for one trial. The movement starts at sample point $n = N$ and ends at sample point $n = 1$. The red line is the regression line fitted to samples from the start of coupling ($n=m-1$) to end of the movement.

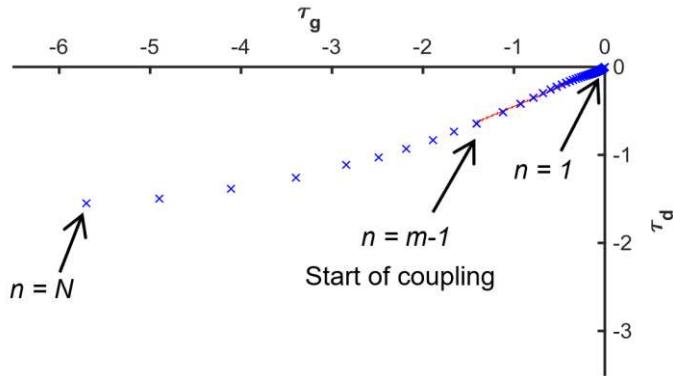
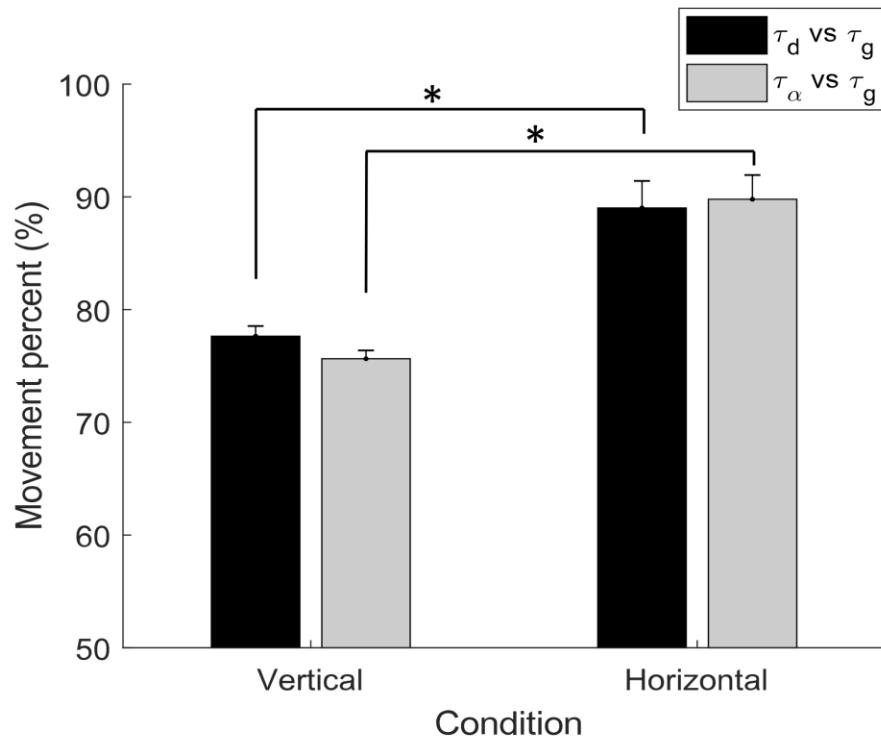


Fig. 4. Movement percentages (MP) for the different coupling types in both the vertical and horizontal conditions. The black columns represent the mean MP values for coupling between τ_d and τ_g while the grey columns represent the mean MP values for couplings between τ_α and τ_g . The error bars represent the standard error and asterisks show the significant differences.



