MECHANISMS UNDERLYING THE INTERPLAY BETWEEN COGNITION AND MOTOR CONTROL: FROM BENCH TO BEDSIDE

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EDITORIAL
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Editorial: Mechanisms Underlying the Interplay Between Cognition and Motor Control: From Bench to Bedside

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Editorial on the Research Topic

Mechanisms Underlying the Interplay Between Cognition and Motor Control: From Bench to Bedside

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Movements allow establishing preferred outcomes in the environment. To set movement parameters optimally, a plethora of brain processes spell out the intended course of action, often termed "cognition." This functional interrelationship between assessment, i.e., cognition, and manipulation, i.e., movement, of the self in the environment suggests that there is crosstalk between "cognitive" and "motor" brain areas. The goal of this Research Topic was to demonstrate and elucidate those mechanisms underlying the interplay between cognition and motor control.

Is there evidence that cognition and movement are interdependent? Lunazzi et al. show that the time taken to decide between equivalent candidate movements depends on their duration: Decisions between lengthy reaching movements were faster than those between short movements, indicating that participants aimed to limit the total time needed to obtain rewards. This implies that decisions and movements follow similar overarching goals and hence are subject to common regulatory mechanisms. Ribot et al. demonstrate that well after onset of reaching movements, trajectories are swayed by visual targets representing alternative candidate movements. Hence, decisional processes continuously control movements, so that changes of mind are reflected in deviating movement trajectories. This competition between alternative movements seems to increase GABAergic intracortical inhibition, as indexed by the silent period duration, observed following the motor-evoked potential elicited by Transcranial Magnetic Stimulation. Hence movements may be continuously subject to changes of mind, with GABAergic inhibition potentially serving as gatekeeper. In a patient pilot study, Kim et al. present preliminary evidence that aspects of cognition and motor learning rely on shared neural resources: Motor accuracy and cognitive speed partly suffered more in dual tasks as compared to single tasks for stroke patients in contrast to controls. Re-learning upper limb movements in stroke patients thus puts a strain on cognitive resources, so that daily situations such as answering a question while reaching for an object may be challenging in these patients.

Which candidate brain structures may promote such interplay? Grill et al. combined Position Emission Topography and functional Magnetic Resonance Imaging (fMRI) to identify brain regions activated by motor and cognitive aspects of a simple finger tapping task. Several sub regions were identified in the striatum, a subcortical region associated with motor functions, attention and motivation. Some were seemingly more involved in regulating motor aspects of the task, whereas others were sensitive to cognitive aspects. These findings provide further support for the idea that the striatum is neither strictly "cognitive" nor "motoric" but organized along a gradient covering cognition and movement. Boen et al. highlight the functional parcellation of the right Inferior Frontal Gyrus (rIFG) by combining Diffusion Tensor Imaging with behavioral measures. This cortical structure had previously been associated with various cognitive and motor-related functions such as motor inhibition and -imagery, attention and speech. Here, results show that the rIFG is richly connected inter-regionally, with complex cortical and subcortical pathways, some of which likely translate cognitive variables into motor control. More specifically, the dorsal pars opercularis of the rIFG was associated with higher response caution in a stop signal task, but not a simple reaction time task. This suggests that this brain region does not merely assist movement production, but specifically modulates movement when cognitive goals call for response caution.

Is cognition needed for motor functions? Thierrien and Wong explore the idea that percepts resulting from simulated movements may play a central role in optimizing behavior over time: Learning to modify movement when environmental or physical states change, i.e., motor adaptation, likely rests on matching predicted and perceived sensory outcomes of own movements. Such sensory prediction errors likely provide important feedback on whether intended movements were successfully executed, but suboptimal in the context of task goals. From this perspective, the line between movement and cognition is blurred in motor adaptation, as matching predicted with actual movement consequences is central to this process. Mathew and Crevecoeur further discuss this idea by arguing that the assumed duality of distinct feedforward and feedback mechanisms in motor adaptation is likely obsolete. Instead, ongoing movement is likely corrected online to match sensory priors set by previous experience, which themselves are optimized over slower time scales to produce better optimized movement. Again, this framework is compatible with the idea that cognition, as assessing the relation between self and environment, and movement, as operation of bringing this relationship to a more favorable state, are inherently intertwined.

Is movement-related brain activity needed for cognitive functions? One fascinating implication of this Research Topic is that motor functions may be recruited for cognitive functions. Ridderinkhof et al. investigated the idea that predicting an opponent's shooting direction in football rests on simulating the observed movement as if done by oneself. Utilizing multivoxel pattern analysis on fMRI data, the authors show that such motor-imagery strategies are indeed likely used to predict the shooting direction. As such, brain processes recruited for simulated movement, largely overlapping with those for actual movement, may help inferring movement goals of others, indicating that cognitive functions may rely on motor functions. In a similar fashion, Nalborczyk et al. propose a theory that verbal thought may rely on such overt, "simulated", movement. In other words, motor-related aspects of thinking such as inner speech, as hallmark of subjective experience underlying cognition, may directly be embedded in motor regions, but inhibited or downregulated to prevent actual speaking. When sensory consequences of speech are simulated instead, such as inner hearing, or when the degree of abstraction is high, verbal thought may rely on motor activity less. When speech and motor inhibition develop during childhood, motor activity may contribute to verbal thought most.

In conclusion, articles collected in this Research Topic suggest that movements are shaped by cognitive functions allowing to reconcile sensory outcomes with cognitive goals. Likewise, cognition may partially rely on "simulated movement" to predict sensory consequences, which are then utilized for abstract operations such as planning, inference or thinking. As such, cognition and movement likely operate as direct functions of each other, rather than in isolation.

AUTHOR CONTRIBUTIONS

TC: writing—original draft preparation. GD, MW, FH, and JD: writing—review and editing. All authors contributed to the article and approved the submitted version.

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Dual Task Effects on Speed and Accuracy During Cognitive and Upper Limb Motor Tasks in Adults With Stroke Hemiparesis

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Background: Adults with stroke need to perform cognitive–motor dual tasks during their day-to-day activities. However, they face several challenges owing to their impaired motor and cognitive functions.

Objective: This case-controlled pilot study investigates the speed and accuracy tradeoffs in adults with stroke while performing cognitive–upper limb motor dual tasks.

Methods: Ten adults with stroke and seven similar-aged controls participated in this study. The participants used a robotic arm for the single motor task and participated in either the serial sevens (S7) or the controlled oral word association test (COWAT) for single-cognitive task. For the dual task, the participants performed the motor and cognitive components simultaneously. Their speed and accuracy were measured for the motor and cognitive tasks, respectively.

Results: Two-sample t-statistics indicated that the participants with stroke exhibited a lower motor accuracy in the cross task than in the circle task. The cognitive speed and motor accuracy registered by the subjects with stroke in the dual task significantly decreased. There was a negative linear correlation between motor speed and accuracy in the subjects with stroke when the COWAT task was performed in conjunction with the cross task ($\rho = -0.6922$, $p = 0.0388$).

Conclusions: This study proves the existence of cognitive–upper limb motor interference in adults with stroke while performing dual tasks, based on the observation that their performance during one or both dual tasks deteriorated compared to that during the single task. Both speed and accuracy were complementary parameters that may indicate clinical effectiveness in motor and cognitive outcomes in individuals with stroke.

Keywords: stroke, cognitive motor interference, dual task, upper limb, movement, speed-accuracy trade-off

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INTRODUCTION

The successful recovery of upper limb (UL) sensorimotor functions allows survivors of hemiparetic stroke to perform daily activities without significant discomfort (Harris and Eng, 2010; Eraifej et al., 2017; Valdes et al., 2020). UL motor activities are more cognitively initiated and driven than activities such as walking, i.e., autonomous movements (Houwink et al., 2013). Modern UL therapies have adopted robotic technologies (Kwakkel et al., 2008) that occasionally demand the application of the visuo-cognitive and UL motor resources of the individuals with stroke. It has been observed that cognitive–motor dual tasks often resulted in cognitive–motor interference instead of motor or cognitive facilitation (Plummer and Eskes, 2015; Shin et al., 2017). Cognitive tasks considerably affect the motor function of the UL during robot-guided movements, thereby proving the presence of cognitive–motor interference (Shin et al., 2017).

Fitts' law (Fitts, 1954) explains various human movement characteristics in terms of speed–accuracy tradeoffs (SATs). It claims that the speed of a movement is inversely related to its accuracy. SATs have been consistently used as a parameter in clinical studies that analyze human motor task performance by focusing on either the emphasis of speed (fast and inaccurate) or accuracy (slow and accurate)(Glenn and Parsons, 1991; Vallesi et al., 2012). In the field of neuro-rehabilitation, recent studies have reported the SATs as a possible parameter for the clinical assessment that estimated decreased capabilities in UL motor skill learning in patients with neurological disorders such as stroke (Fan et al., 2017; Kantak et al., 2018; Doost et al., 2019) and traumatic brain injuries (Korman et al., 2018). These studies evaluated patient's neurophysiological changes that were successfully described in terms of SATs while conducting the paretic arm movement tasks, which were compared with outcomes in healthy controls.

Many neuropathological UL movements display decreased functional characteristics on SATs in individuals with upper motor neuron disorders, such as Parkinson disease (Fernandez et al., 2018), multiple sclerosis (Ternes et al., 2014), Huntington disease (Despard et al., 2015), and cerebral palsy (Davies et al., 2014; Fernani et al., 2017). For example, one study demonstrated that UL paretic movements were faster in contrast to their associated low accuracy during the movement task (Fernandez et al., 2018). A stroke, however, is known to be accompanied by mild to severe cognitive impairments, unlike the neuromuscular diseases mentioned above (Esmael et al., 2021). A hemiparetic stroke tends to cause both motor and cognitive impairments, thereby making it difficult to perform dual tasks that require cognitive resources. In fact, many day-to-day UL activities involve cognitive–motor dual tasks; for instance, typewriting involves simultaneous reading and typing, and it is therefore a visuomotor cognitive–motor task (Yamaguchi et al., 2013). Consequently in rehabilitation clinics, it would be of practical and clinical importance to utilize the dual task paradigm during extensive UL motor rehabilitation. However, to the best of our knowledge, there are limited studies that have investigated the execution of a cognitive–UL motor dual task by people with stroke hemiparesis, and has not previously been explored about the effectiveness of assessing SATs during a cognitive–UL motor dual task. Furthermore, most studies on modern robotic and visuo-cognitive technologies in motor rehabilitation have been increasingly applied to gait-driven dual task paradigm on lower limb motor rehabilitation (Subramanian et al., 2010; Ricklin et al., 2018), not on UL visuomotor cognitive dual task.

The purpose of this study is to investigate the speed and accuracy of a person with stroke while performing a cognitive–UL motor dual task. The first hypothesis that was tested stated that adults with stroke display significantly lower speed and accuracy, and mutual interference during a UL motor and cognitive dual task compared to those displayed by them during a single task. The second hypothesis claimed that, while performing a dual task, the cognitive and motor outcomes of the adults with stroke were less accurate in comparison to those of healthy controls. We analyzed the effects of the motor and cognitive components of the single and dual tasks on the speed and accuracy of the subjects with stroke and healthy controls of similar ages.

MATERIALS AND METHODS

Subjects

Ten adults with chronic stroke (54.7 ± 12.3 years; M: 10) and seven age- and gender-matched controls were recruited; they were asked to perform a series of cognitive–motor tasks. A power analysis using G*Power 3.1.9.4 (Faul et al., 2007) for an independent-sample t-test was conducted assuming one-tailed testing with a large effect size of $d = 1.3$, 80% power and alpha error probability of a= 0.05 (McGough and Faraone, 2009; Taub et al., 2011). This analysis suggested a total sample size of at least 10 subjects with stroke and eight healthy controls. This study was approved by the institutional review board of the National Rehabilitation Center, Seoul, South Korea, and registered clinical human subject registry (cris.nih.go.kr registration: KCT0004873). The written informed consent forms of all the participants were obtained before collecting data. The study followed all STROBE guidelines and reported the necessary information appropriately (see **Supplementary Video 1**).

The eligibility criteria for the participants were given based on the previous studies, and shown as follows: (1) first-time and chronic poststroke hemiparesis (>3 months); (2) > 18 years of age; (3) manual muscle testing (MMT) at shoulder and elbow joints is above the poor grade (Zero/Trace/Poor/Fair/Good/Normal scale) (Cuthbert and Goodheart, 2007); (4) Modified Ashworth scale (MAS) at upper extremities less or equal than 1+ (0/1/1+/2/3/4 scale)(Pandyan et al., 1999); and (5) mini-mental states examination (MMSE) over than 23 (24–30: No cognitive impairment, 18–23: Mild cognitive impairment, 0–17: Severe cognitive impairment)(Zwecker et al., 2002). Individuals with the following conditions were excluded from the study: (1) stroke with multiple or bilateral lesions; (2) recurrent stroke; (3) complications of orthopedic disorders; (4) communication disorders due to aphasia; and (5) mental illnesses.

Single Tasks

The upper limb movements were performed using customized commercial upper limb robotic rehabilitation equipment for the single-motor task, as shown in **Figure 1A** (Camillo 3DBT-61, Man&Tel Inc, South Korea). The participants were seated in a comfortable chair and fastened to it with a trunk seatbelt to

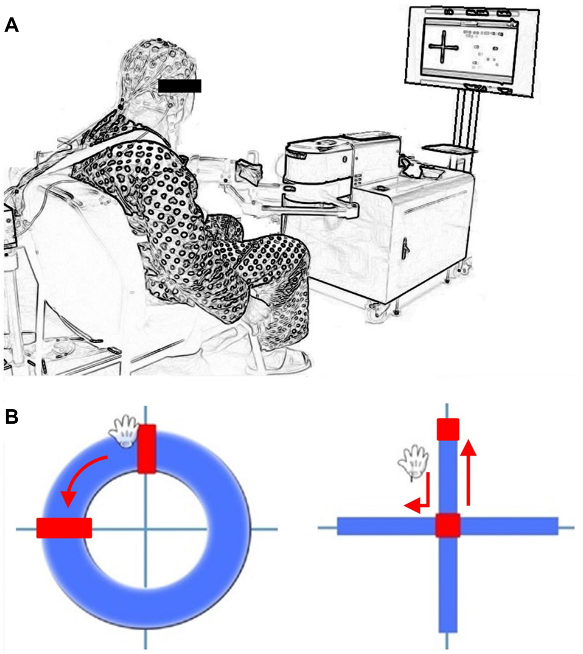

FIGURE 1 | (A) Cognitive-Upper Limb Motor dual task test setup (3DBT-63, Man&Tel Inc., Gumi, South Korea) **(B)** Visual feedback with movement cursor and direction indicator (Circle and Cross movement task).

minimize any additional compensatory movement and prevent an accidental fall. The subject's paretic arm was fastened to a handle with an upper arm support by using the Velcro provided in the equipment. The subjects were required to move a cursor by using the robotic arm to follow a moving red target in the feedback monitor within the designated areas (circle or cross-shapes) and testing time (1 min) for the single task. In the task involving the circular shape, the subject was required to move the cursor along an annulus by using the affected hand. The cross-shaped task required the participants to perform center-in and center-out movements in four clockwise and counter-clockwise directions, as shown in **Figure 1B**. In many modern robotic UL motor equipment, the cross-shaped reaching task was adopted for the UL movement tasks as well as linear- and circular-shaped movements (Brewer et al., 2007). The single-cognitive task consists of a serial sevens subtraction test (S7) that involves the serial subtraction of seven from a randomly chosen three-digit number (for instance, subtracting 7 from 203) or a controlled oral word association test (COWAT) task that requires the subject to orally state related words as much as possible within 1 min (for instance, saying hospital-related words or words beginning with "B"). These S7 and COWAT tests have been widely used to test the diagnostic values about cognitive abilities of subjects with cognitive impairments in clinics (Milstein et al., 1972; Malek-Ahmadi et al., 2011; Cullen et al., 2019).

Dual Task Effect

The subjects were required to perform UL motor tasks identical to those in the single tasks, in addition to performing the serial sevens or COWAT test simultaneously for one minute in the dual task paradigm. The dual task effect (DTE) is used to quantify the effects of the dual task performance on various parameters compared to the single task performance, as demonstrated by Plummer and Eskes [6]. The DTE is calculated as shown below:

$$\mathit{Dual\ Task\ Effect}\ (\mathbf{D}\mathit{TE}) = \frac{\text{Dual task performance} - \text{Single task performance}}{\text{Single task performance}} \times \mathbf{1}00$$

Speed and Accuracy

The verbal answers provided during the cognitive tasks were recorded from the beginning of each task while noting down the correct answers provided by the subjects. This was followed by the calculation of the cognitive speed, which is defined as the ratio of the total number of answers to the task time, and cognitive accuracy, which is defined as the ratio of the number of correct answers to the total answers provided in a task. Similarly, the movement trajectories were recorded during the motor task and used to calculate the motor accuracy and motor speed. The motor accuracy is equal to the percentage of movement trajectories within the annulus, and the motor speed is defined as the ratio of the total distance to the task time.

Statistical Analysis

Descriptive statistics were applied to the motor and cognitive variables to depict the motor accuracy and the number of accurate answers. The hypotheses were tested by comparing the single and dual task performances through a paired two-sided t-test and an independent sample student t-test on the subjects with stroke and healthy controls. The SPSS Analytic Server Version 21.0.0.1 (IBM Corporation, Chicago, Illinois, United States) was used to perform the statistical analysis wherein the significance level was set at 0.05.

RESULTS

Subjects

The 10 subjects with chronic stroke (average onset time: 50.9 months; seven subjects with left hemiparesis) participated in an initial screening (Fugl–Meyer assessment: upper extremity = 40.1 ± 16.5; mini-mental state examination = 28.9 ± 1.4) followed by the single and cognitive–UL motor dual tasks. Seven age- and gender-matched healthy control subjects also participated in the study. The subject's demographics and clinical information is shown in **Table 1**.

Single vs. Dual Tasks

As shown in **Table 2**, comparisons between the results of the single and dual tasks demonstrated that the motor accuracy of the subjects with stroke during the single motor task (circle only) was significantly lower than that observed during the dual task (circle + S7). The motor accuracies of the single and dual tasks were significantly decreased from 84.9% ± 11.2% to 79.0% ± 16.3%, respectively (p = 0.017). The motor accuracy of

TABLE 1 | Subject Demographics.

	ID	Age (yrs)	Ht (cm)	Wt (Kg)	Onset (mths)	Side (L/R)	MMSE	FMA-UEx	MAS		MMT	
									Elbow	Wrist	Shoulder	Elbow
Subjects with stroke hemiparesis	1	61	160	62	10	L	27	49	0	0	F	F
	2	39	190	120	6	L	29	21	0	0	F	F
	3	61	174	74	87	R	30	55	0	0	F	F
	4	53	162	79	36	L	30	57	0	0	F	F
	5	77	167	62	201	L	29	55	0	0	F	F
	6	53	174	80	96	R	30	52	1	1+	F	F
	7	42	170	75	5	L	26	10	1	1	F	F
	8	68	162	63	10	L	30	30	1+	1	F	F
	9	52	177	78	39	L	28	29	1+	1+	F	F
	10	41	178	78	19	R	30	43	1	1	F	F
	mean	54.7	171.4	77.1	50.9	7 L	28.9	40.1	–		–	
	(sd)	(12.3)	(16.7)	(16.4)	(62.1)		(1.4)	(16.5)				
H.C.	mean	58.4	162.2	67.7	–	–	–	–	–	–		
(*n* = 8)	(sd)	(10.6)	(13.1)	(17.5)								

H.C, healthy controls; MMSE, Mini-Mental State Examination. FMA-UEx, Fugl-Meyer Assessment of the Upper Extremity. MAS, Modified Ashworth Scale. MMT, Manual Muscle Test; F, Fair.

TABLE 2 | Cognitive and motor speed and accuracy in single and dual tasks between participants with stroke and healthy controls.

				Healthy controls	Stroke subjects	Healthy controls	Stroke subjects
				Motor Task (O shape)		**Motor Task (+ shape)**	
Motor Task	Speed (cm/sec)	Single Task		23.6 ± 12.3	15.9 ± 4.7	11.3 ± 4.7	11.0 ± 3.5
		Dual Task	S7	19.1 ± 9.8	14.6 ± 3.5	**9.9 ± 4.0***	10.0 ± 3.2
			COWAT	**17.5 ± 10.0***	15.1 ± 5.2	9.4 ± 3.6	11.1 ± 4.3
	Accuracy (%)	Single Task		93.1 ± 5.14	84.9 ± 11.2	88.6 ± 8.2	77.2 ± 13.2
		Dual Task	S7	92.9 ± 8.9	**79.0 ± 16.3***†	87.0 ± 9.8	74.9 ± 13.5
			COWAT	91.8 ± 8.5	86.1 ± 10.7	**90.3 ± 7.7***	**74.6 ± 12.4***†
				Cognitive Task (Serial 7)		**Cognitive Task (COWAT)**	
Cognitive Task		Single Task		12.7 ± 6.3	11.3 ± 5.4	11.6 ± 3.6	11.0 ± 2.6
	Speed (answers/min)	Dual Task	O	13.3 ± 4.9	10.6 ± 5.8	10.2 ± 4.9	11.0 ± 2.2
			+	11.0 ± 5.6	**9.3 ± 4.7***	11.1 ± 5.4	10.4 ± 2.6
	Accuracy (%)	Single Task		79.6 ± 14.7	86.8 ± 9.5	95.3 ± 3.1	95.5 ± 4.7
		Dual Task	O	80.2 ± 20.2	88.4 ± 12.1	93.9 ± 7.9	97.1 ± 3.7
			+	75.7 ± 20.4	84.3 ± 10.8	90.8 ± 9.1	96.4 ± 3.6

*S7 denotes "Serial 7" cognitive task. COWAT denotes a controlled oral word association test; O denotes motor task with circle shape movement track. + denotes a motor task with cross-shaped movement track. *p-value by paired t-test between single and dual task results. †p-value by student's t-test between stroke and control. Bold digits indicate values with statistical significance (p < 0.05).*

the subjects with stroke during the dual tasks (COWAT + cross) was also significantly reduced, with accuracies of 77.2% ± 13.2% and 74.6% ± 12.4% for the single and dual tasks, respectively ($p = 0.034$). The cognitive speed of the subjects with stroke during the dual task (S7 + cross) was significantly less than that observed during the single task. The cognitive speeds of the subjects with stroke during the single and dual tasks were equal to 11.3 ± 5.4 and 9.3 ± 4.7, respectively ($p = 0.008$).

Stroke vs. Control

The paired-t statistics in **Table 2** indicated that the motor accuracy of the stroke subjects was significantly lowered during the cross component of the single task than it was during the circle component ($p = 0.006$). There was no significant change in the number of correct answers and the motor accuracy of the control subjects during the single and dual tasks.

However, there was a significant difference in the movement accuracies between the subjects with stroke and the healthy controls during the dual tasks (**Table 2**). The subjects with stroke and the healthy controls registered movement accuracies of 79.0% ± 16.3% and 92.9% ± 7.9% during the Circle + S7 dual task, respectively ($p = 0.035$). Similarly, the subjects with stroke and the healthy controls reported movement accuracies of

74.6% ± 12.4% and 90.3% ± 7.7% during the Cross + COWAT dual task, respectively ($p = 0.010$).

There was a trend that the motor accuracy of the stroke group was lower than that of the control group, especially during single-motor conditions. The movement accuracies of the stroke and control subjects during the circle test were 84.9% ± 11.2% and 93.1% ± 5.1%, respectively ($p = 0.094$). Similarly, the movement accuracies of the stroke and control subjects during the cross test were 77.2% ± 13.2% and 88.6% ± 8.2%, respectively ($p = 0.062$). No significant difference was found between the controls and the subjects with stroke during the single-cognitive task.

Dual Task Effects

Dual task effects were shown between the results of speed and accuracy during cognitive and motor dual task described in **Table 3** and **Figure 2**. DTE in motor accuracy and cognitive speed during dual task of Circle and Serial 7 was significantly lower motor accuracy ($p = 0.034$) and cognitive speed ($p = 0.032$) in individuals with stroke. Cognitive speed and accuracy were significantly deteriorated in healthy controls during cognitive (Serial 7) motor(cross) dual task. (cognitive speed $p = 0.039$; cognitive accuracy $p = 0.046$) compared to corresponding single task outcomes. There was a significant negative linear correlation between motor speed and motor accuracy in subjects with stroke ($\rho = -0.6922$, $p = 0.0388$) (**Figure 2A**).