Figures

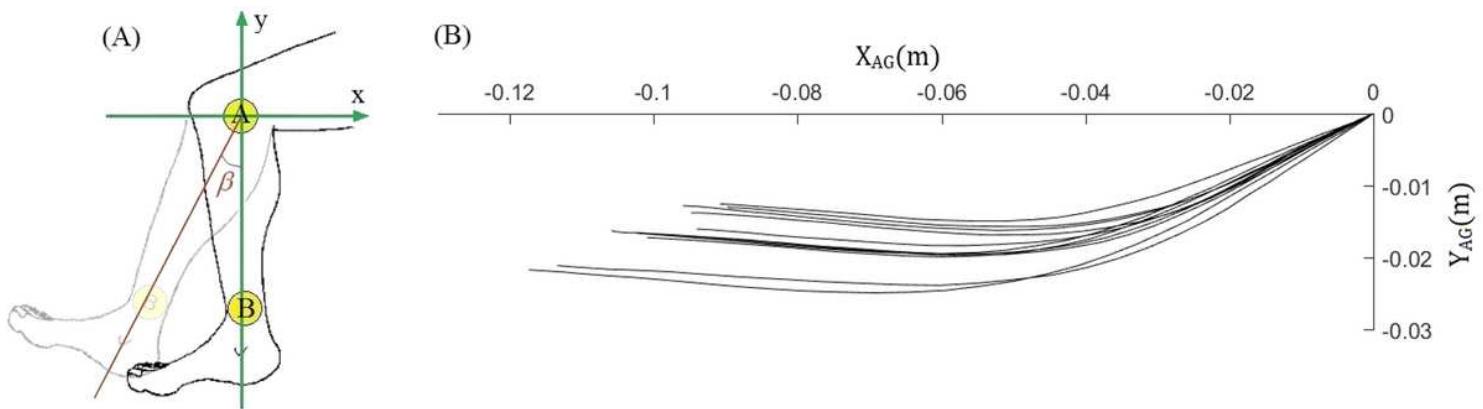


Figure 1

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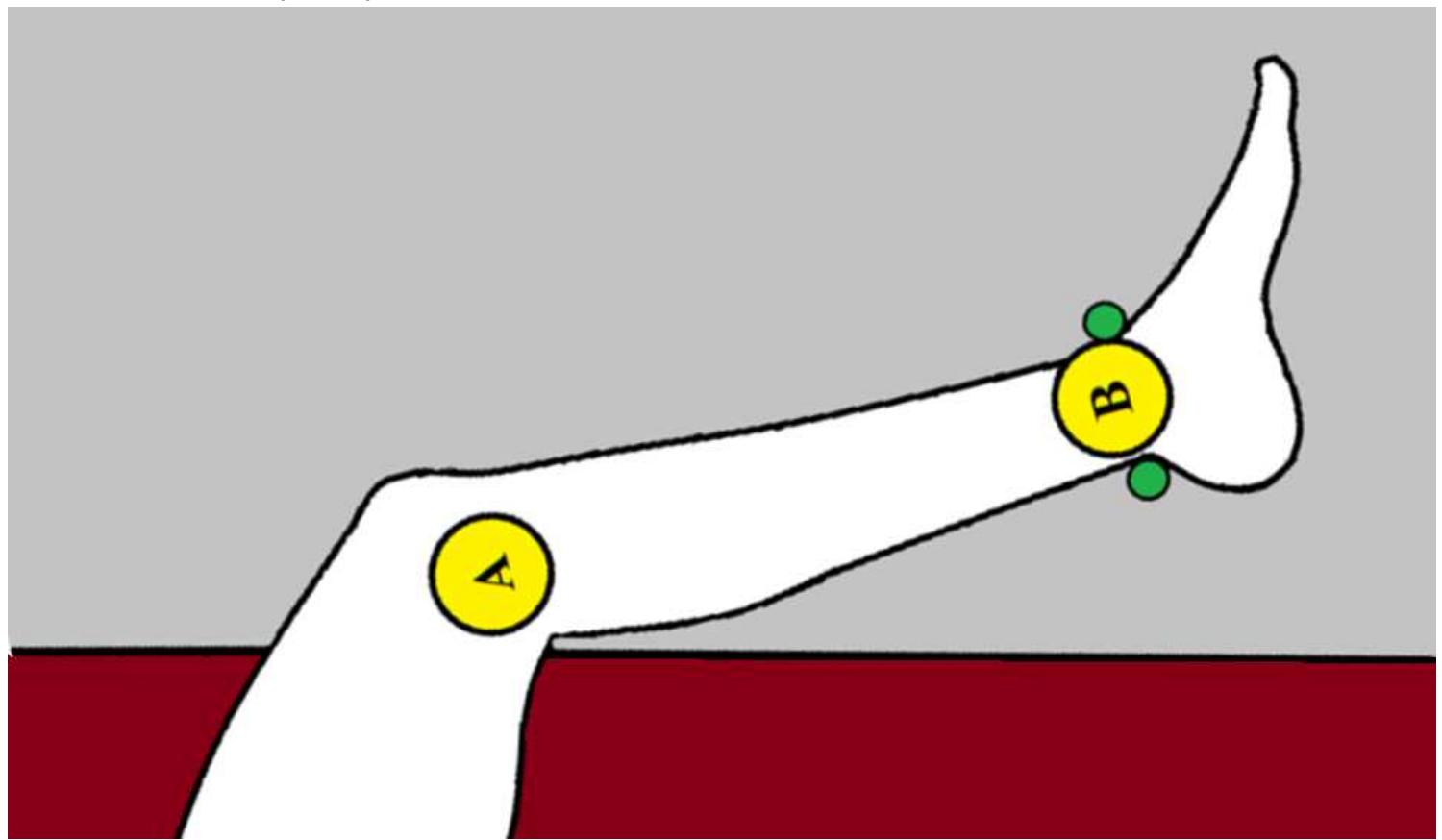