DISCUSSION

In this pilot study, we proved that the individuals with stroke demonstrated speed-accuracy tradeoffs during a cognitive and UL motor dual task, in conjunction with a greater emphasis on deteriorated cognitive performance. The people with stroke exhibited a lower motor accuracy compared to that of the healthy controls. However, the cognitive accuracies of the subjects with stroke and healthy controls were similar during the dual tasks. The people with stroke displayed a tendency to sacrifice motor accuracy to sustain motor speed and cognitive performance. This is contrary to the theory of sacrificing speed for accuracy in motor tasks, as stated by Fitts' Law. However, the healthy controls sacrificed motor speed and produced similar outcomes. It was demonstrated that speed and accuracy were the appropriate parameters for describing the outcome differences in cognitive and UL motor dual tasks between people with stroke and healthy controls.

To perform either a fine motor or challenging cognitive task, exerted cognitive efforts to increase or sustain the accuracy may exist. The people with stroke displayed a significantly lower UL motor accuracy compared to the healthy controls during dual tasks (**Table 1**). This is an acceptable outcome because the hemiparetic movements of subjects with stroke are assumed to be less accurate than those of the healthy participants. The validity of these results was verified by previous studies that have demonstrated the deterioration of the motor capabilities of subjects with stroke while performing cognitive–motor dual tasks, particularly during lower extremity activities such as walking (Bowen et al., 2001; Plummer-D'Amato et al., 2008) or balancing (Bensoussan et al., 2007). These studies also stated that subjects with stroke, unlike the healthy controls, prioritized cognitive tasks, such as maintaining the walking speed, center of pressure, and double support time, when the motor outcomes are significantly affected. Because the primary focus of this study was to analyze the deteriorated motor outcomes due to divided cognitive attention, we have not compared the effects of the single and dual tasks on the motor speed and accuracy of the UL. However, the healthy controls registered a better motor accuracy during the dual task than they did during the single task (**Table 1**). These results prove that the singular and dual natures of the motor and cognitive tasks affect the functional outcomes of the speed and accuracy paradigm differently. In the rehabilitation clinics, for examples, the motor accuracy during dual task may directly indicate the progress in UL motor rehabilitation, which potentially predict future performances of adults with stroke on several UL-involved and cognitive-driven daily activities while living in the community.

The DTE demonstrated that each group applied a different strategy while performing the dual circle (autonomous movement) and cross (cognitively-driven movement) motor tasks. There was no significant difference between the DTE values of the people with stroke and those of the healthy controls during the cross component of the dual task. However, a significant difference was observed in the DTE values of the people with stroke and those of the healthy controls while performing the circle component of the dual task. The people with stroke displayed more interference than the healthy controls in terms of motor accuracy, while the latter facilitated cognitive accuracy. Dual tasks related to walking have been an area of focus in stroke rehabilitation studies. These studies have obtained dual task outcomes that are similar to those obtained in the current study; for instance, they observed postural unsteadiness while demanding attention during walking, which is an autonomous movement (Brown et al., 1999; Yang et al., 2007). Similarly, the cognitive demands associated with the (autonomous) UL movements during the circle component may be lower than those of the UL (cognitive-driven) movements during the cross component of the cognitive–motor dual tasks. The different DTE values indicate that healthy controls are more likely to prioritize motor accuracy, which demands more cognition, compared to people with stroke. People with stroke are less likely to demand cognitive resources to improve their motor accuracy during a dual task because of their cognitive impairments. Therefore, they require more cognitive resources to increase their motor accuracy This study has successfully explored about the effectiveness of assessing SATs during a cognitive–UL motor dual task in adults with stroke. The SATs assessment may provide useful clinical information on UL motor rehabilitation, particularly when applying modern robotic and visuo-cognitive technologies.

Speed and accuracy are complementary parameters to effectively examine the task performance outcomes in people with stroke during cognitive and task-specific UL motor dual tasks. Researchers have encountered several unresolved issues indicating that people with stroke have a higher risk of mild cognitive impairments and dementia (Knopman et al., 2009).

TABLE 3 | Dual Task Effects in Motor and Cognitive Tasks.

					O			+	
	DTE			**Healthy**	**Stroke**	***p*-value†**	**Healthy**	**Stroke**	***p*-value†**
Motor Task									
	Speed (cm/sec)	Dual task	S7	−16.1 ± 17.4	−4.9 ± 17.1	0.213	−10.1 ± 14.3	−6.9 ± 17.0	0.678
			COWAT	−18.8 ± 19.8	−8.4 ± 14.3	0.261	−13.0 ± 19.5	−0.1 ± 15.9	0.173
			p-value	0.786	0.708	–	0.527	0.153	–
	Accuracy (%)	Dual task	S7	−0.3 ± 3.4	**−7.8 ± 9.0**†	**0.034**	0.1 ± 7.1	−2.5 ± 10.3	0.540
			COWAT	−1.6 ± 4.6	**1.8 ± 8.7***	0.312	3.5 ± 6.0	−2.1 ± 7.5	0.106
			p-value	0.120	**0.028**	–	0.382	0.926	–
Cognitive Task					**Serial 7**			**COWAT**	
				Healthy	**Stroke**		**Healthy**	**Stroke**	
	Speed (answers/min)	Dual task	O	11.0 ± 18.4	**−9.3 ± 14.2**†	**0.032**	−13.4 ± 30.1	3.0 ± 22.6	0.246
			+	**−12.3 ± 21.0***	−16.8 ± 23.8	0.684	−7.8 ± 20.9	−2.0 ± 25.5	0.611
			p-value	**0.039**	0.280	–	0.597	0.286	–
	Accuracy (%)	Dual task	O	12.9 ± 36.3	−6.4 ± 18.0	0.228	7.5 ± 27.8	−4.3 ± 23.3	0.372
			+	**−17.6 ± 19.7***	−19.7 ± 18.7	0.832	−1.9 ± 27.8	−0.1 ± 25.6	0.896
			p-value	**0.046**	0.109	–	0.384	0.412	–

*S7 denotes “Serial 7” cognitive task. COWAT denotes; O denotes a motor task with circle shape movement track. +, denotes a motor task with cross-shaped movement track; Bold, significant p-value ($p < 0.05$). *p-value by paired t-test between single and dual task results. †p-value by student’s t-test between stroke and control.*

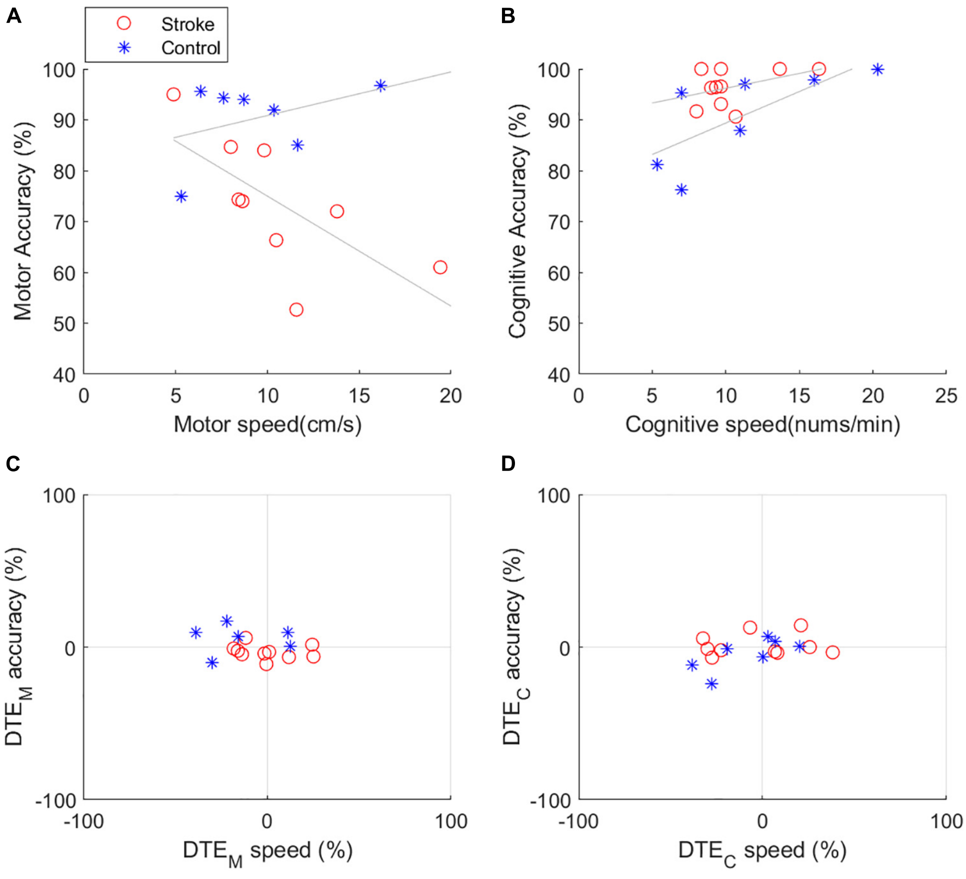

FIGURE 2 | Dual task effects on speed and accuracy during cognitive (COWAT) and upper limb motor (Cross) dual task **(A)** Speed and accuracy relationship in motor task **(B)** Speed and accuracy relationship in cognitive task **(C)** DTE motor speed and accuracy **(D)** DTE cognitive speed and accuracy.

However, mild cognitive impairments in people with stroke have been shown to decrease UL dual-task performance (Toosizadeh et al., 2016). The cause of the decreased performance in dual tasks has been investigated in terms of executive and neurophysiological dysfunctions in people with mild cognitive impairments (Johns et al., 2012; Kirova et al., 2015). In general, tasks that require executive attentional resources have been shown to adversely affect the task performance outcomes (Brown et al., 2015). Therefore, unlike gait training (i.e., autonomous movements), an effective training method for UL movements in people with stroke may concurrently affect other UL movements. A previous study on task-specific UL training methods successfully demonstrated that one trained UL movement task (i.e., feeding) potentially had lasting therapeutic effects on two untrained tasks, (i.e., sorting and dressing) (Schaefer et al., 2013). Therefore, a training paradigm that provides cognitive and UL motor dual-tasks would be appropriate for stroke UL movement rehabilitation; measurements of speed and accuracy provide useful information concerning a patient's rehabilitation.

In the future, a study should be conducted to investigate the clinical effectiveness in comprehensive interventions of cognitive and UL motor dual tasks for people with stroke who exhibit limited UL functions. The current study was preliminary which had limited samples of a gender-biased small number of participants. Future studies should involve an increased number of subjects and an investigation into task-specific motor activities such as the level of difficulty of the motor and cognitive tasks.

In summary, people with stroke were observed to have a UL motor accuracy during cognitive and UL motor dual tasks instead of a slow motor speed. Speed and accuracy were used as complementary parameters that may be capable of effectively indicating clinical progress in motor and cognitive rehabilitation outcomes.

CONCLUSION

In this study, we demonstrated that a cognitive–UL motor interference occurs in people with stroke hemiparesis while performing dual tasks; this was based on the observations of their performances with respect to speed and accuracy during single and dual tasks. Dual task effects indicated a deterioration in performance in the dual tasks compared to that of the single task. Speed and accuracy are the complementary parameters that may indicate clinical effectiveness in motor and cognitive outcomes in people with stroke.

DATA AVAILABILITY STATEMENT

The original data presented in the study are included in the **Supplementary Material**.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Institutional Review board at National Rehabilitation Center, Seoul, South Korea. The patients/participants provided their written informed consent to participate in this study. Written informed consent was obtained from the individual(s) for the publication of any potentially identifiable images or data included in this article.

AUTHOR CONTRIBUTIONS

HK, H-KK, NK, and CSN had equal contributions to the conception, design and methodology of the work, data acquisition, supervision, and project administration. H-KK and HK contributed to analyze the data, validation, formal analysis, and visualization. HK contributed to original draft preparation, review, editing, and funding acquisition. All authors have read and agreed to the published version of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnhum.2021.671541/full#supplementary-material

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Dissociating the Impact of Movement Time and Energy Costs on Decision-Making and Action Initiation in Humans

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Recent theories and data suggest that adapted behavior involves economic computations during which multiple trade-offs between reward value, accuracy requirement, energy expenditure, and elapsing time are solved so as to obtain rewards as soon as possible while spending the least possible amount of energy. However, the relative impact of movement energy and duration costs on perceptual decision-making and movement initiation is poorly understood. Here, we tested 31 healthy subjects on a perceptual decision-making task in which they executed reaching movements to report probabilistic choices. In distinct blocks of trials, the reaching duration ("Time" condition) and energy ("Effort" condition) costs were independently varied compared to a "Reference" block, while decision difficulty was maintained similar at the block level. Participants also performed a simple delayed-reaching (DR) task aimed at estimating movement initiation duration in each motor condition. Results in that DR task show that long duration movements extended reaction times (RTs) in most subjects, whereas energy-consuming movements led to mixed effects on RTs. In the decision task, about half of the subjects decreased their decision durations (DDs) in the Time condition, while the impact of energy on DDs were again mixed across subjects. Decision accuracy was overall similar across motor conditions. These results indicate that movement duration and, to a lesser extent, energy expenditure, idiosyncratically affect perceptual decision-making and action initiation. We propose that subjects who shortened their choices in the time-consuming condition of the decision task did so to limit a drop of reward rate.

Keywords: time cost, reaching, decision making, energy expenditure, reward rate, action, goal directed behavior

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INTRODUCTION

For humans and animals in general, life presents a constant stream of decisions about actions to make regarding food, mobility, social interactions, and many other situations. Crucially, decision and action often involve context-dependent computations during which effort is traded against time to obtain rewards as soon as possible while spending the least possible amount of energy (Shadmehr and Ahmed, 2020). These computations are complex to solve because strong interactions exist between reward valuation, elapsing time, and energy expenditure (**Figure 1A**). For example, human and non-human primates expecting large rewards reduce their reaction time and increase the vigor of the movements executed to obtain these rewards (Kawagoe et al., 1998; Manohar et al., 2015; Reppert et al., 2015; Yoon et al., 2018; Revol et al., 2019). But increasing vigor usually means increasing energetic expenditure, which discounts reward value (Sugiwaka and Okouchi, 2004; Klein-Flügge et al., 2015). Indeed, when an effortful movement is anticipated, reaction times are increased, and action vigor is reduced (Morel et al., 2017; Summerside et al., 2018). Besides, to be rewarded, it is often necessary to execute accurate movements. A fundamental and long-established observation is the so-called speed-accuracy trade-off: when actions are performed faster, they tend to be less precise (Fitts, 1954). This principle applies to both motor and cognitive performances (Heitz, 2014). Individuals could thus benefit from maximizing accuracy and minimizing effort by making slow movements. However, this strategy implies increasing behavior duration, which inevitably delays the completion of the task and the acquisition of the reward, leading to the well-known temporal discounting of reward value (Myerson and Green, 1995; Shadmehr et al., 2010; Haith et al., 2012; Choi et al., 2014; Berret and Jean, 2016). To summarize, both time and effort discount the value of reward, and reducing reward temporal discounting requires increasing energy expenditure, which in turn discounts the value of reward too.

What are the implications of these relationships during goal-directed behavior? For anyone making a decision, the most adaptive strategy is to choose options that maximize the global rate of reward (Bogacz et al., 2010; Balci et al., 2011), which occurs when *both* decision and action are sufficiently accurate but not overly effortful and time consuming. Because trade-offs during decision and action have been typically studied in isolation, mechanisms allowing a coordinated computation of reward rate are still elusive. Recent promising advances suggest, however, that motor control and choices share important principles (Morel et al., 2017; Yoon et al., 2018; Carland et al., 2019). First, motor costs influence human decision-making when choices rely on movements of different costs (Cos et al., 2011, 2014; Morel et al., 2017; Michalski et al., 2020) or when they are driven by perceptual stimuli (Marcos et al., 2015; Hagura et al., 2017). During motor decisions for instance, humans usually prefer close and big targets compared to small and distant ones (e.g., Michalski et al., 2020). Importantly, movements of longer durations are judged by humans as more effortful regardless of amplitude. This suggests that time, and not distance nor speed, increases the perception of effort (Morel et al., 2017). Whether or not this result generalizes beyond motor choices is unknown. Second, in a foraging paradigm, humans make decisions regarding how long to stay and collect rewards from one patch, and then move with certain speed to another patch. In this situation, the harvest duration and the vigor with which subjects move from one site to another are governed by a mechanism allowing to maximize the overall capture rate (Yoon et al., 2018). Finally, both human and monkey level of decision urgency predicts the duration of the movements executed to express these choices, allowing to maximize the rate of reward (Ditterich, 2006; Churchland et al., 2008; Drugowitsch et al., 2012; Thura et al., 2012, 2014; Thura, 2020).

Together, these studies suggest that movement vigor is coordinated with decision-making urgency to optimize the rate of reward. Recently, we provided strong support for this hypothesis by showing that when movement accuracy requirements are relaxed, decision duration is extended, allowing human subjects to increase their choice accuracy (Reynaud et al., 2020). The present work is designed to investigate this coordination between decision and action further and assess whether, how and why motor time and/or energy costs influence perceptual choices in human subjects. More specifically, we aimed at addressing three questions: (1) Does the motor context in which a choice is made, costly or not, influence decision-making? Because decision and action need to be coordinated in order to maximize the rate of reward, we predict that decision speed and/or accuracy will be modulated depending on the cost of the movement executed to express that choice; (2) What is the most impactful motor cost (time or energy) context during perceptual decision-making? Because several studies have shown that movement duration is the parameter that subjects tend to control to increase their rate of reward (Shadmehr et al., 2010; Haith et al., 2012; Choi et al., 2014), we predict that movement duration should have the largest impact on subjects' choices; (3) How variable are these effects between subjects? Recent studies revealed individual "traits" of decision and motor behavior, showing that despite facing identical trials, some subjects could decide and act much faster than others (Berret et al., 2018; Reppert et al., 2018; Labaune et al., 2020; Thura, 2020). This suggests variable sensitivities to motor costs at the population level. We thus predict that the impact of the movement energy and/or temporal costs on decision-making will be idiosyncratic.

MATERIALS AND METHODS

Power Analysis

We performed an *a priori* power analysis to estimate the optimal combination of trials per condition and participant numbers, depending on expected effect sizes and variabilities (Baker et al., 2021). Calculations were performed based on the duration of decisions made by 20 human subjects performing a similar decision task where movement properties were varied between blocks of trials (Reynaud et al., 2020). We estimated a mean difference of decision duration between motor conditions of 150 ms, a within-subject standard deviation (SD) of 420 ms, a between-subject SD of 230 ms, and we set the alpha level to 0.05. For a standard power of 80%, 22 subjects had to be tested on 32 trials per condition. To increase the power and reach 90%, we needed to test at least 28 subjects in about 80 trials per conditions. Given our past experience with similar experiments (Reynaud et al., 2020; Thura, 2020), executing a minimum of 80 trials per condition in an experiment that is designed to include 3 conditions takes about 1 h, which is an acceptable duration for a healthy, young subject. But to further increase the statistical power of our results without increasing session duration, we tested each participant twice, in two separate sessions. The effect of the session on the impact of motor costs on goal-directed behavior will be addressed in another publication.

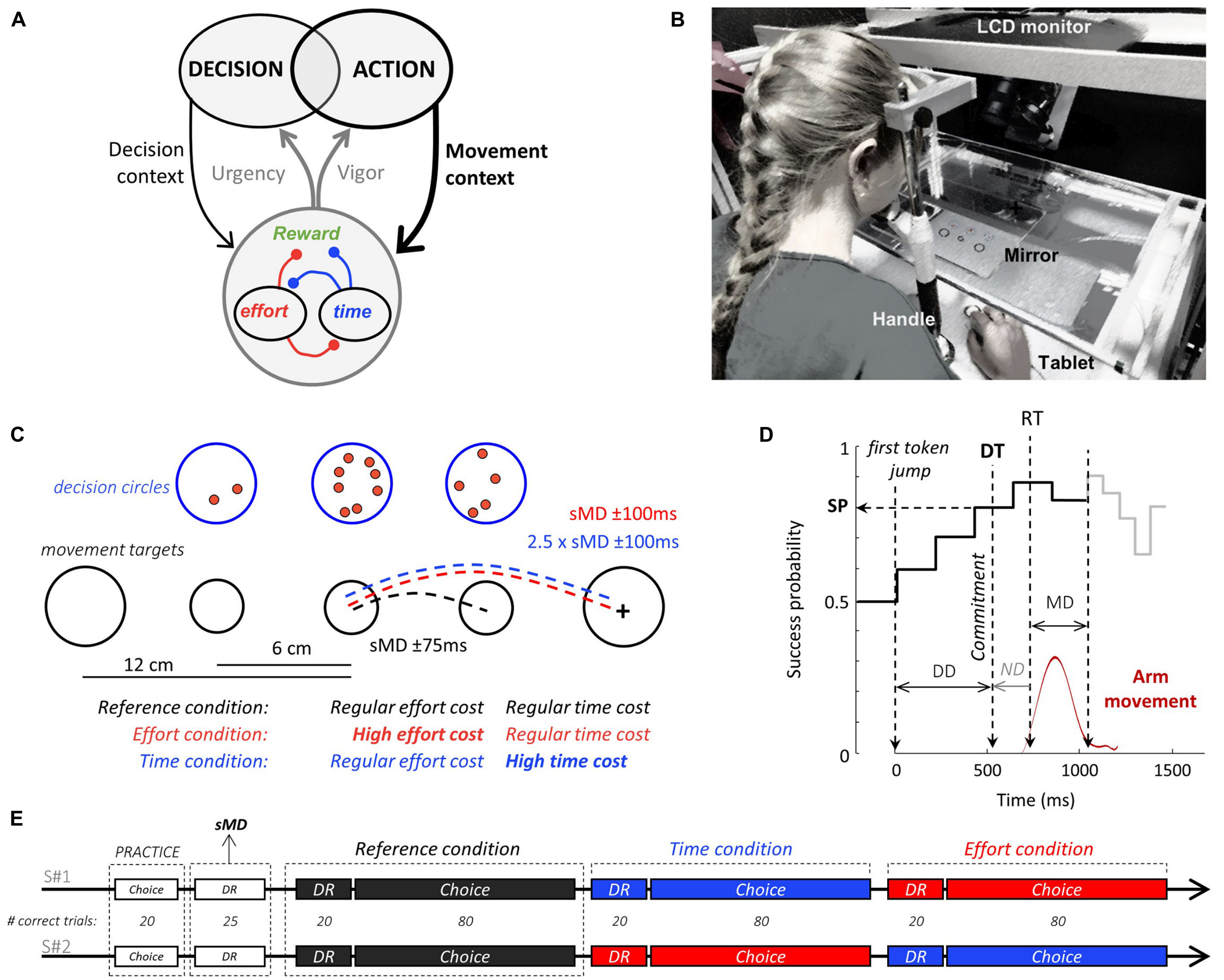

FIGURE 1 | Theoretical framework, experimental set-up and design. **(A)** To maximize the rate of reward during goal-directed behavior, decision and action must be coordinated. Regulation signals (gray arrows) allow such coordination. These signals are determined based on the decisional (thin black arrow) and motor (bold black arrow) context-dependent integration of reward value, elapsed time, and energy expenditure. These three components are intertwined in a trade-off of reciprocal negative interactions (red and blue connections). **(B)** Experimental apparatus (see text for details). **(C)** Visual display and motor conditions in the choice task. Blue circles illustrate the decision stimuli. Tokens successively jump from the central circle to one of the two lateral circles. Black circles show the movement stimuli. Subjects move a handle (cross) from a central start circle to one of the two lateral targets, depending on their choice. Movement amplitude and duration (MD) are imposed in distinct blocks of trials. In the Reference condition (black), both lateral movement targets are located close to the starting circle and a specific movement duration (with a 150 ms tolerance window) is imposed. In the two other conditions, both lateral movement targets are located twice as far apart from the starting circle compared to the Reference condition. In the Effort condition (red), the imposed movement duration is the same as in the Reference condition whereas in the Time condition (blue), the imposed movement duration is about twice longer. For these two costly conditions, the tolerance interval around the imposed movement duration is 200 ms. Note that four movement targets are displayed next to the start circle for illustration purpose. Only two, either at 6 or 12 cm of the starting circle are visible during the experiment. **(D)** Temporal profile of success probability in one example trial of the choice task. At the beginning of the trial, each target has the same success probability (0.5). When the first token jumps into one of the two potential targets (the most leftward vertical dotted line), success probability of that target increases to ∼0.6. Success probability then evolves with every jump. Subjects execute a reaching movement (red trace) to report their choices. Movement onset (RT) and offset times are used to compute movement duration (MD), and movement offset marks the moment when the tokens that remain in the central decision circle jump more quickly to their assigned target (gray trace). The estimated time of the decision (DT) is computed by subtracting the subject's mean non-decision delay (ND) estimated in a simple delayed-reach (DR) task from movement onset time, allowing computation of the success probability (SP) at that moment. Only 10 out of 15 jumps are illustrated on this SP profile. **(E)** Time course of the two sessions (S#1 and S#2). Subjects start each session with 20 trials of the choice task to familiarize themselves with the set-up. Then 25 trials of the DR task with no constraint on movement duration are performed in order to determine for each subject the average spontaneous arm movement duration (sMD) which will be necessary to determine the time constraints of the response movements in each condition. Subjects next need to complete 20 correct trials in the DR task and 80 correct trials in the choice task for each motor condition. They start with the Reference condition, followed by the Time and the Effort conditions in the first session. The order of presentation of the two costly conditions is reversed in the second session.

Participants

Thirty-one healthy human subjects (age range: 18–36, mean ± standard deviation: 24.4 ± 4.2; 20 females / 11 males; 29 right-handed / 2 left-handed) participated in this study. All gave their consent before starting the experiment. The INSERM ethics committee (IRB00003888) approved the protocol on March 19th, 2019. Each participant was asked to perform two experimental sessions (with a maximum of 7 days between sessions) and they received a monetary compensation (15 euros per completed session) for participating in this study. All subjects completed the two sessions and are included in the present dataset.

Experimental Set Up

Subjects sat in an armchair and made planar reaching movements using a handle held in their dominant hand. A digitizing tablet (GTCO CalComp) continuously recorded the handle horizontal and vertical positions (100 Hz with 0.013 cm accuracy). Target stimuli and cursor feedback were projected by a DELL P2219H LCD monitor (60 Hz refresh rate) onto a half-silvered mirror suspended 26 cm above and parallel to the digitizer plane, creating the illusion that targets floated on the plane of the tablet (**Figure 1B**).

Tasks and Experimental Design

Subjects were instructed to perform alternations of two tasks: a choice task, modified from Cisek et al. (2009), and a delayed-reaching (DR) task. In the choice task (**Figure 1C**), participants faced a visual display consisting of three blue circles (the decision circles; 1.5 cm radius) placed horizontally at a distance of 6 cm of each other and three black circles positioned 12 cm below (the movement targets). At the beginning of each trial, 15 red tokens are randomly arranged in the central blue circle. The position of the decision stimuli was constant, but the distance between the central and lateral movement targets varied, set to either 6 cm (short distance) or 12 cm (long distance) from the central circle in distinct blocks of trials. The size of the central movement circle (the starting circle) was constant (0.75 cm radius) whereas the size of lateral movement circles was set to either 1 cm radius in the short distance trials or 1.5 cm radius in the long distance ones to minimize the perceived size and accuracy requirement differences between conditions (Sperandio and Chouinard, 2015). Importantly, the size of the movement target was chosen to be large enough to minimize the motor accuracy constraints and avoid major speed-accuracy tradeoff adjustments. The effect of motor accuracy on decision-making has been investigated in a recent publication (Reynaud et al., 2020).

A choice task trial (**Figure 1D**) starts when the subject places the handle in the starting position and remains still for 500 ms. The tokens then start to jump, one by one, every 200 ms, in one of the two possible lateral blue circles. The subject has to decide which of the two decision circles will receive the majority of the tokens at the end of the trial. To report a decision, the subject has to move and hold the handle into the lateral movement target corresponding to the side of the chosen decision circle for 500 ms. Subjects were allowed to make and report their choice at any time between the first and the last token jump. The tokens that remain in the central circle once the target is reached then jump more quickly (every 50 ms), motivating subjects to answer before all tokens have jumped to increase their rate of correct decisions. Note that this feature entails that movement duration carries a temporal cost with respect to the subject's rate of correct decisions. A visual feedback about decision success or failure (the chosen decision circle turning either green or red, respectively) is provided after the last jump. A 1,500 ms period (the inter-trial interval, ITI) precedes the following trial.

The delayed-reach (DR) task is similar to the choice task except that only one lateral decision circle along with its associated movement target are displayed at the beginning of the trial (either at the right or at the left side of the central circle with 50% probability). Moreover, all tokens move from the central circle to this unique circle at a GO signal occurring after a variable delay (1,000 ± 150 ms). This task is used to estimate the spontaneous movement duration of each subject and their mean reaction (i.e., non-decision) time in each motor condition (see below).

At the beginning of the session, a practice period consisting of performing 20 choice task trials with short and long distance targets (with 50% probability) was proposed, mainly allowing subjects to get familiar and comfortable with the manipulation of the handle on the tablet. Then, the subject had to perform 25 trials of the DR task with short distance movements and no constraint on movement duration. This block of trials was used to determine the average spontaneous arm movement duration (sMD) necessary to reach short distance targets in each subject. Based on this duration, we determined for each subject the spontaneous MD interval (sMD ± 75 ms) and the long-distance MD interval (2.5 × sMD ± 100 ms). The first six subjects performed the tasks with a lower temporal tolerance (± 50 and ± 75 ms for the short and long distance movements, respectively), but based on their motor performance and post-session interviews, we decided to relax the temporal constraints of the movements for the rest of the population (±75 and ± 100 ms for the short and long distance movements, respectively). Subjects then performed alternations of DR and choice task trials in the three different motor conditions described in the next paragraph (**Figure 1E**).

To assess the influence of the time and energy costs of movements on decision-making and movement initiation, the position of the lateral movement targets as well as the movement duration (MD) interval allowed to reach these targets were varied in three distinct blocks of trials (**Figure 1C**). In the "Reference" condition, subjects were instructed to execute short distance movements, within their spontaneous MD interval. In the "Time" condition, subjects had to execute long distance movements within their long MD interval, thus doubling movement duration (**Figure 2A**, left) without much of an increase of energy expenditure compared to the Reference condition (**Figure 2B**). In the "Effort" condition, subjects were instructed to execute long distance movements, just as in the Time condition, but within their spontaneous MD interval. This Effort condition thus required about twice faster movements than

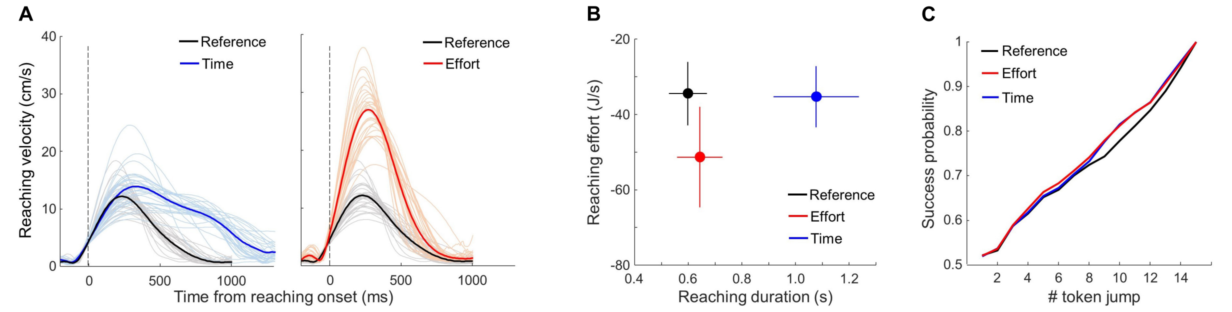

FIGURE 2 | Control analyses. **(A)** Individual (thin) and average (bold) reach velocity profiles in the three motor conditions of the choice task, aligned on movement onset. Only adequate movements are included. Time and Reference conditions are compared in the left panel; Effort and Reference conditions are compared in the right panel. **(B)** Relationship between the average (±SD) reaching duration and effort across subjects in the three motor conditions (see Eq. 2 and details in text). **(C)** Average success probability profiles of trials experienced by subjects in each of the three motor conditions (Eq. 3).

the Reference condition, substantially increasing their energy cost (**Figure 2B**) without increasing their duration (**Figure 2A**, right). Importantly, the decision component of the task was strictly similar between the three motor conditions. For instance, the maximum decision time allowed (15 token jumps, 2,800 ms) wasn't shorter in the Time condition compared to the two other blocks. A trial was considered incorrect if movement did not meet these block-dependent spatio-temporal constraints. In this case, the subject received a visual feedback (both movement targets turned red) as well as a 500 ms audio feedback indicating that movement was too fast or too slow (800 or 400 Hz sound, respectively). If the movement was executed within the imposed duration interval and the subject chose the target receiving the majority of tokens at the end of the trial, that trial was considered as correct. The goal for each subject was to perform in each of the two sessions 20 correct DR task trials in each condition and 80 correct choice task trials in each condition. This objective encouraged them to maximize their rate of correct responses. Subjects started both sessions in the Reference condition. In the first session, the Reference condition was followed by the Time and the Effort conditions, whereas this order was reversed in the second session (**Figure 1E**).

Data Analysis

The present analyses were performed on trials collected from all subjects performing both sessions #1 and #2. Data were analyzed off-line using custom-written MATLAB (MathWorks) and R[1] scripts. Unless stated otherwise, data have been combined across sessions, and are reported as mean ± standard deviation (SD).

We first analyzed the kinematic properties of the reaching movements performed by subjects in each of the three motor blocks. Horizontal and vertical handle position data were filtered using a fifteen-degree polynomial filter and then differentiated to obtain velocity profiles (see one example reach velocity profile depicted in **Figure 1D**). Movement onset and offset were determined using a 3.75 cm/s velocity threshold (1.5 pixel/10 ms for a screen resolution of 0.025 cm/pixel). Peak velocity and movement duration (MD) were, respectively, computed as the maximum value and the time between these two events.

In the present work, we manipulated subjects' reaching speed (for a given amplitude) to vary movement energetic expenditure between conditions, as reaching speed and metabolic rate strongly co-vary (Ludlow and Weyand, 1985; Shadmehr et al., 2016). But we also estimated, *post hoc*, the energy e_r spent during each reaching movement as a function of the reaching distance d (in meters) and duration t (in seconds) using the following equation, from Shadmehr et al. (2016) in which the energetic cost of 2D reaching movements was measured (via expired gas analysis) and parameterized as a function of movement duration, arm mass, and distance:

$$e_r = amt + b\frac{md^i}{t^{j-1}} \tag{1}$$

In Eq. (1), m is a constant which represents the mass of the arm, estimated in the present work based on subjects' weight data (m = weight × ∼0.05, de Leva, 1996). Terms a, b, i, and j are fixed coefficients determined in Shadmehr et al.'s (2016) experiment. For the present estimations, we set $a = 15$, $b = 77$, $i = 1.1$, and $j = 2.7$. Energetic consumption may represent an objective measure of movement effort. We used this estimation to compute participants' expected reward rate in the choice task (see Eq. 4). In the context of reaching movements however, past studies proposed that effort is rather subjectively perceived as the temporally discounted metabolic cost of performing an action (Körding et al., 2004; Shadmehr et al., 2016), resulting in the following equation:

$$E(t) = -\frac{e_r}{1+\gamma t} \tag{2}$$

where γ is the hyperbolic temporal discounting parameter. Thus, assuming that movement duration delays the acquisition of reward, the act of moving fast leads to acquisition of a large reward in exchange for a large effort, whereas moving slowly leads to acquisition of smaller, discounted reward later in exchange for payment of small effort. We used this metric to control for the

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[1] https://www.r-project.org/

efficiency of our experimental conditions to dissociate reaching duration from effort (**Figure 2B**).

The analysis of participants' decision-making behavior in the choice task focused on the duration of the decision (DD) and the success probability of the choice (SP). To estimate the time at which subjects committed to their choice on each trial, we first defined the reaction time (RT) as the time of movement onset with respect to the first token jump. We then subtracted from each RT the mean non-decision delay estimated based on subjects' RTs in the same motor condition of the DR task, providing the time at which the deliberation ends (decision time, DT). RTs measured in the DR task also allowed us to assess the effects of the motor context on movement initiation (**Figure 3**). Then, DD was computed as the duration between the first token jump and DT in the choice task (**Figure 1D**).

The choice task design allows to calculate, at each moment in time during a trial, the success probability $p_i(t)$ associated with choosing each target i (Eq. 3). For instance, for a total of 15 tokens, if at a particular moment in time the right target contains N_R tokens, whereas the left target contains N_L tokens, and there are N_C tokens remaining in the center, then the probability that the target on the right will ultimately be the correct one, i.e., the success probability (SP) of guessing right is as follows:

$$p\left(R \mid N_R, N_L, N_C\right) = \frac{N_C!}{2^{N_C}} \sum_{k=0}^{\min(N_C,\, 7-N_L)} \frac{1}{k!(N_C-k)!} \qquad (3)$$

To control for the average decision difficulty between motor conditions and make sure that this difficulty could not account for potential differences in the subjects' decision strategy, all subjects faced the same sequence of trials in which we interspersed among fully random trials (20% of the trials in which each token is 50% likely to jump into the right or into the left lateral circle) three special types of trials characterized by particular temporal profiles of success probability. Subjects were not told about the existence of these trials. 30% of trials were so-called "easy" trials, in which tokens tended to move consistently toward one of the circles, quickly driving the success probability $p_i(t)$ for each toward either 0 or 1. Another 30% of trials were "ambiguous", in which the initial token movements were balanced, making the $p_i(t)$ function close to 0.5 until late in the trial. The last special trial type was called "misleading" trials (20%) in which the 2–3 first tokens jumped into the incorrect circle and the remaining ones into the correct circle. Crucially, the sequence was designed so that the proportion of trial types was continuously controlled and kept constant within and between motor conditions. Even if the above criteria leave some room for variability within each trial type, the sequence provided subjects with an overall same level of decision difficulty between motor conditions (**Figure 2C**). In all cases, even when the temporal profile of success probability of a trial was predesigned, the actual correct target was randomly selected on each trial.

We computed subjects' mean reward rate in each motor condition in order to assess the impact of each motor cost on this metric. We quantified the expected reward rate in each trial i with the following equation:

$$RR_i = \frac{(\Delta . SP_i) - e_i}{DD_i + ND + MD_i + rT_i + ITI} \qquad (4)$$

where Δ is a hypothetic value (in Joules) assigned by the brain to a positive outcome in each trial (arbitrarily set to 500), SP is the probability of choosing the correct target in trial i (Eq. 3), e is the energetic consumption of reaching toward the chosen target in trial i (Eq. 1), DD is the decision duration for trial i, ND is the condition-dependent non-decision delay (estimated in the DR task), MD is the duration of the movement in trial i, rT is the time taken by the remaining tokens to jump in their assigned target in

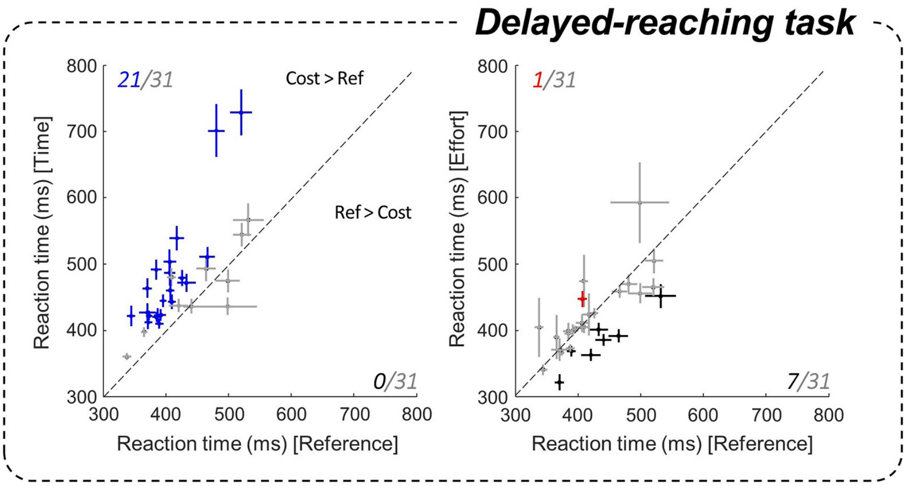

FIGURE 3 | Effect of motor conditions on motor initiation duration. Comparison of subjects' reaction times (RTs) in the delayed-reach task between the costly conditions (ordinate, left panel: Time / right: Effort) and the Reference condition (abscissa). Pluses indicate the mean and standard error (SE) for each subject. Left panel: blue pluses indicate data that are significantly larger in the Time condition compared to the Reference condition. Right panel: red (black) pluses indicate RTs that are significantly larger (smaller) in the Effort condition compared to the Reference condition.

trial i, and ITI is the fixed inter-trial interval. We then computed the average reward rate across trials and compared this average rate between motor conditions at the population level.

Statistics

We used linear mixed effects models to examine the effect of motor conditions on the different dependent measures described above for each subject. Analyses were performed using the "lme4" package for R (Bates et al., 2015). We defined a model containing the most appropriate random effects (i.e., factors of non-interest) for each variable using Likelihood Ratio Tests. For the DR task variable (i.e., RT), *sessions* (#1 and #2) were included in the model as a random intercept. For the motor (duration, velocity peak, effort) and decision (duration, success probability, and reward rate) variables of the choice task, *sessions* (#1 and #2), and *trial types* (random, easy, misleading, and ambiguous) were included as a random intercept. We then tested the effect of the motor conditions (Reference, Time, and Effort) as a fixed factor in order to evaluate their influence on each dependent variable tested. We also computed a linear mixed effect model for each dependent variable tested across all subjects by adding *subjects* as a random factor. Finally, *post-hoc* comparisons were carried out using pairwise comparisons through the "lsmeans" package for R (p-adjusted with false discovery rate method, Benjamini and Hochberg, 1995; Lenth, 2016) to assess the effect of the different motor conditions (Reference vs. Time and Reference vs. Effort). For each *post-hoc* comparison, we report p-values and absolute z-ratios, which corresponds to the ratio between estimated effect size and the standard error of this effect.

RESULTS

Across the two sessions, subjects performed 179 ± 36 trials (average ± SD, correct and incorrect) in the Reference condition, 128 ± 23 in the Effort condition and 202 ± 51 in the Time condition. Subjects' movement error rate was 40% (session #1: 46%; #2: 32%) in the Reference condition, 22% (session #1: 24%; #2: 19%) in the Effort condition and 48% (session #1: 49%; #2: 44%) in the Time condition. When movements were adequate, the overall percentage of correct choices was 80% across the population (Reference condition: 79%; Effort condition: 83%; Time condition: 80%).

Control Analysis: Effect of Motor Conditions on Movement Kinematic

To verify that the motor conditions effectively induced time- or energy-consuming reaching movements with respect to the reference condition, we analyzed reaching velocity peak and duration in each of the three motor blocks. We only report data collected in the choice task but results are similar in the DR task. Only trials in which an adequate movement was performed to express a choice, irrespective of the outcome of that choice, were included. As expected, reaching movement velocity peaks and durations were significantly modulated by the motor context in which movements were executed. **Figure 2A** shows each subject's mean reaching velocity profile averaged across trials as a function of the motor condition. On average (±SD), for a similar duration (642 ± 85 ms vs. 597 ± 71 ms), movement peak velocity was about twice higher in the Effort condition compared to the Reference (28.5 ± 5.3 cm/s vs. 13.3 ± 2.6 cm/s, $|z| = 246.0$, $p < 0.001$), whereas movement duration was about twice longer in the Time condition compared to the Reference condition (1,076 ± 159 ms vs. 597 ± 71 ms, $|z| = 245.9$, $p < 0.001$). In the Time condition, the average (±SD) movement peak speed was slightly higher compared to the Reference condition (15.2 ± 3.3 cm/s vs. 13.3 ± 2.6 cm/s, $|z| = 32.1$, $p < 0.001$), but still much lower compared to the Effort condition (28.5 ± 5.3 cm/s, $|z| = 213.3$, $p < 0.001$).

As noted above, it has been proposed that reaching effort is subjectively perceived as the temporally discounted metabolic cost of performing the movement. By estimating the effort of each reaching movement using (Eq. 2), we observed that the effort level associated with executing reaching movements in the Effort condition is largely increased compared to the Reference condition (−51.3 ± 13 J/s vs. −34.4 ± 8 J/s, $|z| = 165.0$, $p < 0.001$, **Figure 2B**). In the Time condition, however, by imposing the same motion speed as in the Reference condition and doubling the distance to be covered, participants subjective reaching effort is much comparable, yet significantly different, to the Reference condition (−35.2 ± 8 J/s vs. −34.4 ± 8 J/s $|z| = 8.3$, $p < 0.001$, **Figure 2B**).

Effect of Motor Conditions on Motor Initiation

We first address the effects of motor conditions on action initiation. Indeed, the fully instructed delayed-reach (DR) task allows to assess the effects of the motor context on non-decision delays, mainly reflecting the motor initiation process. To do so, we compared subjects' average reaction times (RTs) under each motor condition of the DR task. At the population level, we found that RTs in the DR task were significantly longer in the Time condition, i.e., when reaching duration was longer, compared to the Reference condition (475 ± 79 ms in Time and 420 ± 53 ms in Reference, $|z| = 12.13$, $p < 0.001$). The increase of a temporal motor cost extended RTs in the vast majority of subjects (21/31, $p < 0.05$) compared to the Reference condition (**Figure 3**, left). This increase of RT was not observed in the Effort condition at the population level (414 ± 53 ms). The effect of effort was also less pronounced and more variable at the individual level (**Figure 3**, right). Within-subject data indeed show that energy-consuming movements usually led to similar RTs compared to the Reference block ($p > 0.05$ for 23/31 subjects), although some participants (7/31) reacted significantly faster ($p < 0.05$).

Effect of Motor Conditions on Decision Behavior

To investigate subjects' decision behavior in the choice task, we analyzed their decision durations (DDs) and success probabilities (SPs) as a function of the motor context in which choices were reported. We first found at the population level that DDs were significantly shorter in the Time condition than in the Reference condition (1,033 ± 334 ms vs. 1,104 ± 321 ms, $|z| = 9.91$, $p < 0.001$). This observation is robust within subjects, as about

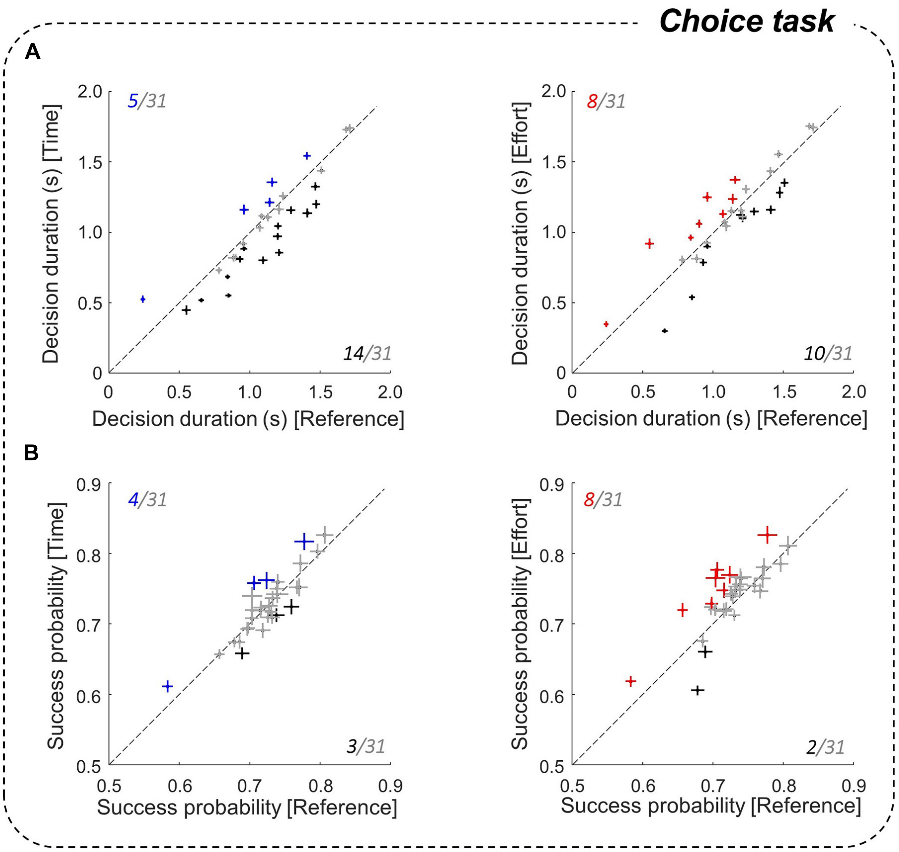

FIGURE 4 | Effect of motor conditions on decision duration and success probability. **(A)** Comparison of the mean (±SE) subjects' decision durations between the costly conditions (left panel: Time/right: Effort) and the Reference condition in the choice task. Same conventions as in **Figure 3**. **(B)** Same analysis as A for success probabilities at decision time.

half (14/31) of them made significantly faster decisions when the required movement duration was doubled (**Figure 4A**, left). Only five subjects showed the opposite pattern, i.e., a decrease of decision speed in the Time condition compared to the Reference condition. By contrast, we found no significant difference in DDs between the Reference and Effort conditions at the population level (1,104 ± 321 ms vs. 1,092 ± 333 ms), and effort had a mixed influence on decision speed at the individual level (**Figure 4A**, right). 13 out of 31 participants did not adjust their DDs in the Effort condition compared to the Reference block, 8 were longer to decide in the Effort condition compared to the Reference condition, and 10 participants showed the opposite pattern.