Figure 2

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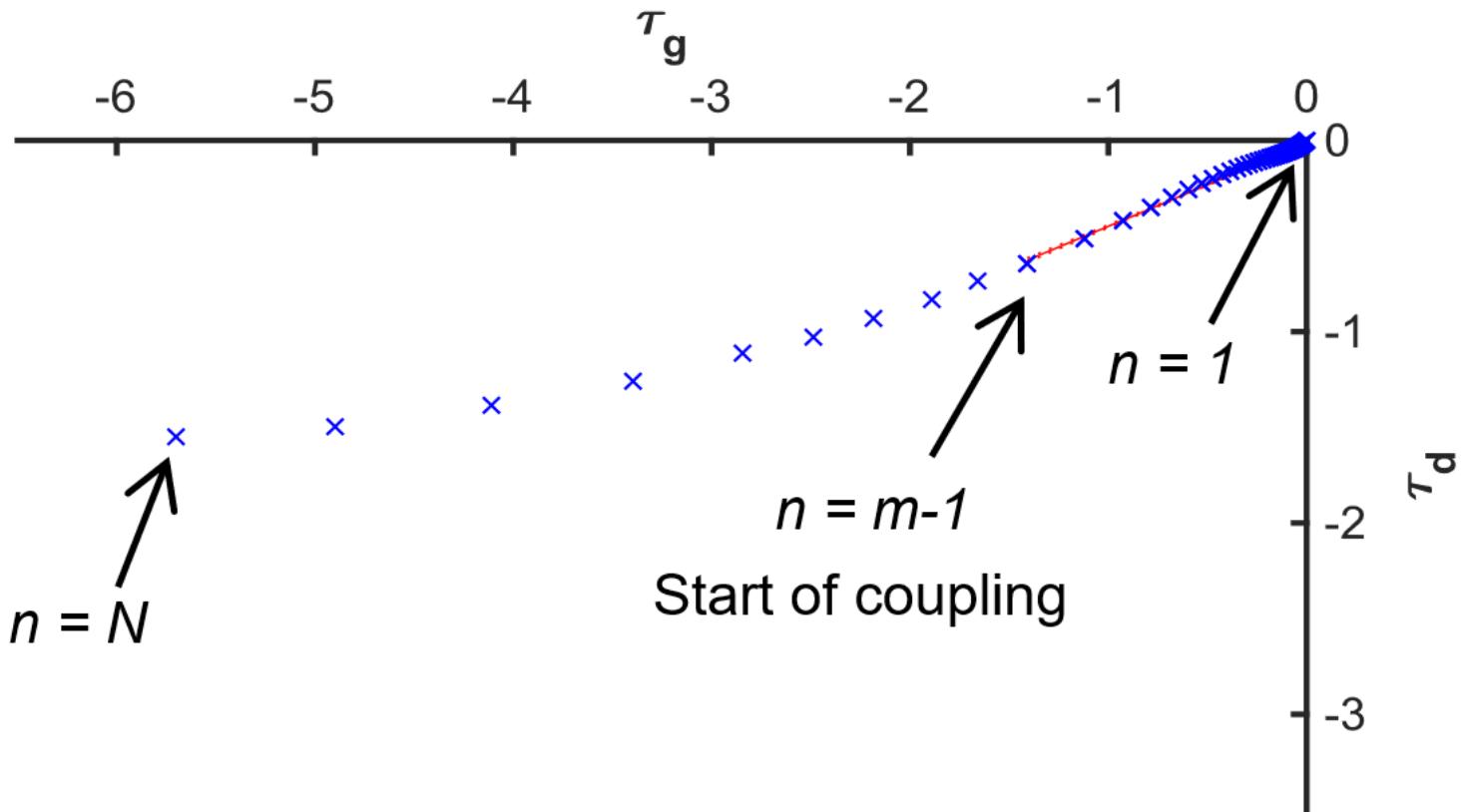


Figure 3

τ_g plotted against τ_d for one trial. The movement starts at sample point $n = N$ and ends at sample point $n = 1$. The red line is the regression line fitted to samples from the start of coupling ($n=m-1$) to end of the movement.