To assess the consequences of a modulation of DDs on choice accuracy, we calculated subjects' SPs at decision time (**Figure 4B**). At the population level, SPs at decision time were similar in the Time and the Reference conditions (0.73 ± 0.05 vs. 0.72 ± 0.04) and were significantly higher in the Effort condition compared to the Reference condition (0.74 ± 0.05 vs. 0.72 ± 0.04, $|z| = 5.98$, $p < 0.001$). However, individual data revealed inconsistent effects, with only 8 subjects that showed a higher SP in the Effort condition compared to the Reference condition and for the majority of subjects (21/31), SPs were similar between conditions. Thus, despite the modulation of DDs described above, choice SP was not significantly impacted by movement duration and only marginally impacted by energy-consuming movements.

Effect of Motor Conditions on the Rate of Reward

We computed the expected rate of reward (according to Eq. 4) for each subject in each trial, averaged it across each motor condition trials and found at the population level that reward rate was lower in the Effort condition compared to the Reference condition (70 ± 6 vs. 74 ± 6 J/s, $|z| = 15.3$, $p < 0.001$, **Figure 5A**). Reward rate was even more significantly reduced in the Time condition compared to the Reference condition (63 ± 7 vs. 74 ± 6 J/s, $|z| = 40.7$, $p < 0.001$, **Figure 5A**). These observations are robust at the individual level since all subjects had a lower reward rate in the Time condition compared to the Reference condition ($p < 0.05$). In the Effort condition, however, effects were more variable within subjects, as reward rate decreased for 20 participants, it increased for 1 subject and it did not significantly vary for the remaining 10 subjects compared to the Reference condition.

It is interesting to note that the most penalizing motor condition (the Time condition) is also the one in which

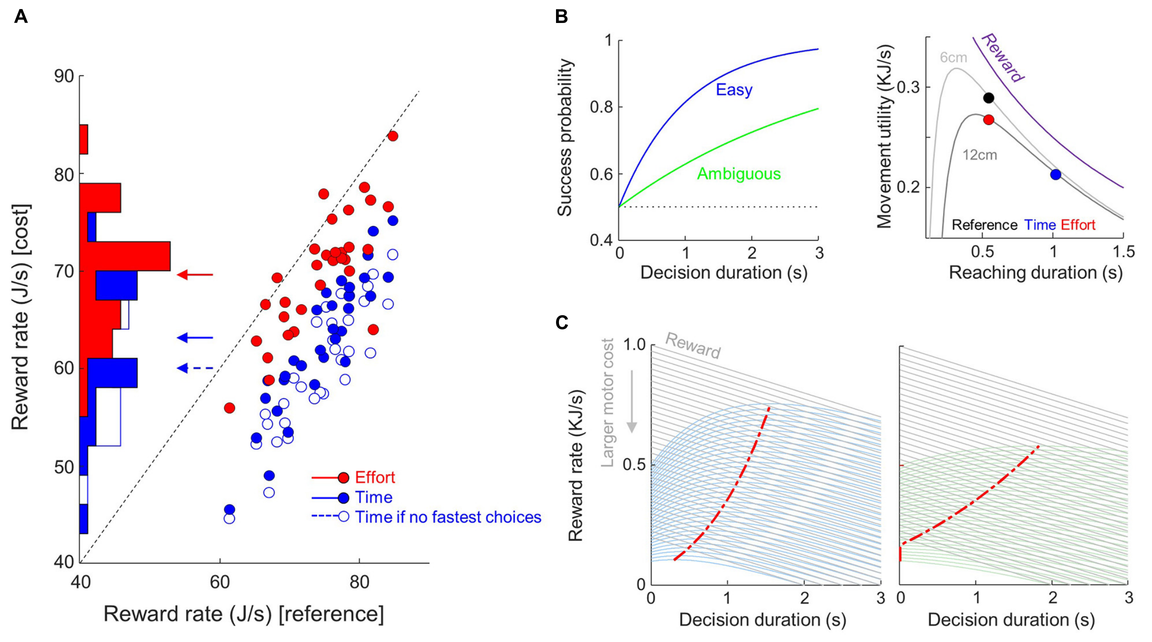

FIGURE 5 | Observed and theoretical effects of motor conditions on reward rate. **(A)** Distributions and comparisons of the average reward rate of each subject (dots) between costly conditions (ordinate, filled blue dots for Time, red for Effort) and the Reference condition (abscissa). Arrows mark the mean values for each condition. Unfilled blue dots show the rate of reward if subjects who shortened their decision durations in the Time condition compared to the Reference condition did not accomplish this shortening. **(B)** Left: Hypothetic success probability (SP) profiles of one easy (blue) and one ambiguous (green) trials. Right: Reward temporal discounting and movement utility according to movement duration (abscissa) and amplitude (see text for details). **(C)** Reward rate computed as the product between the reward value linearly discounted during decision duration (gray lines) and the SP (**B**, left) in easy (left panel) and ambiguous (right) trials for various initial reward values. The initial value of reward is reduced as motor cost increases (downward gray arrow). The red dots mark the maximal value for each reward rate function.

most of the decision adjustments occurred, mostly in terms of decision duration. We describe in the following paragraphs a theoretical demonstration that offers an explanation linking these adjustments and the participant willingness to maximize their rate of reward.

Suppose we consider a family of hypothetical success probability functions:

$$hSP_i\,(t) \;=\; 1 - \frac{1}{2}e^{-c_i t} \tag{5}$$

where c_i is a parameter controlling trial difficulty that can vary from trial to trial. For the present demonstration, we simulate one hypothetic easy trial (**Figure 5B**, left, blue curve) and one hypothetic ambiguous trial (**Figure 5B**, left, green curve). Because these functions increase monotonically with time, waiting until the end of the sensory evidence presentation before committing sounds like the best policy in the choice task. However, spending time to collect sensory information also delays the acquisition of the reward, and time discounts the value of that reward. Assuming that in the choice task the reward is linearly (for simplicity) discounted by time t according to the function (**Figure 5C**, gray lines):

$$R_d\,(t) \;=\; \alpha - \beta.t \tag{6}$$

where α is the value assigned by the brain to a positive outcome given movement utility U_m (see below), and β is the rate of discount, then we can define a theoretical reward rate function during the deliberation process as (**Figure 5C**, blue and green curves):

$$RR_d\,(t) \;=\; hSP_i\,(t)\,.R_d(t) \tag{7}$$

Because of the assumptions made above about $hSP_i(t)$, RR_d has a single peak for each trial i. On any given trial, the probability of success starts at a point (0.5) and grows at some rate (fast in easy trials, more slowly in ambiguous trials). As long as the peak of the RR_d function is not crossed, then one should continue to process information. However, as soon as that peak is crossed, one should commit.

Note that we include the cost of executing a movement in the definition of the rate of reward during the decision process [in $R_d(t)$]. To quantify this cost, we assume that each movement carries a penalty, with respect to its duration and its energetic expenditure, that reduces the initial value (Δ) of the reward at the beginning of the trial. As mentioned in the introduction, movement duration and energetic expenditure are two costs that are intertwined in a trade-off: executing the slowest movements in order to minimize effort sounds like a good strategy, but passage of time t during movement discounts reward value, just like time discounts reward value during deliberation. For this demonstration, the temporal discounting of reward value during movement is expressed as **Figure 5B**, right, purple curve:

$$R_m\,(t) \;=\; \frac{\triangle}{1+\gamma t} \tag{8}$$

where $\gamma = 1$ determines how rapidly reward is discounted (Shadmehr et al., 2016). As a result, the utility of the movement is expressed as the sum of the temporally discounted reward value and the temporally discounted energy consumption (or effort, Eq. 2) during movement production:

$$U_m(t) = R_m(t) + E(t) \tag{9}$$

Thus, if we assume that the context-dependent utility of the movement impacts the rate of reward that subjects expect in a trial, theory predicts that in order to keep reward rate at its maximum when movement cost increases (or movement utility decreases), decision duration should be shortened, especially when the trial is difficult (see the red dots that mark the maximum value of the reward rate functions in **Figure 5C**).

In our experiment, movements executed in the Time condition carried much less utility (assuming the present $\Delta = 500$ and $\gamma = 1$ parameters) compared to movements executed in the Reference and, to a lesser extent, in the Effort conditions (see the color dots in **Figure 5B**, right).

Theory thus suggests that the 14 subjects who shortened their decision duration in the Time condition compared to the Reference condition did so to limit a drop of rate of reward induced by the strong temporal cost associated with executing reaching movements in this condition. If these subjects did not speed up their choices in the Time condition, their rate of reward would have been lower (60 vs. 63 J/s, $|z| = 4.9$, $p < 0.001$, **Figure 5A**, open blue dots).

DISCUSSION

Adapted behavior involves computations during which multiple trade-offs between reward value, accuracy requirement, energy expenditure and elapsing time need to be solved so as to obtain rewards as soon as possible while spending the least possible amount of energy. However, whether, how and why animals integrate movement time and energy costs into a decision-making policy is not fully understood. In this study, we asked 31 healthy human subjects to perform a perceptual decision-making task where the motor context in which a choice is reported was manipulated to dissociate the role of movement time and energy costs on participants' decisions. We found that most subjects were influenced by motor costs during their deliberation process. Both duration and energy expenditure impacted decision-making but increasing reaching duration affected decision and motor initiation more consistently than increasing reaching energy expenditure. While time-consuming movements strongly extended reaction times in a fully instructed task compared to a reference condition, they often led to faster decisions in the choice task. We propose that subjects who shortened their choices in the time-consuming condition did so to limit a drop of reward rate at the session level. Importantly, effects of costs on decision-making and motor preparation often varied between subjects, especially when movement energy was manipulated, suggesting an idiosyncratic nature of the motor cost integration during goal-oriented behavior.

Decision Computations Take Motor Costs Into Account

Decision-making has been traditionally described as a process that is completed prior to the preparation and execution of the action that reports the choice (Pylyshyn, 1984; Padoa-Schioppa, 2011). In ecological scenarios, however, sensory or value-based decisions are very often expressed by actions that are themselves associated with risks and costs (Cisek and Kalaska, 2010). In line with this embodied view of the decision process, the present results indicate that motor costs are part of the decision-making and movement initiation computations.

Among costs, both duration and energy expenditure discount the value of rewards (Shadmehr et al., 2019; Shadmehr and Ahmed, 2020). As a consequence, individuals tend to decide and act in a way that reduces these costs. For instance, when humans make rapid choices between reaching movements, they choose actions that carry the lowest biomechanical cost (Cos et al., 2011). Moreover, when the decision primarily relies on perceptual information, human subjects are biased in their decisions depending on the physical effort or the biomechanical cost associated with the movement executed to report a choice. If one movement carries a large cost, the probability of choosing that option decreases, even if the movement by itself does not influence success probability (Burk et al., 2014; Marcos et al., 2015; Hagura et al., 2017). In these studies, however, each of the two potential targets was assigned with a specific motor cost, and the relative contribution of movement energy expenditure and duration was not addressed.

In the present work, the two targets were always associated with the same motor cost, and time and energy costs were independently varied between blocks of trials. This design allowed us to study the relative contribution of time- and energy-consuming motor contexts on subjects' perceptual decision strategy. Recent studies addressing the relative contribution of motor costs on motor decisions suggest that time-related costs are the most impactful ones. Morel et al. (2017) found for instance that humans avoid time-consuming movements more often than other types of costly movements. Michalski et al. (2020) observed that movement amplitude, direction and accuracy influence the probability of switching from one ongoing movement to another more than energy expenditure. Our results support these studies by showing that varying movement duration impacts perceptual decision-making and movement initiation more often and more consistently than varying movement energy expenditure.

Decision and Action Are Two Modes of One Integrated Process

Why would the motor context in which a decision is made have an influence on the decision itself? During natural behavior, decision and action are tightly linked. It is thus natural to imagine that both functions could share operating principles to maximize behavior utility. Indeed, for anyone making a decision, the most adaptive strategy is to choose options that maximize one's global reward rate (Bogacz et al., 2010; Balci et al., 2011), which occurs when *both* decision and action are sufficiently accurate but not overly effortful and time consuming. In this view, decision and action define a continuum, coordinated by unified or interacting choice and motor regulation signals (Thura and Cisek, 2016, 2017; Cisek and Thura, 2018; Carland et al., 2019; Shadmehr et al., 2019). Recent observations support such coordination between decision and action during goal-directed behavior (Thura et al., 2014; Yoon et al., 2018; Reynaud et al., 2020; Thura, 2020).

In the present delayed reaching task in which both where and when to reach were instructed, the imposed extended movement duration increased reaction times for the vast majority of the subjects. Usually, if the distance to a rewarded target increases, individuals increase their reaching speed to limit the impact of the temporal discounting of reward (Reppert et al., 2018). In the present study, however, subjects could not reduce movement duration. It is thus possible that the larger temporal discounting of reward expected by subjects in this context reduced their implicit motivation to behave (Mazzoni et al., 2007; Shadmehr et al., 2019), leading to longer reaction times. By contrast, almost half of the subjects reduced their decision durations in the Time condition of the choice task compared to a control condition. Because the Time condition strongly reduced subjects' expected reward rate (**Figure 5A**), it is possible that those subjects attempted to compensate the time-consuming movements by reducing their choice duration during the deliberation period. Theoretical simulations (**Figure 5B**) indicate that such strategy limits a drop of reward rate. This observation suggests a flexible mechanism allowing to trade decision speed for movement speed in order to maintain a decent rate of reward despite constraining motor conditions (Reynaud et al., 2020). Interestingly, the analysis of error movement trials (too short or too long with respect to the instructed temporal interval, see section "Materials and Methods") supports such an integrated view of goal-directed behavior. We show in **Supplementary Figure 1** that the too short movements were overall made when decisions were long, and the too long movements were made when decisions were short, suggesting that many subjects were primarily concerned about computing a global trial duration rather than computing decision and action durations separately.

The Question of the Reaching Effort Cost

Compared to the effects of the time-consuming movements discussed above, the impact of the energy-consuming movements on decision and action initiation were less pronounced, especially in the DR task, and more variable at the population level. This result does not fully support the implicit motor motivation hypothesis (Mazzoni et al., 2007), according to which effortful movements discount reward value, thus motivation, delaying movement initiation and reducing movement vigor (Wickler et al., 2000; Summerside et al., 2018; Shadmehr et al., 2019). We even observed the opposite effect for 7 and 10 out of 31 subjects in the delayed reaching and the choice tasks, respectively. For those subjects, it is possible that the instruction to produce more vigorous movements energized their behavior at a global level, leading to faster choices and shorter movement initiations as predicted by the shared regulation hypothesis, according to which one unique context-dependent urgency signal invigorates both decision-making and movement execution (Thura et al., 2014; Cisek and Thura, 2018; Carland et al., 2019; Thura, 2020). By contrast, subjects who spent more time to make their decisions in the effortful condition compared to the control condition possibly aimed at collecting more sensory evidence to avoid choice errors and to ultimately minimize the total number of trials to perform. Alternatively, the more metabolically demanding movements may have, as mentioned above, diminished subjects' motivation to perform the task, leading to longer decisions (Mazzoni et al., 2007).

The lack of consistent effects of reaching effort on decision making and movement initiation at the population level can be explained by several reasons. First, movement effort could not be as directly compensated in the choice task as the time-related cost. Indeed, the deliberation period of the choice task gives a very large window for temporal adjustments, whereas the task does not incorporate a similar effort domain that could have allowed energy costs to be as directly compensated. Moreover, in the present study, subjects faced only two levels of motor effort. It is thus possible that the chosen parameters fell outside of the range that would have been efficient to affect subjects' behavior in a more consistent manner. Finally, the way to manipulate movement energy expenditure often differs between studies. It can be performed through variation of movement trajectories, leading to different biomechanical costs (Cos et al., 2011), through loads or resistances applied on the moving segments (Morel et al., 2017), through isometric manipulations such as handle squeezes (Körding et al., 2004), etc. Here we chose to manipulate movement energy expenditure by imposing various durations for a given amplitude, thus manipulating movement speed. The relation between movement speed and energy expenditure has been well documented, and it offers a convenient theoretical framework to study the impact of motor costs on decision-making (Shadmehr et al., 2016; Shadmehr and Ahmed, 2020). It is still possible that some of the present results would have been different if other types of effort manipulations had been performed.

Influence of Motor Costs Across Subjects and Behavioral Repertoires

Studies of the neural basis of perception and motor control often focus on the shared principles across individuals and thus often neglect inter-individual differences. The present results indicate, however, that motor costs effects on decision and action initiation are highly variable at the population level, especially with respect to energy expenditure. This observation was expected as previous work demonstrated that motor cost is a subjective estimation that does not impact behavior in a consistent way across individuals. For instance, some people consider the effort produced during physical activities as a reward whereas others tend to favor sedentary behavior (Cheval et al., 2018a,b). Regarding elapsing time, Choi et al. (2014) showed in a saccadic task that some individuals exhibit a much greater sensitivity to temporal costs than others. Similarly, Berret et al. (2018) showed that self-selected vigor of pointing movements strongly differs between subjects but tend to be relatively constant within each subject, even when biomechanics-related costs are taken into account. These results suggest that both effort sensitivity and the temporal discounting rate differ between people, possibly explaining why some subjects did not adjust their decision policy as a function of motor costs in the present study while other did. In addition, the temporal discounting rate varies throughout individual's life as well. In humans, the temporal discounting tends to be steepest in adolescence and then declines with age (Green et al., 1999). Despite the present population age range was rather narrow, we cannot exclude that age influenced how some subjects reacted with respect to motor costs in both tasks. Future research may address these variable effects by testing sub-groups of subjects specifically selected based on personality traits.

Finally, it's worth mentioning that subjects expressed their choices via reaching movements. One may also ask whether similar effects would have been observed in other movement types, such as locomotion or saccades. Locomotion-related computations seem to share many of the utility principles described for reaching movements. For instance, the preferred walking speed correlates with a minimization of the metabolic cost during displacement (Zarrugh et al., 1974; Donelan et al., 2001; Summerside et al., 2018). Moreover, consistent inter-individual differences of vigor between reaching and walking tasks are generally found (Labaune et al., 2020). By contrast, the oculomotor system seems to differ from the reaching and the locomotion systems with respect to behavior utility (Reppert et al., 2018; Labaune et al., 2020). More studies are needed to test the questions addressed in the present work in other behavioral repertoires.

To summarize, the present study demonstrates that human subjects are idiosyncratically influenced by motor costs during deliberation and movement initiation. Reaching duration affects decision and motor initiation more consistently than reaching energy expenditure. We propose that subjects who shortened their choices when reaching was time-consuming did so to limit a drop of reward rate.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The present study was reviewed and approved by the INSERM ethics committee (IRB00003888) on March 19th, 2019. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

AUTHOR CONTRIBUTIONS

CSL, AJR, and DT contributed to conception, design of the study, and wrote sections of the manuscript. CSL collected the data. CSL and AJR performed the statistical analysis. CSL and DT wrote the first draft of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnhum.2021.715212/full#supplementary-material

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Dissecting Motor and Cognitive Component Processes of a Finger-Tapping Task With Hybrid Dopamine Positron Emission Tomography and Functional Magnetic Resonance Imaging

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Striatal dopamine is involved in facilitation of motor action as well as various cognitive and emotional functions. Positron emission tomography (PET) is the primary imaging method used to investigate dopamine function in humans. Previous PET studies have shown striatal dopamine release during simple finger tapping in both the putamen and the caudate. It is likely that dopamine release in the putamen is related to motor processes while dopamine release in the caudate could signal sustained cognitive component processes of the task, but the poor temporal resolution of PET has hindered firm conclusions. In this study we simultaneously collected [11C]Raclopride PET and functional Magnetic Resonance Imaging (fMRI) data while participants performed finger tapping, with fMRI being able to isolate activations related to individual tapping events. The results revealed fMRI-PET overlap in the bilateral putamen, which is consistent with a motor component process. Selective PET responses in the caudate, ventral striatum, and right posterior putamen, were also observed but did not overlap with fMRI responses to tapping events, suggesting that these reflect non-motor component processes of finger tapping. Our findings suggest an interplay between motor and non-motor-related dopamine release during simple finger tapping and illustrate the potential of hybrid PET-fMRI in revealing distinct component processes of cognitive functions.

Keywords: finger tapping, PET, fMRI, dopamine, cognitive component, striatum

INTRODUCTION

Simple motor tasks like finger tapping have frequently been used to probe the human motor system both in health (Riecker et al., 2003; Turesky et al., 2018) and disease (Elsinger et al., 2003; Wu et al., 2010; Wurster et al., 2015). The striatum is involved in the facilitation of desirable movements and inhibition of undesirable movements; striatal dopamine (DA) release patterns mediate the execution of desirable movements (Albin et al., 1989; DeLong, 1990; Calabresi et al., 2014).

Additionally, the striatum supports the processing of information related to both higher cognitive functions (Cohen and Frank, 2009) and incentives (e.g., Haber and Knutson, 2010). The striatum receives projections from most of the cerebral cortex as well as DAergic input from the midbrain (Haber and Knutson, 2010), which makes the striatum a convergent area where DA modulates limbic, associative and sensorimotor functions.

Positron emission tomography (PET) is the primary imaging method to investigate DAergic functions in humans. [11C]Raclopride is an antagonist for the DA D2 receptors (Farde et al., 1986), and the binding profile of [11C]Raclopride has been shown sensitive to competition with endogenous DA (Laruelle, 2000). Binding competition occurs when endogenous DA levels are increased in the striatum, reducing the concentration of free D2 receptors available for [11C]Raclopride binding (Dewey et al., 1993). Using [11C]Raclopride and the "binding competition" principle, DA release in the bilateral putamen and the caudate during unrewarded finger tapping has been demontrated (Badgaiyan et al., 2003; Goerendt et al., 2003). Both Badgaiyan et al. (2003) and Goerendt et al. (2003) speculated that DA release in the putamen was reflective of motor demands, consistent with known anatomical projections to the motor cortex, while the caudate responses may have reflected non-motor processes such as learning or attention, which are likely to occur at different timescales than the transient motor specific aspects of the task. Indeed, [11C]Raclopride displacement studies have revealed DA release in the caudate and putamen during executive processes (Monchi et al., 2006; Dahlin et al., 2008; Lappin et al., 2009) and in the ventral striatum (VS) during rewarded conditions (Pappata et al., 2002; Joutsa et al., 2012; Jonasson et al., 2014). Thus, comparisons across studies support the hypothesis that DA release in striatal regions during motor tasks is reflective not only of the motor demands *per se* but also cognitive contributions. By this view, the striatum emerges as an important locus for the interplay between cognition and motor control. With the DA system playing a key role in many psychiatric and neurological disorders (Brisch et al., 2014; Belujon and Grace, 2017; Martini et al., 2018), a precise understanding of spatiotemporally specific DAergic functions in the human striatum is important. Several lines of work indicate a regionally distinctive functional architecture of striatal DA (Haber and Knutson, 2010), but direct evidence for such distinctions in humans has remained elusive. This omission primarily pertains to the inherently limited temporal resolution of *in vivo* PET-techniques (at the timescale of minutes at best), inhibiting the separation between transient motor activity and sustained cognitive component processes.

Recent technological developments have allowed the simultaneous acquisition of PET and fMRI. This opens up the possibility to investigate neurochemical processes such as DA release from PET concomitant with neurovascular responses [i.e., the blood-oxygen-level-dependent (BOLD) response from fMRI] during tasks in humans. Using the BOLD response, it is possible to investigate brain activity non-invasively at a timescale of seconds, which provides an opportunity to disentangle short periods of task states (i.e., finger movements) from sustained task set (e.g., related to attention or motivation; for review see Petersen and Dubis, 2012). In a simple finger tapping task, modeling the fMRI data as periods of movement vs. rest yields a robust BOLD response mostly confined to the putamen (Lehéricy et al., 2006; Witt et al., 2008).

In this study, we simultaneously collected [11C]Raclopride PET and fMRI to investigate DA release and BOLD response in nine human participants while they performed a finger tapping task consisting of long (several minutes) blocks of tapping and blocks of rest. Importantly, the task design permitted us to capture neuronal activation specific to the transient component of finger movements at the timescale of seconds using fMRI, while PET was used to identify striatal regions where DA release was related to the task at both faster and slower temporal scales. That is, the fMRI analysis was tuned to identify the regions that were more likely related to the fast component of motor activity, while the maps identified by using PET provided an overall spatial DAergic activity pattern regardless of task component process. By comparing the statistical spatial maps from both modalities, we hence theorized that signal overlap would reflect striatal DA release in response to the transient motor components of task, while DA release without task-specific BOLD response was hypothesized to reflect non-motor components of the task, e.g., motivation or attention. The aim of this study was to test the hypothesis that striatal DA release during motor function is associated with motor as well as non-motor processes, in a spatially distinct manner. In order to further understand the nature of non-motor contributions, we used the non-overlapping areas as seeds in a resting state functional connectivity analysis to map their functional coupling to cortical systems, thereby constraining the interpretation of their functional contribution.

MATERIALS AND METHODS

Participants

Participants were recruited via ads placed around Umeå University campus, targeting young healthy adults between 20–40 years of age. Exclusion criteria included history of head trauma, current or past diagnosis of neurological or psychiatric illness, drug or alcohol dependence, and use of psychopharmaceuticals or stimulants other than caffeine or nicotine for the past 6 months. Individuals with MR-incompatible metallic implants or objects in their body were excluded. Pregnant or breast-feeding women, as well as individuals having previously undergone PET scanning for research purposes were excluded due to radiation safety reasons. All included participants were right-handed. One participant was excluded due to excessive head motion during the scan. The resulting sample size consisted of 9 healthy young adults (mean age = 24.9, *SD* = 4.2, range 20–34; mean height = 172.7, *SD* = 12.9, range 151–196; mean weight = 71.78, *SD* = 13.1, range 55–98; 5 females). This study was approved by the Regional Ethics Committee at Umeå University (2015/239-31).

Procedure

Upon arrival, participants were informed about the study and signed an informed consent form. An intravenous needle used for infusion was placed in the left arm. Participants were then placed

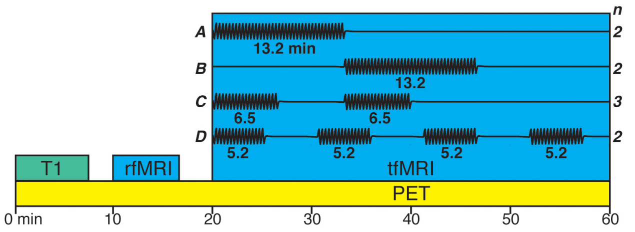

FIGURE 1 | Variations of the finger tapping task paradigm. Black line in **(A–D)** represents blocks of tapping. Two participants had a single block (13.2 min; **A**) with the onset 20 min from PET acquisition start. Two participants had a single block (13.2 min; **B**) with the onset 33.33 min from PET acquisition start. Three participants had two blocks (6.5 min; **C**) with the onset 20 and 33.33 min from PET acquisition start. Two participants had four blocks (5.2 min; **D**) with the onset 20, 30.66, 41.33, and 52 min from PET acquisition start.

into the scanner bore where a mirror mounted on the scanner coil directed their gaze toward a screen located behind the scanner. Task instructions were prompted on the screen during the experiment. A T1-weighted structural image was collected, followed by a resting state T2*-weighted sequence. Participants were injected with [11C]Raclopride at the start of the PET scan. Twenty minutes later the task T2*-weighted sequence started.

Experimental Design

The task consisted of sequential finger tapping with the right hand (index, middle, ring, little finger). Participants were told to self-pace their tapping and were visually cued to tap for 10 s and then rest for 10 s until they were cued to start tapping again. The embedding of this on-off design within the task periods was chosen to fit the temporal resolution of BOLD response so that the BOLD signal would increase during the tapping event while allowing it to decrease during the rest inter trial intervals. The tapping task was partitioned into blocks with differing number of blocks, duration, and onset times between participants which can be seen in **Figure 1**. Note that, since the individual displacement maps were averaged across subjects for the main analysis, the individual differences in design were not of interest to the current study. Nevertheless, since it is unknown how short task blocks may be in [11C]Raclopride displacement study, we present the analyses of individual maps in **Supplementary Material**. These analyses showed that all task block lengths between 5 and 13 min were able to elicit displacement.

PET/MRI Acquisition, Processing, and Analysis

Imaging was performed on a 3T General Electric Signa PET-MR system with a 15-channel head coil. Behavioral data (button presses) were recorded with an MR-compatible 4-button response pad from Cambridge Research Systems. The data was collected between November 2015 and March 2016.

T1-Weighted

Structural T1-weighted images were acquired for 7.36 min with the following acquisition parameters: [FOV: 25 × 20 cm^2, matrix: 256 × 256, Slice Thickness: 1 mm, Slices: 180, TE: 3.1 ms, TR: 7,200 ms, Flip Angle: 12, Bandwidth: 244.1 Hz/Pixel]. T1 images were used for segmenting the brain into anatomical compartments using Freesurfer (Fischl, 2012) and normalization to standard MNI space using a preliminary 12 degrees of freedom registration with FMRIB's Linear Image Registration Tool (FLIRT) followed by a non-linear registration using FMRIB's Non-linear Image Registration Tool (FNIRT), resulting in 2 mm isotropic voxels.

Positron Emission Tomography

The participants were injected with a bolus plus constant infusion of [11C]Raclopride (Kbol = 105 min, Watabe et al., 2000) commencing at start of PET scan. Following the local standard protocol for [11C]Raclopride studies (e.g., Jonasson et al., 2014; Nevalainen et al., 2015), 250 MBq was delivered to the participant during the experiment. A 60 min (20 × 60 s, 30 × 80 s) dynamic time-of-flight acquisition and an MR-based attenuation correction was collected. The data was reconstructed to a voxel size of $1.56 \times 1.56 \times 2.78$ mm^3, employing a resolution recovery OSEM algorithm (3 iterations, 28 subsets, 3.0 mm post filter), with decay, randoms, scatter, and attenuation corrections applied. The data were then motion corrected using FSL's mcflirt with mutual information as cost function to the 25th frame using framewise rigid body alignment, processed using a HYPR filter (Christian et al., 2010), and temporally smoothed using a three-frame Gaussian kernel ([0.25 0.50 0.25]).

Linear parametric neurotransmitter PET (lp-ntPET) was used to estimate voxelwise dynamic binding potentials (Normandin et al., 2012; Sander et al., 2013; Johansson et al., 2019). First, multilinear reference tissue modeling with fixed *k2'* was conducted. An additional time-dependent term was then fitted to the data for each task block to account for [11C]Raclopride displacement. The time-dependent term was defined as the best least-squares solution of a library of gamma functions (Madsen, 1992) with varying α controlling growth and decay rate. This approach takes into account inter-individual as well as inter-regional differences in [11C]Raclopride displacement, adaptive with the unknown shape and onset of dopamine release related to finger tapping. The best solution for each voxel results in individual t-statistics maps of [11C]Raclopride displacement during the tapping task.

Individual task timings were considered only in the first-level model. The individual t statistics maps were then taken to a second level analysis using FSL's randomize function (512 permutations; uncorrected p-value) which estimated the group mean [11C]Raclopride displacement using a one-sample t-test, independent of each person's individual on- and offsets (which were not of interest to the current analysis). Thus, the final group map provided a statistical map of coherent spatial locations of DA release during task as compared to rest.

Functional Magnetic Resonance Imaging

All BOLD fMRI data were collected with the same sequence parameters (FOV: 25.6, Matrix: 96 × 96, Slice Thickness: 3.6 mm, TE: 30 ms, TR: 4,000 ms, Flip Angle: 80°, Acceleration Factor: 2.0). Acquisition of BOLD resting state data started after the T1-weighted image and data was collected for 6.67 min. Acquisition of BOLD task data commenced 20 min after the PET acquisition started and was collected for 40 min (**Figure 1**).

The task data was pre-processed following conventional steps for fMRI as implemented in FSL FEAT[1]. Briefly, this included motion correction by volume-wise rigid body transformation to the first volume, slice timing correction, spatial smoothing (FWHM 5 mm), high pass (50 s) temporal filtering. Single subject task data was analyzed using a general linear model (GLM) with a single on-off regressor of interest describing finger tapping events. The beta estimates from the single subject analysis were taken into a second level group analysis using FSL's randomize function (512 permutations; uncorrected *p*-value) estimating the group mean using a one-sample *t*-test.

The resting state data was motion corrected by volume-wise rigid body transformation to the first volume, slice timing corrected, and 24 motion parameters as well as framewise displacement outliers were regressed out from the data. Minimally preprocessed images were then non-linearly registered to MNI-space using FNIRT. White matter, cerebrospinal fluid, and global signal was regressed out and the data was spatially smoothed (FWHM 5 mm) and band pass filtered (high pass 0.01 Hz, low pass 0.1 Hz). Striatal seeds identified from the lp-ntPET analysis were used in a whole brain functional connectivity analysis to provide indications of their connected cortical targets and thereby constrain the interpretation of their functional contribution. For this, each time-series from the striatal seeds were individually correlated (Pearson's correlation) with each voxel's time-series for the whole brain. Individual correlation maps were then Fisher's r-to-z transformed and entered to a second level group analysis. The resulting group t-statistic maps were given a threshold of $t > 2.9$ corresponding to an uncorrected *p*-value (one-tailed; df = 8) of 0.01 to investigate each seed's strongest functional coupling. The group t-statistics maps were projected to a cortical surface for visualization purposes.

Modality Overlap

A first pass qualitative assessment of overlap/non-overlap between modalities was performed at an (arbitrary) t-threshold of 2.9 ($p = 0.01$) for the fMRI group map and a p-threshold of 0.05 for the group PET map. To ensure robustness of assessment a voxel overlap percentage count was conducted for stepwise [$t(\text{step}) = 0.1$] increasing t-thresholds [$t(\min) = 1$, $t(\max) = 3.5$]. This analysis was made to confirm that overlap/non-overlap definitions were threshold-independent. Overlapping and non-overlapping clusters were then assigned to their appropriate anatomical compartment (putamen, caudate, VS). Once overlap/non-overlap and anatomical compartment ROIs were established, the lp-ntPET analysis was performed again on the time activity curves extracted from the ROIs to confirm [11C]Raclopride displacement for each ROI and individual (**Supplementary Material**).

TABLE 1 | Group-level significant [11C]Raclopride displacement clusters.

	Location	Number of voxels	Mean t-stat	Peak t-stat	Overlap
Putamen	Left middle-anterior	78	2.63	6.19	YES
	Right anterior	28	2.37	3.26	YES
	Right middle	24	2.90	5.38	YES
	Right posterior	63	3.07	6.07	NO
Caudate	Left anterior	19	2.36	2.87	NO
	Right anterior	106	2.70	7.80	NO
	Right posterior	24	2.63	3.49	NO
VS	Left	27	2.36	3.34	NO
	Right	16	2.55	3.84	NO

RESULTS

Widespread Dopamine Release in Response to Finger Tapping

Mean finger tapping frequency during the task blocks was 1.95 ± 0.11 Hz. The voxelwise lp-ntPET analysis showed [11C]Raclopride displacement in several areas of the striatum. Four clusters were observed in the bilateral putamen, three clusters in the bilateral caudate, and two clusters in the bilateral VS (**Table 1**). Because of close spatial proximity of these smaller clusters within anatomically defined regions such as the caudate, the clusters within each anatomically defined region were combined for further analysis (**Table 1**).

Putamen BOLD Response and Modality Overlap/Non-Overlap

The voxelwise fMRI GLM contrast [tapping > rest] showed a bilateral response in the putamen (left: $p = 0.002$, cluster size 990 voxels, peak t-stat = 8.06; right: $p = 0.002$, cluster size 953 voxels, peak t-stat = 5.25). The response was more wide-spread and stronger in the left putamen than in the right putamen (**Figure 2**), consistent with predominant contralateral activation during movement.

Overlap between [11C]Raclopride displacement and task fMRI response was observed in distinct parts of the putamen (**Figure 2**). The clusters overlapped well at all thresholds, with 84% of voxels overlapping at an fMRI threshold of $p = 0.01$. Conversely, the non-overlapping clusters showed poor overlap even at lower threshold, indicating that overlap/non-overlap definitions were relatively threshold-independent. Four general patterns were established: bilateral putamen overlap, ipsilateral putamen non-overlap, caudate non-overlap, and VS non-overlap (**Figure 2**). An exploratory analysis of the BOLD timecourse in the non-overlapping clusters showed that non-overlap was not driven by a shifted or negative BOLD signal in relation to the task regressor (**Supplementary Figure 1**, top).

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[1] https://fsl.fmrib.ox.ac.uk/

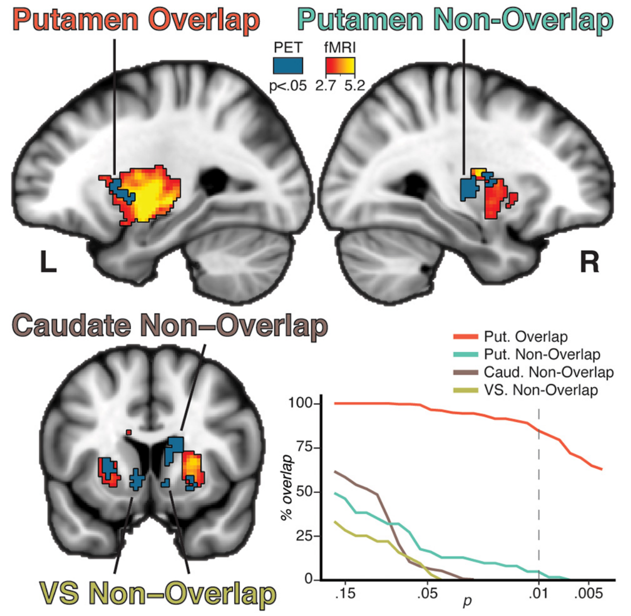

FIGURE 2 | Results from the group lp-ntPET analysis (blue solid color) and the group analysis of the fMRI GLM (red to yellow gradient). Four unique patterns of clusters were observed based on modality overlap and anatomical belonging: putamen overlap, putamen non-overlap, caudate non-overlap, and VS non-overlap. Percentage overlap of the PET clusters was calculated for different fMRI thresholds (bottom right plot). Increasing the threshold reduced the percentage intersection of the non-overlapping clusters, while the overlapping clusters remain at a high level of intersection even at more conservative thresholds. Dotted line represents the threshold used in the brain figures.

A supplementary ROI based lp-ntPET analysis of the four clusters of interest confirmed [11C]Raclopride displacement for each ROI (**Supplementary Figure 1**, bottom). Moreover, this ROI-based lp-ntPET showed that differences in task block timing between individuals did not affect the ability to detect [11C]Raclopride displacement, supporting our approach that individual maps can be collapsed across subjects (**Supplementary Material**).

Functional Coupling of Dopamine Release Clusters

The voxelwise seed-based functional connectivity analysis showed that putamen overlap was functionally coupled to the bilateral motor cortices, supplementary motor area (SMA), anterior cingulate cortex (ACC), and insula. Putamen non-overlap showed similar functional coupling as the putamen overlap. Caudate non-overlap showed functional coupling to the ACC. VS non-overlap showed functional coupling to the medial prefrontal cortex and ACC (**Supplementary Figure 2**). Overlapping functional coupling between the putamen non-overlap, caudate non-overlap, and VS non-overlap seeds was observed in the ACC (**Figure 3**).

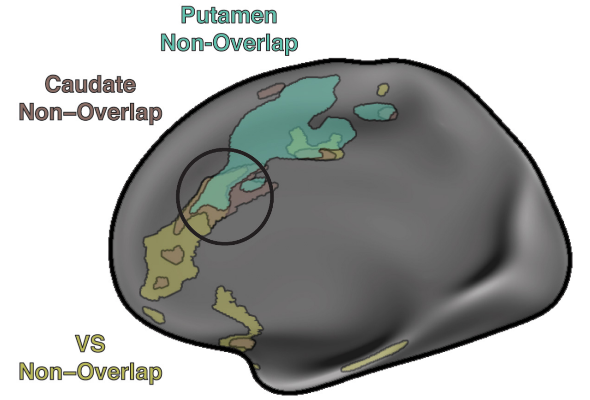

FIGURE 3 | Cortical resting state functional coupling of the non-overlapping clusters. The putamen non-overlap cluster shows functional connectivity to the supplementary motor area and anterior cingulate cortex, the caudate non-overlap cluster shows functional connectivity to the anterior cingulate cortex, the VS non-overlap cluster show functional connectivity to the ventromedial prefrontal cortex and anterior cingulate cortex. A trilateral intersection of functional coupling is observed in the anterior cingulate cortex (black circle) possibly indicating a locus of integration among attentional (caudate), motivational (VS), and motor (putamen) component processes.

DISCUSSION

Striatal DA release is known to facilitate movements (Albin et al., 1989; DeLong, 1990; Calabresi et al., 2014). Previous studies have shown that unrewarded finger tapping elicits widespread striatal DA release (Badgaiyan et al., 2003; Goerendt et al., 2003) providing support for models that assert an important role for DA during motor function. In this study we utilized a novel multimodal PET and fMRI approach to provide support for the hypothesis that striatal DA release during finger tapping can be dissociated into both motor and non-motor component processes, which previously has not been possible with PET alone. Specifically, we exploited the temporal fidelity of fMRI to identify the spatial loci related to the direct motor component, while the PET measure of DA release was temporally insensitive thereby revealing the overall pattern of striatal DA during the task. The complementary information provided by both modalities permitted us to make conclusions about the overlapping and non-overlapping regions of responses. Overlap of responses was interpreted as DA signaling specifically related to motor function, while non-overlap was interpreted as DA related to the task as a whole which includes component processes related to attentional demands. Below, we discuss these findings in relation to existing knowledge on striatal functional organization.

Dopamine Release and BOLD Response Overlap in the Bilateral Putamen During Finger Tapping

In line with previous comparisons across studies (Badgaiyan et al., 2003; Goerendt et al., 2003; Witt et al., 2008) and known anatomy, we observed overlapping loci of DA release and fMRI responses to finger tapping only in the putamen. As expected, this outcome concords with the putamen as the primary motor region of the striatum (Albin et al., 1989; DeLong, 1990; Calabresi et al., 2014), and provides direct evidence that fMRI responses in humans are spatially congruent with dopaminergic activity. Moreover, the location of overlapping BOLD response and DA release was functionally coupled in fMRI with the SMA and bilateral motor cortex (as well as ACC), providing further support that signals from both modalities reflect the modulation of activity in cortico-thalamic loops that regulate motor functions (Alexander et al., 1986). Because fMRI is cheaper, faster and less invasive than functional PET, this finding, albeit expected, highlights the potential for fMRI as a biomarker of dopaminergic function in the motor pathway, for example in studies of Parkinson's disease (Bloem et al., 2019). The spatial convergence between sites of DA release and fMRI task activity encourages a larger study in which individual differences are probed to establish whether larger fMRI responses are proportional to greater DA release during a simple tapping task, which additionally would establish task fMRI as a biomarker of neurochemical dysfunction.

An intriguing and unexpected finding with respect to the motor compartment was that of DA release in the ipsilateral (right) posterior putamen, which was incongruent with the BOLD pattern. The lack of BOLD response in this area suggests a divergence of DA function compared to where the PET and fMRI modalities overlap, possibly relating to differences in DA release patterns (Liu et al., 2021) or differences of co-release of inhibitory, excitatory, or other modulatory neurotransmitters (Hnasko and Edwards, 2012; Tritsch et al., 2016). The posterior putamen was functionally coupled to similar areas as the overlapping putamen clusters (SMA, bilateral motor cortex, and ACC), suggesting a role in modulation of cortico-thalamic regulating motor functions. However, the exact nature of such modulation remains unclear. The putamen non-overlap cluster was uniquely identified by combining PET and fMRI imaging, which speaks to the value of multimodal imaging for researching novel biomarkers.

Dopamine Release in the Caudate and Ventral Striatum Related to Finger Tapping

Striatal DA release in the caudate during finger tapping has been assumed to reflect learning, response selection, predictability of events, and progression tracking (Badgaiyan et al., 2003; Goerendt et al., 2003). Such interpretations have been made based on the locus of DA release, but it has not been possible to definitively dissociate this response from DA release concurrently observed in the putamen. The current task did not involve any apparent learning component nor complicated motor sequence executions, but it did involve predictable events. The BOLD response to event prediction could be expected to precede the event, causing a moderate fit to the defined regressor or even negatively correlating with the regressor. However, in an additional analysis, the observed BOLD response in caudate neither positively nor negatively correlated with the regressor (**Supplementary Figure 1**), which speaks against event prediction or other event-tied component process. An alternative possibility may then be a role in some form of sustained external or internal monitoring, which is common across different finger tapping tasks. The caudate is known to be related to executive functions such as generation and monitoring of appropriate strategies needed to achieve certain goals (Grahn et al., 2008). In support of this interpretation, the caudate DA release cluster was functionally coupled with the ACC (**Figure 3**). Among many functional roles assigned to the ACC, it is part of the brain's attention network (Posner and Petersen, 1990; Weissman et al., 2005; Yeo et al., 2011), and has been associated with error monitoring (Kiehl et al., 2000; Swick and Turken, 2002). Thus, DA release in the caudate might be related to attentional demands associated with tracking the progression of a tapping sequence, consistent with the interpretation by Goerendt et al. (2003).

More generally, the present finding of dissociable PET-MRI pattern in putamen and caudate encourage the design of functional imaging experiments that are able to isolate component processes (e.g., by a mixed design that allows to model both sustained set and events). Such designs may then be able to identify and monitor regionally specific courses of DA degeneration in disease. To give a concrete example, in an fMRI-experiment the caudate response to task set may serve as a within-patient reference to infer the severity of Parkinson's disease-pathology in the motor-putamen.

DA release was also observed in the bilateral VS, which to our knowledge has not been reported in the literature during unrewarded finger tapping which may reflect the fact that our PET model was less constrained than in previous work. The VS is an area integrally linked with incentive processing (e.g., Ikemoto and Panksepp, 1999; Knutson and Greer, 2008; Haber and Knutson, 2010; Sescousse et al., 2013; Salgado and Kaplitt, 2015; Wang et al., 2016; Grill et al., 2020), and VS DA release has been observed during rewarded conditions (Pappata et al., 2002; Joutsa et al., 2012; Jonasson et al., 2014). Recent findings have pointed to unidirectional open feedforward loops between the VS and sensorimotor areas of the striatum through the DAergic midbrain, through which the VS can influence selection and invigorate action based on emotional and motivational states (Aoki et al., 2019). The VS was most strongly functionally coupled to the vmPFC and ACC (**Figure 3**), replicating previous functional connectivity findings (Di Martino et al., 2008). The functional connectivity analysis of the striatal DA release clusters thus reveals trilateral functional coupling in the ACC (**Figure 3**), supporting the ACC being viewed as an integrative area for component processes related to motivation, attention, and motor control (Paus et al., 2001).

In conclusion, we could separate motor from non-motor component processes of finger tapping based on the complementary information from PET and fMRI, but the current experimental design did not support strong conclusions as to what the non-motor components represent. Thus, what is interpreted as non-motor components may reflect sustained executive components of the task or they may be essential parts of finger tapping, for example involving aspects of rhythm or timing of the current task structure.

Methodological Advances

An exciting avenue of research has opened up with hybrid PET/MR systems allowing the investigation of concomitant neurochemical and vascular changes in response to various stimuli. Advances in functional PET analysis (lp-ntPET; Normandin et al., 2012; Sander et al., 2013; Johansson et al., 2019) have made it possible to more accurately model onset and durations of experimental manipulations, thereby allowing for more flexible and "fMRI like" PET paradigms. In our main results we use lp-ntPET to voxelwise identify spatial regions indicating [11C]Raclopride displacement. The lp-ntPET method is also able to dynamically estimate binding potentials during the task which can be translated into DA D2 occupancy in the case of [11C]Raclopride (**Supplementary Figure 1**). Future studies with a larger sample could potentially characterize regional and inter-individual differences in occupancy functions associated with traits and/or behavioral manipulations related to motor, executive, and/or incentive processing. In this study, we pushed the temporal limits of lp-ntPET utilizing various onsets, durations, and number of experimental manipulation blocks. For our main results, it was possible to collapse spatial maps across participants and task paradigms since we were investigating voxels that exhibited DA release. Further methodological considerations are needed when interpreting occupancy functions of more than a single task block.