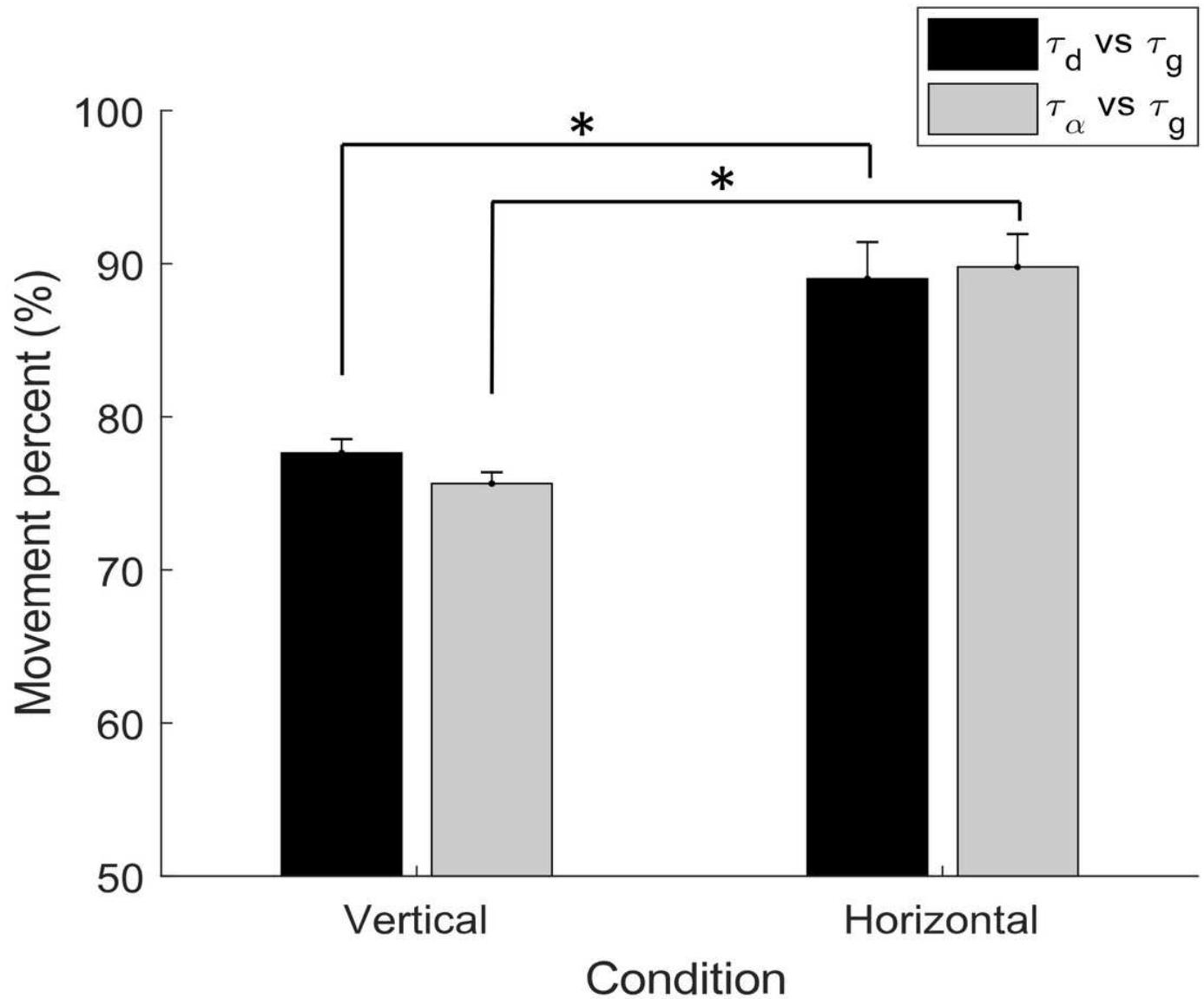


Figure 4

Movement percentages (MP) for the different coupling types in both the vertical and horizontal conditions. The black columns represent the mean MP values for coupling between τ_d and τ_g while the grey columns represent the mean MP values for couplings between τ_α and τ_g . The error bars represent the standard error and asterisks show the significant differences.