Limitations

There are several limitations to consider in this study. The study has low power compared to contemporary neuro imaging studies, and larger-scale studies are called for. With this caveat we note that previous PET studies investigating striatal DA release in relation to finger tapping have shown a robust effect at the single subject level (Badgaiyan et al., 2003) as well as stable group effects for small samples (Goerendt et al., 2003), and robust single-subject BOLD responses have been observed in fMRI studies (Moritz et al., 2000).

The logic of interpreting spatial overlap/non-overlap between [11C]Raclopride displacement clusters and concomitant BOLD response also has its limitations. For overlapping modalities to be related to each other it assumes a neurovascular coupling between DA and the BOLD response. Neurovascular coupling of DA receptors has been observed (Choi et al., 2006; Knutson and Gibbs, 2007; Sander et al., 2013) but the exact nature of the coupling and how it impacts the BOLD response is still unclear. Also, if modality overlap represents signals related to each other, a closer peak-to-peak overlap could be expected. Even if both modalities are collected at the same time, spatial resolution and field of view between modalities differ, possibly causing discrepancies when normalizing to a common template. The stepwise percentage overlap evaluation did nevertheless support the overlap/non-overlap definitions.

Finally, DA release in [11C]Raclopride displacement clusters not accompanied by a BOLD response may still impact the BOLD signal but at a time scale not detectable by the *a priori* defined fMRI GLM regressor. Unfortunately, the current task design did not lend itself to be analyzed for neither more sustained BOLD response (due to the exceedingly long task blocks) nor faster BOLD response (due to TR limitations). Similarly, the current task design did not lend itself for finer control of the relation between finger tapping speed and dopamine release since we let participants determine their own speed. Controlling tapping frequency across individuals may be an improvement over the current design. Alternatively, using similar methods as described here, a better powered study could potentially investigate individual differences of self-paced tapping frequency and striatal DA response. To substantiate our interpretations of component processes related to DA release clusters, we utilized seed-based resting state functional connectivity. This method has previously been used to identify brain networks associated with a seed (Di Martino et al., 2008). Here, we use it as a proxy for function which should not be taken as a definitive component process description, but rather as an indication of functional role.

CONCLUSION

In this study we explore DA release patterns during an unrewarded finger tapping task using a novel hybrid PET-fMRI imaging approach. DA release in bilateral putamen spatially overlapped with concomitant BOLD response. This finding highlights the potential for fMRI as a biomarker of dopaminergic function in the motor pathway, for example in studies of Parkinson's disease. We also observed DA release that did not overlap with the striatal BOLD response in caudate and VS, indicating component processes of finger tapping that are reliant on DA but unrelated to motor action. The non-overlapping areas showed distinct functional connectivity profiles that intersected in the ACC, supporting the view of ACC as an integrative area for component processes related to motivation, attention, and motor control.

DATA AVAILABILITY STATEMENT

Neuroimaging data on the group level can be viewed and downloaded from https://neurovault.org/collections/11584/.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Regional Ethics Committee at Umeå University. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

FG conducted the final analysis and wrote the first draft. JJ conducted analysis and edited the manuscript. JA developed the

PET protocol and edited the manuscript. PB developed the MR protocol and edited the manuscript. LN conceived the study and edited the manuscript. AR conceived the study, conducted analysis, and edited the manuscript. All authors contributed to the article and approved the submitted version.

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Adaptive Feedback Control in Human Reaching Adaptation to Force Fields

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Sensorimotor adaptation is a central function of the nervous system, as it allows humans and other animals to flexibly anticipate their interaction with the environment. In the context of human reaching adaptation to force fields, studies have traditionally separated feedforward (FF) and feedback (FB) processes involved in the improvement of behavior. Here, we review computational models of FF adaptation to force fields and discuss them in light of recent evidence highlighting a clear involvement of feedback control. Instead of a model in which FF and FB mechanisms adapt in parallel, we discuss how online adaptation in the feedback control system can explain both trial-by-trial adaptation and improvements in online motor corrections. Importantly, this computational model combines sensorimotor control and short-term adaptation in a single framework, offering novel perspectives for our understanding of human reaching adaptation and control.

Keywords: feedback control, motor adaptation, reaching control, sensorimotor integration, computational models

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INTRODUCTION

Sensorimotor adaptation can be characterized by an update of motor commands following changes in body or environment dynamics. This critical function of the nervous system allows humans and other animals to improve the efficiency of their movements with practice. Traditionally, studies on upper limb reaching movements in laboratory settings have described trial-by-trial improvement performance in terms of two interacting processes: *feedforward* and *feedback* control. Feedforward control can be defined as the formation of motor commands independent of sensory feedback, and it is typically associated with predictive aspects and planning. Feedback control refers to real-time adjustments of motor commands based on sensory inflow. These two controllers can be modified between movements (i.e., offline) or within a movement (online). Characterizing how adaptation impacts feedforward and feedback control has recently been a lively research topic.

In the context of force field learning, it is assumed that the difference between actual and expected sensory information, also called sensory prediction error, is used internally to re-calibrate an internal model of limb and environment dynamics (Shadmehr et al., 2010; Wolpert et al., 2011). Here, we adopt a generic definition of an internal model, as a neural mechanism that can simulate the consequences of an action, and drive estimation and control based on this knowledge (McNamee and Wolpert, 2019). Accordingly, adaptation has often been understood as an iterative update of the feedforward controller following sensory prediction errors from the previous movement. Recently, mounting evidence has highlighted that adaptation was not confined to the feedforward process, as it also occurs in the feedback control system. Yet a theory linking feedforward and feedback adaptation has been lacking.

Here, we present computational models of reaching adaptation and review current evidence that adaptation also impacts feedback control. We highlight that the feedback control system can adapt without necessarily implying changes in behavioral proxies of feedforward control such as initial movement directions. Moreover, evidence suggests that adaptation in feedback pathways can occur within a time interval shorter than the time of a reaching movement, which is difficult to reconcile with a sequential adaptation of feedforward and feedback controllers across trials. These observations suggest that models of sensorimotor adaptation require revision to include adaptation in feedback pathways explicitly. We describe a candidate model to accommodate these behavioral findings.

COMPUTATIONAL MODELS OF HUMAN REACHING ADAPTATION

Models of human reaching adaptation have typically dissociated trial-by-trial changes in movement performances from continuous variables that the nervous system handles within a movement, thereby separating control and adaptation mechanisms. A standard definition of a trial is a single point-to-point movement, but it is clear that this artificial construct has impacted models of adaptation and that translating the concepts developed below to continuous tasks, such as cyclic movements or tracking, is an important question for prospective work. Although it is accepted that adaptation is a continuous process (Krakauer et al., 2019), the main computational models characterize discrete-time adaptation with a time step is equal to a trial. The categories presented below also correspond to model properties, which are not exclusive, thus some previously published models fall into several categories.

A first category corresponds to *time-series* models, which aim at capturing the evolution of learning curves across trials. A prominent example is the two-states model proposed by Smith and colleagues (Smith et al., 2006), who demonstrated that there exist fast and slow processes that learn and forget at different rates. Kording et al. (2007), added that multiple timescales could underlie the dynamics of memory. The addition of multiple timescales was also associated with a parallel architecture in the context of visuomotor adaptation (Lee and Schweighofer, 2009). Although these models differ by their structure, they make the same assumption that any error [or filtered error (Wei and Körding, 2010)] perceived on a given trial influences the next trial. Indeed, in Smith et al. (2006), the time unit was the trial. In Kording et al. (2007), it was hypothesized explicitly that the fastest timescale in the adaptation model was slower than the movement time, thereby only allowing trial-by-trial adjustments. These models also describe the evolution of an abstract state variable (or *motor gain*), without considering continuous variables related to movement execution, hence it is it difficult to link adaptation and control in this framework.

A second category of adaptation models can be referred to as *partial compensation*. Contrary to time-series models, these models express a control problem in continuous time with partial knowledge of environment dynamics. For instance, Shadmehr and Mussa-Ivaldi (1994) used a model based on trajectory tracking with an adaptive internal model. Mistry and colleagues (Mistry et al., 2013) made similar assumptions in the context of Linear-Quadratic-Gaussian (LQG) control (Todorov and Jordan, 2002), with an estimated plant dynamics that differed from the true plant dynamics including the force field. Recently, Ikegami and colleagues (Ikegami et al., 2021) used the same approach to demonstrate that both target failure and altered hand path may interact to drive adaptation hierarchically. In these models, the level of adaptation depended on how much the force field was compensated during movement by the approximate internal model, which simply takes the form of a function used in the controller. While they explicitly formulated a control problem in continuous time, these models did not include any learning rule that transforms sensory mediated errors into a novel model estimate for the next movement.

A relationship between discrete-time adaptation and continuous control can be found in the following classes of models. The first includes *motor primitives* as building blocks linking continuous control during a movement and updates between movements. Motor primitives are defined as basis functions available in the brain tuned to position and velocity (Thoroughman and Shadmehr, 2000; Hwang et al., 2003), which are combined to minimize the error between actual and ideal or expected forces. In this framework, the internal model takes the form of a weighting matrix used to combine the primitives. The power of this theory has been to capture human generalization patterns. The main question toward linking adaptation and control with motor primitives is whether this model can reproduce behaviorally the same properties as state-feedback controllers, which characterize human motor responses to perturbations (Crevecoeur and Kurtzer, 2018).

In favor of this idea, Sing and colleagues (Sing et al., 2013) argued that limb motion determined adaptation independent of the disturbance profile, suggesting that the variables underlying adaptation are limb position and velocity. However, this hypothesis is at odds with the fact that similar patterns of motion evoke different feedback responses dependent on the limb configuration and context, suggesting that an internal model of limb dynamics and externally applied loads are used in the brain for online control (Kurtzer et al., 2008, 2009; Crevecoeur and Scott, 2013; Maeda et al., 2017). Moreover, assuming that the weighting matrix of motor primitives can be used with time varying signals, it could be taken for a linear feedback controller. But in this case, this model does not include time-varying control gains known to characterize goal-directed reaching control in human (Liu and Todorov, 2007; Dimitriou et al., 2013; Poscente et al., 2021). Hence, the possibility that adaptation rests on the combination of motor primitives tuned to position and velocity may not capture all properties of human state-feedback control. The question arises as to whether it is still biologically plausible to assume the existence of a library of primitives including a broader set of variables as well as time-varying mixing matrices.

The other class of discrete time models: *adaptive impedance-control*, proposes muscle co-activation as a link between feedforward adaptation and online movement execution. According to this view, it is proposed that trial-by-trial adjustments were complemented by within-trial rejection of disturbances, inherent during early phases of adaptation, mediated by the limb intrinsic properties (Shadmehr and Mussa-Ivaldi, 1994; Franklin et al., 2003, 2008). In Shadmehr and Mussa-Ivaldi (1994), it was hypothesized that disturbances are countered by instantaneous opposition to deviation in position and velocity. Franklin and colleagues (Franklin et al., 2008) further demonstrated that trial-by-trial adjustments could be captured by changes in co-activation following unexpected muscles stretches ("V-shape" learning rule), while limb stability during movement was preserved in the model by the muscles viscoelastic properties. This model featured a simple learning rule, but the main shortcoming was that common estimates of limb stiffness are strongly impacted by feedback components. Indeed, measurements of stiffness are calculated up to ∼100 ms after an abrupt limb displacement (Burdet et al., 2000, 2001), thereby including proprioceptive, visuomotor, and early voluntary responses (Scott, 2016). Consequently, the relationship between online control and movement adaptation remains elusive.

To summarize, current computational models have in common the assumption that control during a movement is performed with a fixed internal model, and that adjustments are performed between two trials based on an error signal coming from the previous trial. In this view, it is easy to consider motor adaptation as an update in a feedforward pass across two trials. However, as we review in the next section, the expression of adaptation in feedback control makes feedforward and feedback adaptation mechanisms increasingly difficult to dissociate.

ADAPTATION IN HUMAN FEEDBACK CONTROL SYSTEM

Assuming separate forward and feedback passes with the adaptation of the feedforward pathway only can now be rejected in light of compelling evidence that adaptation of reaching movements also evokes changes in feedback control. A seminal study by Bhushan and Shadmehr proposed to include internal models in feedforward and feedback pathways (Bhushan and Shadmehr, 1999). Wagner and Smith (2008) demonstrated that resisting or assisting forces applied after adaptation to a lateral velocity-dependent force field evoked feedback responses with a lateral force component, indicative that the online correction took into account the acquired knowledge of the force-field. Subsequent studies showed that exposure to a force field evoked a modulation of visuomotor (Franklin et al., 2012), and long-latency pathways, that is as early as ∼60 ms following an abrupt load applied to the limb (Ahmadi-Pajouh et al., 2012; Cluff and Scott, 2013; Maeda et al., 2018). Long-latency responses have played a key role in understanding the neural basis of feedback control since they include a transcortical pathway through primary sensorimotor areas, premotor cortex, parietal areas, and cerebellum (Flament et al., 1984; Pruszynski et al., 2011; Omrani et al., 2016). Hence, it could be deduced from a modulation in long-latency responses that the underlying neural structures have access to the acquired knowledge of the force field.

It was further shown that changes in long-latency feedback gains paralleled the learning curve and correlated with the extent of adaptation (Cluff and Scott, 2013). More recently, a modulation in long-latency feedback gains has been linked to the fast time-scale of movement adaptation in a dual-rate model (Coltman and Gribble, 2020). A comparable change in long-latency response gain has been associated with transient and unpredictable disturbances, evoking co-contraction and modulation of overall control gains (Crevecoeur et al., 2019). It remains unclear when changes in long-latency responses start expressing knowledge of the new force field rather than reflecting a robust control strategy. But clearly, over the course of a few trials, the imprint of movement errors in the brain produces adjustments in the neural bases of both feedforward and feedback controllers.

These previous studies still implicitly assumed that feedforward adaptation occurred and the feedback control system inherited or shared the novel reach representation to produce adapted feedback responses. However, there is also evidence that adaptation occurs in the feedback control system without adapting the feedforward mechanism. Indeed, Maeda and colleagues (Maeda et al., 2020) trained volunteers to counter perturbation while blocking shoulder motion physically. They observed that participants reduced their shoulder response, which in turn affected reaching movements performed when the shoulder was suddenly unlocked. Thus, internal representations of dynamics (in this case, the limb dynamics) could be acquired by exposing the feedback control system only. It is therefore necessary to at least consider adaptation in both feedforward and feedback pathways with reciprocal interactions (**Figure 1A**). An additional property must still be added to the picture: the possibility that adaptation occurs online, within a movement, as suggested in our recent series of reports.

Indeed, we documented evidence for adaptation in feedback responses to unpredictable application of a force field during reaching. By looking at the whole movement execution, we showed that participants learned to correct for the unexpected disturbance without anticipation, and that the tuning of the force profiles applied by participants to the handle, displayed the same properties as adapted movements measured in a standard adaptation paradigm (Crevecoeur et al., 2020b). The possibility that movement representation was different at the beginning (no anticipation) and end (adapted feedback) of a single reaching movement means that the controller changed online. The improvement in feedback corrections was observed for force fields of different directions and different kinds, and was expressed while relearning to move in a previously experienced force field (Crevecoeur et al., 2020a; Mathew et al., 2021). These responses also evoked rapid and stable re-planning when they were performed in a rapid sequence of movements (Mathew et al., 2020).

Measuring the timescale of this process was crucial. When we trained participants to perform a rapid movement including a

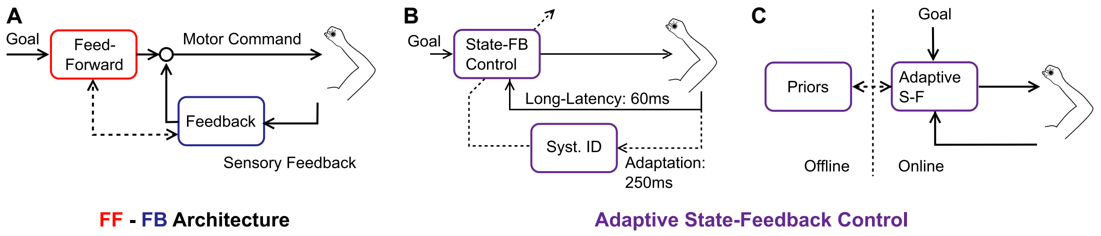

FIGURE 1 | (A) Feedforward-feedback control architecture, each pass corresponds to different neural structures that share knowledge of the environmental dynamics. Feedforward and Feedback are associated with red and blue colors, respectively. **(B)** Adaptive state-feedback control model in which an identification of the system parameters (Syst. ID) updates a state-feedback controller online (State-FB Control). The timescales are represented: it is assumed that state-feedback control is supported by long-latency feedback loops (timescale: ∼60 ms), and the online updates are associated with a slower timescale (∼250 ms). **(C)** Conceptual representation of the adaptive state-feedback controller which can replace feedforward and feedback mechanisms, while different time scales are associated with online and offline mechanisms.

stop-over at a via point, we observed that the second movement, from the via-point to the goal, was quickly updated according to a force field perturbation experienced before the via-point. This update was visible in hand kinematics as early as ∼0.5 s following reach onset (Crevecoeur et al., 2020b; Mathew et al., 2020). In a different experiment, we observed that adaptive changes in muscles recordings that correlated with force modulation occurred after ∼250 ms following reach onset (Crevecoeur et al., 2020a). Thus, the timescale of adaptation may lie between 250 ms (from EMG) and 500 ms (from hand kinematics).

Including such a fast timescale of adaptation in a computational model of reaching control is a two-sided story: on the one hand, there is no difference with previous models since it also considers that sensory prediction errors update internal representations. On the other hand, the fact that adaptation happens faster than a trial blurs the distinction between feedforward and feedback mechanisms.

ADAPTIVE STATE-FEEDBACK CONTROL MODEL

The candidate model to explain the forgoing observations was based on adaptive state-feedback control (Bitmead et al., 1990). It must be noted that the computational advantage of an adaptive neural controller was first discussed by Fortney and Tweed (2011). The basic premise is that the state-feedback controller is parameterized based on knowledge of the limb and environment dynamics, coupled with an identification procedure that can change the parameters of the controller online (**Figure 1B**). The model can be viewed as two nested loops: the state-feedback controller describes how the nervous system responds to changes in state variables for a fixed parameterization, and the adaptive loop consists in online tuning of the model parameters. When mapped onto human neural mechanisms, we submit that the state-feedback control loop is mediated by long-latency circuits (∼60 ms) (Crevecoeur and Kurtzer, 2018), while adaptation is associated with a longer timescale (>250 ms, **Figure 1B**).

This model is very close to the standard view of human reaching adaptation while offering novel perspectives. In theory, the learning rate must not be too high, but there is no lower bound on the timescale at which the controller can be re-parameterized. Thus it accommodates adaptation in real time and within a reaching movement. Second, the learning rule corresponds to a standard gradient descent: at each time step the parameter estimate makes a step in the direction that reduces the difference between expected and actual sensory input. It is of course a strong assumption to state that the nervous system performs a kind of gradient descent, however, this assumption is inherited from even the simplest learning models that make a step proportional and away from an error signal. It is the same learning rule as in previous models based on motor primitives, but it is applied to different variables. In the framework of motor primitives, the difference between sensed and expected forces (or trajectory) is used to change the mapping between primitives and force output, whereas in the framework of adaptive control, the difference between actual and expected sensory input is used to update a parametric representation of the system dynamics.

Importantly, the variables used to update the model are not abstract variables, such as learning states, instead they are the same state-variables as those assumed by the controller, i.e., neural encoding of joint angles, velocities, torques, muscles state, and potentially higher order derivatives. Thus, if we assume that these variables are used for control, we do not add complexity by assuming that they are also used for adaptation.

The adaptive feedback control model bridges together discrete-time models, and control models with partial compensation, simply by assuming that the time unit of adaptation is smaller than reaching time. This consideration suggests that the function of motor adaptation is not only to support changes in internal models over medium to long-term horizons but also to complement state-feedback control online. Hence, instead of considering separate feedforward and feedback processes (**Figure 1A**), we suggest that it is more accurate to consider online and offline mechanisms (**Figure 1C**). The online mechanism is an adaptive state-feedback controller. There is a daily life example of this mechanism: the adjustment of grip force that follows from lifting an unexpectedly heavy or light object. In this case, the object mass is a model parameter that is used to select control, and errors about this parameter produce not only feedback corrections but also changes in the parameter estimate. We propose that the same mechanism applies to online adaptation to velocity-dependent force fields. Other processes linked to consolidation and memory may work offline and follow longer timescales. Their expression takes the form of an internal prior, reflecting the expected dynamics during movement planning.

CONCLUSION AND PERSPECTIVE

The adaptive feedback control model opens many questions and challenges. From a computational perspective, it is clear that non-linear dynamics and delays limit the range of feasible online adaptation rates. This theoretical limit is currently unknown and it may impact the generalizability of the model. Moreover, by adapting parameters online the adaptive feedback controller becomes a non-linear control model. A theoretical bound on the adaptation rate would also limit the range of non-linear effects that this model can handle. We believe that it offers the opportunity to understand which classes of movements can be handled with adaptive linear approximations and which movement properties require a forward pass to cope with non-linear effects.

Another clear challenge is to link adaptive feedback control with other learning mechanisms. We focused on adaptation to force fields, but evidence for online adaptation has been also reported with random visuomotor perturbations (Braun et al., 2009). Besides, there are different ways the nervous system expresses improvements in behavior including use-dependent learning, reinforcement learning, and explicit strategies (Krakauer et al., 2019). The relationship between adaptive state-feedback control and these different learning schemes remains to be established.

Finally, we believe that rapid feedback adaptation could become a behavioral proxy of fast neural learning mechanisms recently hypothesized (Sohn et al., 2021). On the one hand, changes in connectivity in a network model of sensorimotor adaptation may capture plasticity mechanisms and long-term adaptation, on the other hand rapid or online adaptation must rely on changes in neural trajectories for a fixed network configuration (Sohn et al., 2021). It is expected that the imprint of online adaptation is visible as changes in dimension or shape of neural trajectories associated with reaching control.

AUTHOR CONTRIBUTIONS

Both authors listed have made a substantial, direct, and intellectual contribution to the work, and approved it for publication.

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Mechanisms of Human Motor Learning Do Not Function Independently

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Human motor learning is governed by a suite of interacting mechanisms each one of which modifies behavior in distinct ways and rely on different neural circuits. In recent years, much attention has been given to one type of motor learning, called motor adaptation. Here, the field has generally focused on the interactions of three mechanisms: sensory prediction error SPE-driven, explicit (strategy-based), and reinforcement learning. Studies of these mechanisms have largely treated them as modular, aiming to model how the outputs of each are combined in the production of overt behavior. However, when examined closely the results of some studies also suggest the existence of additional interactions between the sub-components of each learning mechanism. In this perspective, we propose that these sub-component interactions represent a critical means through which different motor learning mechanisms are combined to produce movement; understanding such interactions is critical to advancing our knowledge of how humans learn new behaviors. We review current literature studying interactions between SPE-driven, explicit, and reinforcement mechanisms of motor learning. We then present evidence of sub-component interactions between SPE-driven and reinforcement learning as well as between SPE-driven and explicit learning from studies of people with cerebellar degeneration. Finally, we discuss the implications of interactions between learning mechanism sub-components for future research in human motor learning.

Keywords: cerebellar degeneration, adaptation, reinforcement learning, explicit and implicit motor learning, sensory prediction error

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INTRODUCTION

The field of motor neuroscience has greatly advanced our understanding of how humans learn to produce and control new movements. There are many contexts in which motor learning occurs, such as when learning to perform movements *de novo* or learning the appropriate sequence of movements necessary to execute a skilled action. Here, we focus on studies of a third motor learning context, often termed motor adaptation, in which one must learn to modify an existing movement pattern to account for persistent changes to the body, task, or environmental dynamics (Krakauer et al., 2019). All types of motor learning likely rely on multiple interacting mechanisms that, in turn, rely on different neural circuits. However, the mechanisms underlying motor adaptation have received particular attention in recent years, with most literature studying the interactions between three mechanisms: learning driven by sensory prediction errors (SPEs, or the difference between the sensory outcome of a movement and a prediction of that outcome), explicit (or strategy-based) learning, and reinforcement (or reward-based) learning.

Studies of interactions between these mechanisms have largely treated them as modular, focusing on how each mechanism's outputs are combined to produce overt learning behavior. To isolate one or more learning mechanisms, studies have modified the attentional cues and/or sensory feedback provided during behavioral learning tasks. Intriguingly, these manipulations have produced evidence of additional interactions between the sub-components of the different learning mechanisms. Here, we propose that understanding these sub-component interactions is needed to advance our knowledge of how learning mechanisms combine to produce overt behavior. We first summarize the current literature studying interactions between SPE-driven, explicit, and reinforcement mechanisms of motor learning. We then present evidence of sub-component interactions between SPE-driven and reinforcement learning, as well as between SPE-driven and explicit learning, from studies of people with cerebellar degeneration. We conclude with a discussion of considerations for future research.

Motor Adaptation Results From the Interaction of Multiple Mechanisms

While several mechanisms have been proposed to contribute to motor learning, three have largely been assumed to account for the vast majority of observed behavioral changes in simple motor adaptation tasks (Krakauer et al., 2019). These three mechanisms are SPE-driven learning, explicit learning, and reinforcement learning (**Figure 1**). Each of these mechanisms is thought to respond to a different kind of feedback signal, and consequently, drive changes in behavior in different (and occasionally opposing) ways and at different rates (Mazzoni and Krakauer, 2006; van der Kooij et al., 2018; Albert et al., 2020; Morehead and Orban de Xivry, 2021). In general, the study of these mechanisms has treated them as modular, typically assuming that observed behavior can be described as the summation of the outputs of the individual mechanisms. Thus, when the contribution of a single mechanism cannot be easily isolated experimentally, it is often estimated by subtracting out the influence of a second, more easily measured mechanism (Taylor et al., 2014; McDougle et al., 2015; Maresch et al., 2021).

One commonly used task to study motor adaptation has participants generate a movement such as a reach or a saccade toward a target. Participants are then presented with a predictable perturbation that alters the outcome of that movement, which necessitates learning to alter the movement pattern to account for the imposed perturbation. For example, in a task requiring the adaptation of reaching movements to a visuomotor rotation, individuals observe a cursor move at a fixed non-zero angle relative to their actual hand motion, which is hidden from view. Over many trials, participants learn to adjust their motor plans to reach in a direction opposite the perturbation to reduce the error. Trial-to-trial learning in this adaptation task has been shown to be supported by all three mechanisms.

SPE-driven learning was the first mechanism recognized to contribute to behavioral changes in adaptation tasks. SPEs convey the difference between the sensory outcome of a movement and a prediction of that outcome based on a copy of the outgoing motor command (Kawato, 1999; Tseng et al., 2007; Shadmehr et al., 2010; Morehead et al., 2017). The SPE signal is thought to be computed by the cerebellum (Medina, 2011; Schlerf et al., 2012); hence people with cerebellar damage are known to exhibit poor performance in adaptation tasks (Criscimagna-Hemminger et al., 2010; Izawa et al., 2012; Therrien et al., 2016; Wong et al., 2019). SPEs do not necessarily reflect task failure, but rather the fact that a movement did not result in the predicted sensory outcome according to the planned motor command. Thus, if an inappropriate motor command was executed accurately (e.g., reaching toward the target when the task is to reach in the opposite direction from the target), it would result in a task error but not an SPE. More recently, such task errors (specifically, the observed difference between the movement outcome and the intended movement target or goal) have also been suggested to drive learning under this mechanism (Miyamoto et al., 2014; Leow et al., 2018; Albert et al., 2020). Regardless, SPE-driven learning requires sensory information about the direction and magnitude (i.e., vector information) of movement errors. In motor adaptation tasks, vector error information is typically provided by contrasting the desired target location with a visual representation of the index fingertip position during reaching movements (e.g., a cursor on a screen). The signature of SPE-driven learning (and the most reliable measure of its impact on behavior) is the existence of after-effects—behavioral changes reflecting a new mapping of motor commands to predicted sensory outcomes that persist even after the perturbation has been removed. SPE-driven learning is described as occurring without conscious awareness, possibly due to a concomitant recalibration of perception (Ostry and Gribble, 2016; Rossi et al., 2021), and can be expressed even at low reaction times (approximately 130 ms, Haith et al., 2015; Leow et al., 2017; Hadjiosif and Krakauer, 2021); hence, it is often referred to as implicit learning. By most accounts, SPE-driven learning is thought to be the primary driving force behind motor adaptation (Izawa and Shadmehr, 2011; Therrien et al., 2016; Cashaback et al., 2017; Wong et al., 2019).

In addition to SPE-driven learning, prior work has emphasized a large contribution of an explicit learning mechanism. In the context of adaptation tasks, explicit learning is often described as the acquisition of an aiming strategy or learning to deliberately move somewhere other than the target location. For example, if a cursor is rotated 45° clockwise relative to the hand, people can accurately move their hand to a target if they adopt a strategy of aiming their reach 45° counterclockwise from the target. Broadly speaking, explicit learning arises as a result of a task error (i.e., awareness that the task objective was not achieved), although exactly how task errors are quantified and how they lead to changes in behavior are not well understood. Nevertheless, studies probing the relationship between SPE-driven and explicit learning often assume that these mechanisms have an additive impact on behavior (Mazzoni and Krakauer, 2006; Benson et al., 2011; McDougle et al., 2015; Long et al., 2016; Miyamoto et al., 2020). Researchers often subtract explicit aiming reports from net learning to measure SPE-driven learning (e.g., Taylor et al., 2014). Alternatively, researchers might measure the SPE-driven learning process using a process dissociation procedure and

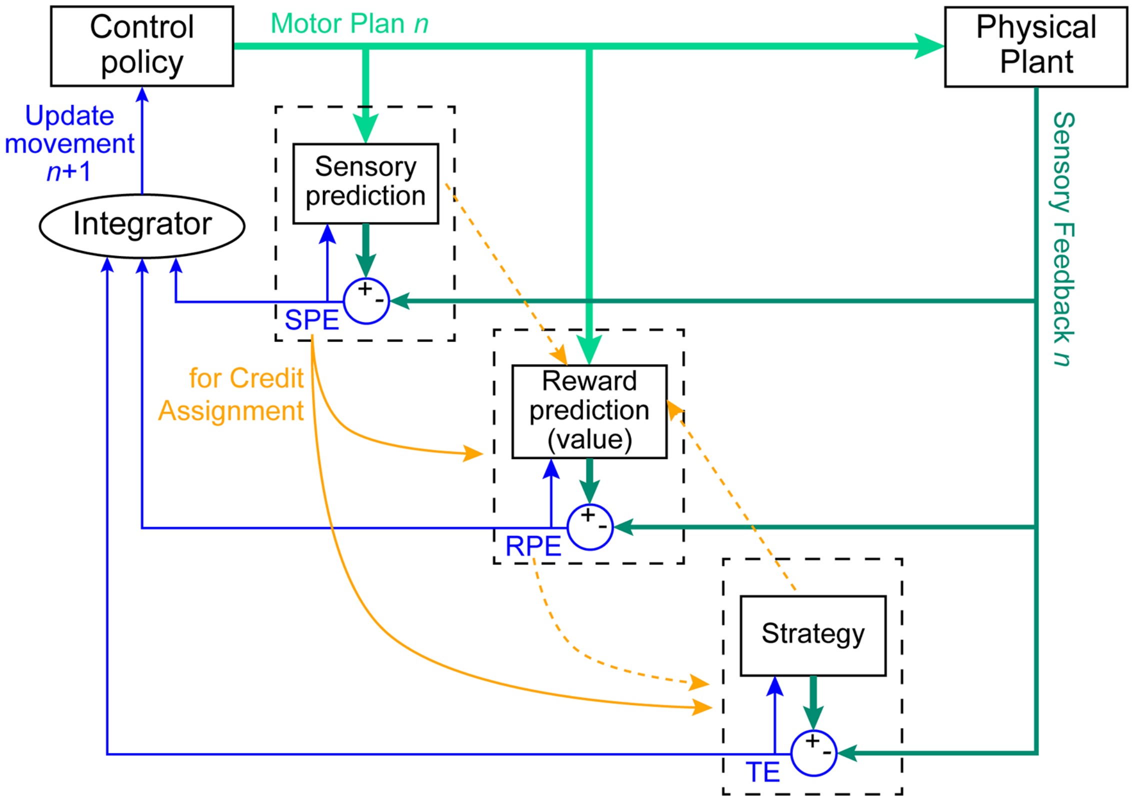

FIGURE 1 | Control policy updates arising from the interactions of three learning mechanisms. On trial *n*, a control policy is issued to perform the current movement (light green thick arrows). This plan is executed by the body (physical plant), and sensory feedback is detected (dark green arrows). The SPE-driven learning system predicts the expected sensory consequences of the movement, which is compared against sensory feedback of the actual executed movement to compute a sensory prediction error (SPE). The reinforcement learning system predicts the expected reward associated with that movement and this is compared against the actual reward outcome to compute a reward prediction error (RPE). The explicit learning system compares the expected outcome of the strategy against the observed movement outcome to compute a task error (TE). In all cases, the computed error signals (thin blue arrows) update both the respective prediction mechanism as well as the control policy for the next (*n* + 1) movement. Most studies treat this control-policy update as the combination of the contributions of the individual learning systems (here labeled as the Integrator). We suggest that these systems also interact in other ways. For example, SPE signals are a means by which the reinforcement-learning and explicit-learning systems could solve the credit-assignment problem in determining whether the policy or the execution of that policy led to the observed result (solid orange arrows). Additional speculated interactions may exist (dashed orange arrows), although more behavioral evidence is needed to support the existence of such connections in humans.

subtract it from net learning to estimate the contribution of an explicit process (Werner et al., 2015). Many studies have used these methods to examine adaptation across the age span and have suggested that impaired performance in older individuals is largely due to a reduced contribution of the explicit learning mechanism, while the SPE-driven learning system remains intact (McNay and Willingham, 1998; Bock, 2005; Heuer and Hegele, 2008; Hegele and Heuer, 2013; Vandevoorde and Orban de Xivry, 2019).

Finally, there is reinforcement learning. Despite being one of the earliest learning mechanisms to have been studied in the context of behavior modification (Thorndike, 1905), studies have only recently begun to carefully examine its contribution to adaptation tasks. Reinforcement learning occurs in response to scalar feedback about performance outcomes. In the extreme case, scalar feedback may be a binary signal (e.g., an auditory tone indicating success or failure), but reinforcement learning can also occur in response to a success gradient (e.g., hot/cold). Studies of motor adaptation have attempted to leverage reinforcement learning by providing binary or gradient feedback in place of a visual cursor representing the position of the hand during reaching movements. In this way, an individual does not have access to the direction or magnitude of movement errors; rather, the individual must explore possible task solutions to discern those that yield success. Reinforcement learning induces a change in behavior by increasing the likelihood of generating movements associated with rewarding outcomes. It is thought to depend on reward-prediction errors (RPEs), computed in midbrain dopaminergic circuits, which convey the difference between predicted and actual rewards (Schultz, 2006; Lee et al., 2012). Although learning in response to rewards could occur as part of a deliberate decision-making strategy, here we classify such situations as examples of explicit learning since they are primarily driven by task errors (where the "task" in this case is to choose the most rewarding option). Instead, we view reinforcement learning as an implicit process, in line with the notion that behavioral conditioning can occur without needing to explicitly learn the relationship between stimulus, response, and outcome (Skinner, 1937). Indeed, in motor learning tasks, exploration of the response space (characteristic of a reinforcement learning process) can be driven by unconscious motor variability (Wu et al., 2014), and reinforcement learning has been shown to couple with other implicit processes such as use-dependent learning (Mawase et al., 2017). However, more work is needed to carefully dissociate the explicit and implicit effects of learning in response to reinforcement.

Reinforcement learning can occur either as a stand-alone process that is independent of the other learning mechanisms, or by interacting with either the SPE-driven or explicit process. In the former case, reinforcement learning drives motor learning without recalibrating perception (Izawa and Shadmehr, 2011). It may operate by inducing both exploration of the reward landscape as well as the repetition of more successful movements (Nikooyan and Ahmed, 2015; Cashaback et al., 2017; Uehara et al., 2019). Thus, reinforcement learning may complement other learning mechanisms by contributing in an additive manner to the net observed behavior (Kim et al., 2019), although if only scalar feedback is provided this could alternatively reduce the amount of learning arising from another mechanism like SPE-driven learning (Izawa and Shadmehr, 2011; van der Kooij et al., 2018). On the other hand, reinforcement learning may have a more intimate interaction with SPE-driven or explicit learning. It could do so by increasing the likelihood of selecting more successful behaviors that have been identified through these other learning mechanisms (Shmuelof et al., 2012; Nikooyan and Ahmed, 2015). For example, reinforcement learning may help individuals to identify and preferentially select more successful explicit strategies (Bond and Taylor, 2015; Codol et al., 2018; Holland et al., 2018; Rmus et al., 2021) because the explicitly-identified action also becomes associated with greater reward. Regardless of its exact mechanism of action, reinforcement learning is typically treated as acting in conjunction with other learning mechanisms to modify behavior (Haith and Krakauer, 2013).

Evidence of Interactions Between Sub-components of Learning Mechanisms

Although the interactions between SPE-driven, explicit, and reinforcement learning mechanisms have largely been modeled as a summation or integration of each mechanism's outputs, imperfect additivity has been noted (e.g., Maresch et al., 2021). Deviations from model predictions have sometimes been attributed to additional learning processes not measured or, alternatively, to the inability of measurement methods to fully capture a given mechanism's output. However, some work suggests the additional possibility that sub-components of each mechanism may also interact. That is, the computations underlying one learning mechanism may serve a critical role in the functioning of another. Understanding the nature of sub-component interactions is crucial, as their presence significantly complicates attempts to experimentally parse the contribution of different learning mechanisms in behavioral tasks. To date, the clearest evidence of sub-component interactions comes from studies of people with cerebellar degeneration. With the cerebellum's role in SPE-driven learning well established, one hypothesis has been that cerebellar damage selectively disrupts this learning mechanism. Yet studies attempting to distinguish SPE-driven, explicit, and reinforcement learning in people with cerebellar degeneration have not shown the hypothesized dissociation (McDougle et al., 2016; Therrien et al., 2016; Wong et al., 2019).

Therrien et al. (2016) attempted to distinguish supervised and reinforcement learning in people with cerebellar degeneration by modifying error feedback in an adaptation task. In one condition, SPE-driven learning was leveraged by providing full vector feedback of movement errors in the form of a visual cursor representing the index fingertip position throughout reaching movements. In a second condition, reinforcement learning was leveraged by providing only binary feedback of reach success or failure. People with cerebellar degeneration showed distinct behaviors in the two learning conditions: no retention of learning (i.e., no after-effect) when provided with vector error feedback, but significant retention when provided with binary feedback. If examined only at the output level of each mechanism, these results are consistent with cerebellar degeneration impairing supervised learning and leaving reinforcement learning intact. However, people with cerebellar degeneration learned more slowly with binary feedback compared to age-matched control participants, suggesting that cerebellar degeneration may reduce the efficiency of reinforcement learning. Importantly, this latter result pointed to a previously unknown interaction between cerebellar computations and reinforcement learning.

How could cerebellar computations contribute to reinforcement learning? Cerebellar SPEs may be used to solve reinforcement learning's credit-assignment problem (Taylor and Ivry, 2014; McDougle et al., 2016; Therrien et al., 2016, 2018). In reinforcement learning, the valence of RPE signals is used to update the future probability of selecting a particular motor response to a given stimulus (Dayan and Niv, 2008; Haith and Krakauer, 2013). However, motor response execution is rife with uncertainty due to a combination of noise inherent in the sensorimotor system and variable properties of the environment (Franklin and Wolpert, 2011). Sensorimotor uncertainty makes determining the true cause of reward signals (i.e., credit-assignment) ambiguous. Cerebellar SPEs convey whether a movement was executed as intended, and thus constitute a particularly useful solution to the credit-assignment problem (**Figures 2A,B**).

Reinforcement learning behavior is known to account for higher-order statistical properties of sensorimotor uncertainty, such as the distribution standard deviation (Trommershäuser et al., 2008; Wu et al., 2009, 2014; Landy et al., 2012). However, behavioral variability reflects variance in both motor planning (i.e., response selection) and motor execution (van Beers et al., 2004; van Beers, 2009). Therrien et al. (2016, 2018) modeled reinforcement learning with behavioral variability parsed into exploration, representing planning variability, and motor noise, representing execution variability. Their conjecture was that, after positive reinforcement, response selection is updated in a manner that accounts for exploration, but not motor

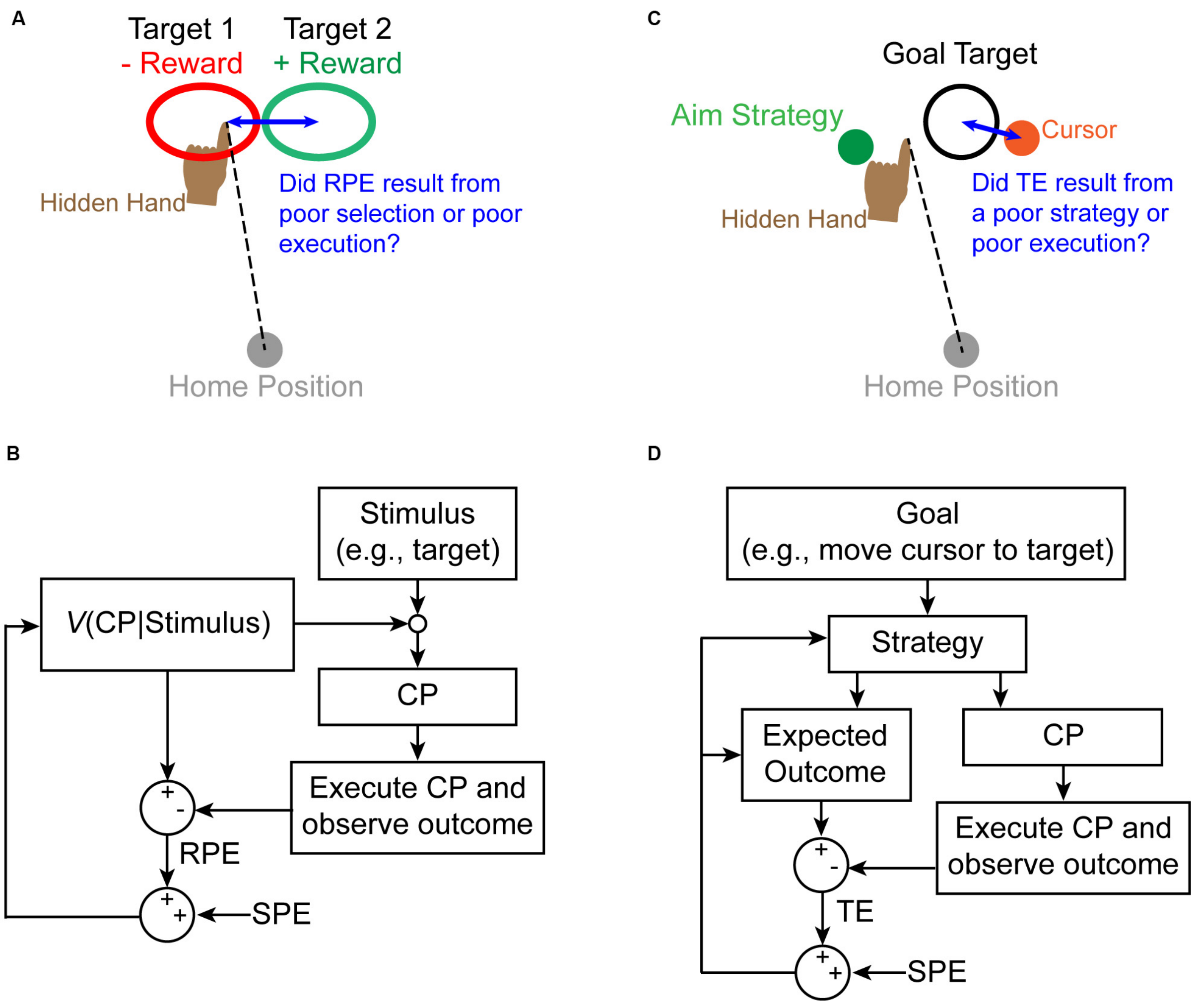

FIGURE 2 | Proposed interactions between the SPE signal and other learning mechanisms to solve the credit-assignment problem. **(A)** On a given trial, individuals receive positive or negative reward feedback about reach outcome. If this feedback is unexpectedly negative (i.e., a negative RPE signal), for example, individuals must determine whether they erroneously selected the wrong control policy or simply executed the correct policy poorly. **(B)** An example state diagram corresponding to the situation in panel **(A)** describes how an update signal is generated based on an RPE (indicating an error has occurred). An SPE is used to determine if the RPE should be attributed to a poor policy choice or a poor execution of that policy. **(C)** During explicit learning, an individual adopts a strategy (e.g., aim location) to attain a goal (hit the target with the cursor). If a task error arises, individuals must determine if they erroneously selected the wrong explicit strategy or if they poorly executed the correct strategy. **(D)** Although it remains unclear exactly how explicit learning occurs, we propose that updates to the strategy choice occur as a result of a task error (TE), which is modulated by an SPE informing about the accuracy of executing the chosen strategy.

noise. In their studies, people with cerebellar degeneration displayed reinforcement learning behavior consistent with excessive variability being allotted to motor noise—a pattern indicative of impaired estimation of action execution. People with cerebellar degeneration also showed reduced exploration after negative reinforcement (Therrien et al., 2018), suggesting that cerebellar degeneration impacts the integration of both positive and negative reinforcement signals. The cumulative result is a reduced updating of action selection in response to reinforcement signaling that slows learning in this population.

McDougle et al. (2016) examined the role of SPE-like sensorimotor error signals in solving a credit-assignment problem in reinforcement-based decision making. Participants were required to select between two visual targets, each associated with a different magnitude of reward, by reaching to hit one or the other. On some trials they were given false feedback about the accuracy of their reach, which generated RPEs—the actual reward received differed from the expected outcome. In contrast to neurologically healthy participants, people with cerebellar degeneration were unable to determine if RPEs should be attributed to themselves or the experimental manipulation (i.e., solve the credit-assignment problem) in this task, suggesting that reach-related sensorimotor error signals play an important role in reinforcement learning.

Reinforcement learning is not the only situation in which a credit-assignment problem must be resolved. Although it is less clear exactly how explicit learning operates, sensorimotor uncertainty likely contributes to a credit-assignment problem similar to that identified above. For example, one must determine if an error arose because of a poor choice of strategy, or because of poor execution of the chosen strategy. Here again, the involvement of an SPE signal would be beneficial to formulate and modify explicit strategies by informing how well the intended strategy was executed (**Figures 2C,D**).

Evidence supporting the involvement of an SPE-like signal in explicit learning arises from a series of studies investigating the ability of people with cerebellar degeneration to develop *de novo* strategies for learning. As noted above, cerebellar degeneration disrupts the signal supporting SPE-driven learning, which impairs performance during a visuomotor rotation paradigm. Previous work had demonstrated that in such tasks, people with cerebellar degeneration could follow a provided strategy to aim in a direction other than the target (i.e., opposite the visuomotor rotation), allowing them to overcome the perturbation and successfully hit the target (Taylor et al., 2010). Such an observation led to a puzzling question—if their ability to employ strategies was so successful, why did not people with cerebellar degeneration use strategies all the time to compensate for their movement deficits instead of continuing to rely on an impaired SPE-driven learning system? Butcher et al. (2017) showed that, on their own, people with cerebellar degeneration had great difficulty invoking explicit learning to identify a successful aiming strategy that would minimize task errors. That is, some people with cerebellar degeneration continued to aim directly for the target despite the presence of the visuomotor rotation perturbation. However, Wong et al. (2019) revealed that this was only part of the answer. Under certain circumstances, people with cerebellar degeneration could successfully develop *de novo* strategies using explicit learning. Wong and colleagues demonstrated that when people with cerebellar degeneration were able to view their actual hand moving simultaneously with the cursor, they could resolve the credit assignment problem by recognizing that task errors were not a result of a mis-executed motor command but instead caused by a manipulation of the cursor. That is, people with cerebellar degeneration could use visual feedback to appropriately attribute performance errors to task errors rather than execution errors. Consequently, people with cerebellar degeneration were able to invoke explicit learning to modify their movement goals (i.e., change their aiming direction) akin to that of age-matched neurotypical controls. This work thus suggests a role for SPE signals in supporting explicit learning. While more work is needed to parse the specific role that such SPE signals may play, together these studies provide compelling evidence of interactions between cerebellar computations and both explicit and reinforcement learning mechanisms.

CONCLUSION

We have reviewed current literature on the interactions between SPE-driven, explicit, and reinforcement learning mechanisms in motor adaptation. It is generally agreed that overt learning behavior results from the combined outputs of each mechanism, but interactions between these mechanisms likely occur at multiple levels. For example, studies of people with cerebellar degeneration provide evidence of a role for SPE signals in the functioning of both reinforcement and explicit learning. These studies suggest that an SPE signal may be needed by reinforcement and explicit learning systems to know whether RPEs or task errors, respectively, arose from poorly executed movements or poor selection of an action or strategy. By helping to resolve this credit-assignment problem, SPEs can optimize learning by informing reinforcement and explicit learning systems whether an action or strategy truly needs to change.

It is notable that some of the neuroanatomy needed to support these proposed interactions has been shown. With regard to a role for cerebellar SPE signals in reinforcement learning, the cerebellum communicates directly with the dorsal striatum *via* a short-latency disynaptic connection that modulates corticostriatal plasticity (Hoshi et al., 2005; Chen et al., 2014). The posterior lobules of the cerebellum are also reciprocally connected with prefrontal cognitive regions of the cerebral cortex, which are hypothesized to support the explicit learning process (Ramnani, 2006; Strick et al., 2009). The nature of the information sent through these pathways is unclear, but there is recent evidence to suggest homologous function across cerebellar projections (Pisano et al., 2021). However, the cerebellum contributes to a diverse set of behaviors, both motor and non-motor (Diedrichsen et al., 2019; King et al., 2019; Sereno et al., 2020). Further work is needed to understand whether different regions of the cerebellum may be preferentially involved in the interactions proposed here or whether variability in the pattern of cerebellar damage across individuals and studies can explain some contrasting results. Sharing of the SPE signal represents one of the multiple possible interactions among SPE-driven, reinforcement, and explicit learning mechanisms below the level of their output stages (see **Figure 1**), and future research is needed to elucidate others. Importantly, the presence of such multi-level interactions means that learning mechanisms cannot be easily isolated.

When it comes to motor adaptation, studies of people with cerebellar degeneration suggest that SPE-driven learning may be the primary system responsible for resolving performance errors. Only when the influence of SPE-driven is minimized, such as by eliminating the need or ability to compute a meaningful SPE signal (e.g., by removing cursor feedback altogether or providing visual feedback of the hand), can reinforcement learning or explicit learning become the predominant driver of changes in behavior (Therrien et al., 2016, 2021; Cashaback et al., 2017; Wong et al., 2019). This has important implications for future studies aiming to manipulate or leverage individual learning mechanisms.

Finally, the work reviewed here begs the question of whether further insight into the interactions between SPE-driven, explicit, and reinforcement learning mechanisms can be gained from studies of motor adaptation in other patient populations. Parkinson's disease (PD) is often studied as a model of basal ganglia dysfunction, a structure known to play an integral role in reinforcement learning (Schultz, 2006; Lee et al., 2012). A sizable body of literature has studied motor adaptation in people with PD but has noted inconsistent findings. While some studies show similar adaptation behavior between people with PD and age-matched control participants (e.g., Stern et al., 1988; Marinelli et al., 2009; Leow et al., 2012, 2013), other studies have noted adaptation impairments in people with PD (Contreras-Vidal and Buch, 2003; Venkatakrishnan et al., 2011; Mongeon et al., 2013). Discrepant results may stem from differences in the size of the imposed perturbation (Venkatakrishnan et al., 2011; Mongeon et al., 2013) or medication status of participants across studies (Semrau et al., 2014). To date, no study has attempted to parse the contributions of SPE-driven, explicit, and reinforcement learning to motor adaptation in this population (but see Cressman et al., 2021), but it would be highly interesting for future studies to do so. Overall, this literature, along with the other studies reviewed here, underscores the complexity of interactions occurring between motor learning mechanisms and argues for the importance of not treating such learning mechanisms as predominantly modular.

AUTHOR CONTRIBUTIONS

Both AT and AW contributed equally to development of the idea, writing the manuscript, and generation of figures. All authors contributed to the article and approved the submitted version.

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Competition, Conflict and Change of Mind: A Role of GABAergic Inhibition in the Primary Motor Cortex

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Deciding between different voluntary movements implies a continuous control of the competition between potential actions. Many theories postulate a leading role of prefrontal cortices in this executive function, but strong evidence exists that a motor region like the primary motor cortex (M1) is also involved, possibly *via* inhibitory mechanisms. This was already shown during the pre-movement decision period, but not after movement onset. For this pilot experiment we designed a new task compatible with the dynamics of post-onset control to study the silent period (SP) duration, a pause in electromyographic activity after single-pulse transcranial magnetic stimulation that reflects inhibitory mechanisms. A careful analysis of the SP during the ongoing movement indicates a gradual increase in inhibitory mechanisms with the level of competition, consistent with an increase in mutual inhibition between alternative movement options. However, we also observed a decreased SP duration for high-competition trials associated with change-of-mind inflections in their trajectories. Our results suggest a new post-onset adaptive process that consists in a transient reduction of GABAergic inhibition within M1 for highly conflicting situations. We propose that this reduced inhibition softens the competition between concurrent motor options, thereby favoring response vacillation, an adaptive strategy that proved successful at improving behavioral performance.

Keywords: decision, executive control, behavioral adaptation, reaching movement, transcranial magnetic stimulation, silent period, inhibition, primary motor cortex (M1)

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INTRODUCTION

Because most decisions are implemented through concrete action, understanding their neuronal bases requires to address eventually the question of competition between potential responses. Among the several tasks designed for studying response competition, those designed to produce a conflict gave rise to a strong interest because they offer distinct cognitive conditions with sharply defined chronometric and psychometric behavioral evidences (Smith, 1968; MacLeod, 1991).

Among the numerous and distributed brain areas involved in motor decisions (Cisek, 2012), it is now well admitted that primary motor cortex (M1) does not only operate as a pure output in the motor process, but also contributes to the integration of cognitive variables that influence and bias movement execution (Georgopoulos, 2000). It is thus expected that this core brain region plays an active role in the conflict decision process (Michelet et al., 2010; Klein et al., 2014), in addition to other frontal and prefrontal regions like the anterior cingulate cortex emphasized by the classic conflict-monitoring theory(Botvinick et al., 2004).

Among several studies that helped to better understand the role of M1, those using transcranial magnetic stimulation (TMS) are of particular interest because they associate both excellent spatial and temporal resolution with a direct access on the motor output function. The majority of these studies (Leocani et al., 2000; Michelet et al., 2010; Klein et al., 2012) used single pulse TMS during the RT period, defined since Donders as the time elapsing between the onset of the stimulus and the onset of the response, and consequently considered to represent the time during which a decision is made (Meyer et al., 1988). Thanks to precise analyses of the amplitude of motor evoked potentials (MEP) that reveal the corticospinal excitability (CSE), they generated a great deal of knowledge about the chronometry and the network organization of the cortical mechanisms involved in conflict. Importantly these studies strongly suggest that M1 is not just a blind executor of a decision made upstream but is also biased and modulated by cognitive influences during the RT period (Michelet et al., 2010; Klein et al., 2014).

However, at least in complex behaviors, decision is not always limited to the RT period and the decision process is supposed to evolve after movement onset, as suggested by behavioral adjustment or correction during ongoing execution of movement (Rabbitt and Vyas, 1981).

Hence it seems of particular interest to further study the involvement of M1 during movement execution, and more particularly to address the inhibitory processes that are thought to shape movement execution (Bari and Robbins, 2013). Among the different possibilities allowing to measure inhibition within the central nervous system, the silent period (SP) is of particular interest as it must be elicited during voluntary electromyographic (EMG) activity (Ziemann et al., 1993; Chen et al., 1999). More particularly, this SP is characterized by a pause in the EMG signal whose cortical origin has been clearly proven (Chen et al., 1999). Although debate still exists on a spinal contribution to its earliest component (Schnitzler and Benecke, 1994), the SP is proven to be a reliable measure of GABA intracortical inhibition (Siebner et al., 1998). Unfortunately, the vast majority of studies interested in conflict have used experiments involving ballistic-like movements (e.g., quick button presses mediated by adduction/abduction of the index finger), lacking the biomechanical complexity of most natural actions as well as post-onset control requirements.

To fill this gap, here we designed a novel conflict task in order to assess the potential role of cortical inhibition during ongoing movement execution. We based our paradigm on a center-out reaching task which, contrary to simple categorical decision, is subject to factors such as effort, biomechanical complexity, and ongoing movement control (Cos et al., 2011; Cos et al., 2012; Coallier et al., 2015).

For this pilot study, twenty subjects performed our directional Stroop-like task (DSLT) allowing to study a broad range of competition level and conflict situations. Two potential targets arrayed randomly in a circle are presented simultaneously with a central cue. The choice is imposed by a simple shape-matching rule, but the color feature of the cues is manipulated to provide an irrelevant and conflicting dimension, thereby allowing to generate three cognitive situations, corresponding to control, congruent, and incongruent conditions (**Figures 1A,B**). Additionally, we also carefully controlled the angular distance between the target and distractor in order to influence the competition effect within each condition (**Figure 1B**).

This DSLT coupled with TMS allowed us to address specifically the role of gabaergic inhibition during post-onset decision period within the primary motor cortex. We hypothesized that, in addition to pre-movement (RT), conflict can still influence the decision process within the M1 during the ongoing movement.

As a whole, the present experiment aimed at addressing the following questions:

(1) Is the DSLT a valid task to study behavioral impact of response competition and conflict?
(2) Is conflict resolution based on the same neuronal processes as other competition for the selection of a target between several options?
(3) Can the inhibitory activity within the primary motor cortex account for the behavioral results found in a complex conflict task?

This study will incidentally provide information on the general concept of response competition and on the peculiar role of incongruent situations, appealing for a necessary clarification of the terms "competition" and "conflict" to prevent research's misdirection.

MATERIALS AND METHODS

Participants

Twenty subjects (9 females), mean age 24.2 (±3.4) participated in the experiment. All had normal or corrected-to normal visual acuity, were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971), and were free from any contraindication to transcranial-magnetic stimulation (TMS; Rossi et al., 2009). The experimental procedure was approved by the national ethics committee (CPP N° 2013A01444936), and was carried out in accordance with the principles of the revised Helsinki Declaration [World Medical Association General Assembly (WMAGA), 2008]. All subjects gave written informed consent prior to the experiment and were financially compensated for their participation.

Apparatus

The task apparatus consists of a digitizing tablet (GTCO Calcomp, Columbia, MD, United States; 0.915 × 0.608 m) and a half-silvered mirror suspended 16 cm above and parallel to the digitizer plane. Visual stimuli were projected onto the half-silvered mirror by an LCD monitor suspended 16 cm above the mirror, producing the illusion that the targets lie on the plane of the digitizing tablet. Subjects made reaching movements in the horizontal plane using a digitizing stylus (moving the

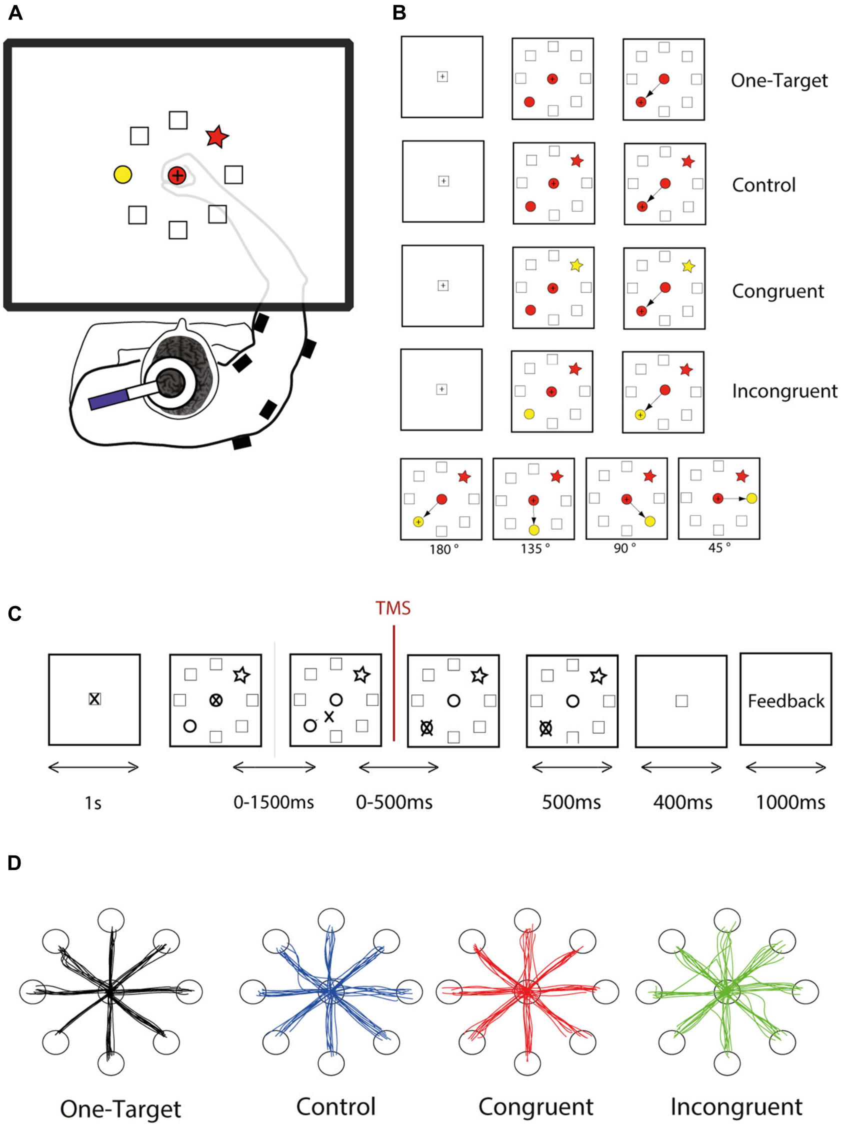

FIGURE 1 | Experimental design. **(A)** The subject responded to the task by moving a cursor on a digitizing tablet. Stimuli and cursor feedback are projected onto a mirror placed between the table and the monitor. Single-pulse transcranial magnetic stimulation (TMS) was applied over left primary motor cortex, and EMG activity was measured thanks to wireless electromyographic surface electrodes attached to the main muscle groups of the right upper arm. **(B)** The task follows a shape-matching rule, and color dimension is an irrelevant feature of the stimuli. However, shapes and colors were assembled to form different cognitive situations, of three different levels of difficulty. For each cognitive condition, the target could be located in every one of 8 positions arrayed in a circle, and the distractor could be spaced from 45 to 180°. **(C)** The DSLT task began (after a 1,000-ms rest period during which the cursor rests in the home position) with the simultaneous presentation of one central shape and the peripheral target and distractor. The subject had up to 1,500 ms to initiate the movement and up to 500 ms to reach the correct target and stay inside for 500 ms. Then a positive or negative visual feedback, depending on the response accuracy appeared for 1,000 ms. **(D)** Examples reach trajectories in one-target, Control, Congruent, and Incongruent conditions from one subject.

cursor) embedded within a 3D-printed cylinder held by the subject's right hand. The semi-silvered mirror was such that the hand was mostly invisible to subjects, who mostly saw the cursor they controlled and the visual stimuli delivered to them (**Figure 1A**). The stylus position was sampled at 125 Hz with a spatial resolution of 0.006 ± 0.127 mm. The control of the task, stimulus display, and synchronization of task events and signal recording were performed by a custom written LabVIEW program (National Instruments, Austin, TX, United States). The data were stored in a Matlab structure and analyzed using custom Matlab scripts (Mathworks, Natick, MA, United States).

Task Design

We designed a new experimental paradigm based on a center-out reaching task combined with an analog of the original Stroop test. Because of the combination of these two features, we called this task the DSLT (for Directional Stroop like task).

The principle used here is the shape-matching protocol in which the subject had to select the peripheral target with the same shape as the central cue, whatever the colors filling these shapes (**Figure 1**). The color of the stimuli is consequently an irrelevant information. Using different combinations of color and shape, we were able to assess interference between 2 competing tendencies (shape or color association), and consequently present three cognitive conditions comparable to those of the classical Stroop: control, congruent, and incongruent conditions (**Figure 1B**). In the control condition, all the shapes are filled with the same color (e.g., red, **Figure 1B**), such that the color is not supposed to bias the movement toward one particular peripheral shape. In the congruent condition, the target is colored with the same color as the central cue (e.g., red) while the distractor is filled with another color (e.g., yellow), such that the color should bias the movement toward the target. Finally, in the incongruent condition, the distractor as the same color as the central cue (e.g., red), such that the color should bias the movement toward the distractor. Because the cue is in the central position and the target in 1 of 8 potential positions at the circumference of a 12 cm radius circle (equidistantly arranged, at 45° intervals), this task involved a wide range of movement directions. Moreover, the relative distance between the target and the distractor can also be easily manipulated in this task (**Figure 1B**, bottom panel).

Task stimuli were manipulated and presented in a pseudo random order in order to satisfy the following constraint: (1) control, congruent, and incongruent trials were presented in equivalent proportion; (2) similar number of trials for the eight movement directions (3) similar number of trials for angular distance between target and distractor (i.e., 45, 90, 135, and 180°) (4) similar number of trials using the red or yellow color to fill the central cue, and (5) similar number of occurrence for each of the four shapes (triangle, star, square, or heart symbol). Each shape has an equivalent surface and are filled either with a red or yellow color with equal luminance.

Each trial comprised the same succession of events (**Figure 2C**). A trial started when the cursor is within the home position represented by a square at the center, followed by a 1 s rest period during which the subject was instructed to remain still. Next the task itself (DSLT) appeared, i.e., the simultaneous presentation of one central shape and the peripheral target and distractor, followed by the response period during which the hand leaves the home position to reach the peripheral target. The evaluation period ended the trial with the appearance of a positive or negative visual feedback. Subjects had 1,500 ms to leave the home position, and 500 additional ms to reach the target. Despite this temporal constraint which was easy to comply with, subjects were instructed to move as quickly and accurately as possible. The trial aborted if the hand position cursor was moved outside an acceptable diameter of the central cue (±10% of the cue diameter) before the target and distractor appearance.

In addition to the DSLT, a one-target task was also performed to obtain control values for behavioral variables as well as SP duration when no choice had to me made (see below: RT, initial deviation, and SP). All reaching curvature and dispersion measures were normalized for each direction by those control values obtained in the one-target experiment. Each subject performed one session that comprised 657 trials (with a short pause every 100 trials) and lasted about 2 h, including the threshold hunting phase. After a first series of 200 trials without TMS, TMS was applied for each trial. The three trial conditions and the four angles were interleaved in a pseudorandom order, and the mean number of SP in a single muscle computed for each of these 12 different experimental conditions was 31 per subject. Eighty trials were also used for measuring the SP in the One Target condition in the eight different direction, with 10 SP for each movement direction and for a single muscle.

Electromyographic, Motor Evoked Potential, and Silent Period Recording

The silent period (SP) is induced when a TMS pulse is applied during an ongoing movement execution, and corresponds to a transient suppression of the EMG activity. The TMS pulse was applied 30 ms after the cursor left the central zone (2 cm diameter) in order to stimulate during an active EMG period, yet soon after movement execution (but in every trial, after the 100 ms following action onset, hence allowing to measure the initial deviation in the absence of TMS perturbation).

Surface electromyographic recording was performed in nine muscles, eight of each chosen on the basis of their involvement in the reaching movements (**Supplementary Figure 1**): biceps long head, biceps short head and anterior deltoid as flexors, triceps brachii and posterior deltoid as extensors, pectoralis major as arm adductor, lateral deltoid as arm abductor and trapezius as shoulder elevator. Finally, the FDI (a finger abductor) was recorded in order to measure the resting motor threshold (RMT). EMG activity was acquired with a Trigno^{TM} Wireless EMG Systems (Delsys Inc., Boston, MA, United States) amplified (by a factor of 909), band-pass filtered (Bandwidth 20 ± 5 Hz, >40 dB/dec), digitized on line (rate 2 kHz), and later rectified and integrated.

During experimental recording sessions, subjects were seated in a chair. Their heads were slightly immobilized on the right to counteract the pressure exerted by the TMS coil positioned over the left M1, and their left arm rested on their knees. For the first twelve subjects, a figure- of-eight coil (Double 70 mm Coil, Magstim Company Ltd., Whitland, Dyfed, United Kingdom) was used to stimulate M1 over the left hemisphere. During this first part of the experiment, the duration of the SP obtained were too short to be confidently attributed to a cortical inhibition (mean duration: around 60 ms, but see the section "Discussion" and **Supplementary Material**). In order to increase the SP duration, and because the effect of simulation intensity on the SP duration is well documented (Taylor et al., 1997; Säisänen et al., 2008), we used for the remaining eight subjects a circular coil (90 mm Coil, Magstim Company Ltd., Whitland, Dyfed, United Kingdom) with a larger surface of stimulation allowing to stimulate a larger region, with a higher intensity, corresponding to the forelimb region of the primary motor cortex. The rest of the protocol was exactly the same regardless of the coil used. In the following section, the results correspond to the

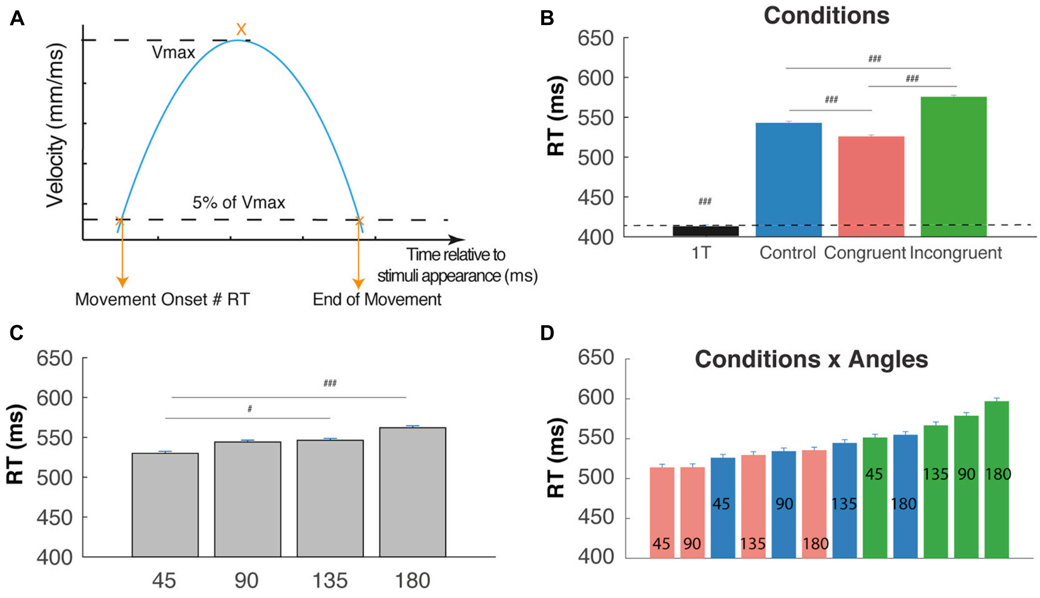

FIGURE 2 | Reaction time (RT). **(A)** RT corresponds to the movement onset time relatively to the appearance of the cues; it is defined by the time at which the velocity cross a threshold defines as 5% of the maximal tangential velocity (Vmax). **(B)** RT are significantly shorter for the one-target condition in comparison with two targets cognitive conditions. RT trials are significantly longer than control and congruent trials RTs (interference effect) and Congruent trials are faster than control trials (congruency effect) (###$P < 0.0001$). **(C)** RT increase with the angular distance between targets. **(D)** Almost linear increase of RT when considered the (12) conditions x angles trial types and revealing a continuum in the competition level induced by these trials-types. $^{\#}p < 0.01$.

circular coil experiment, while the results obtained with the figure- of-eight coil are presented in **Supplementary Material**. The coil was held tangentially on the left hemi-scalp with its handle pointing backward at an angle of about 45 degrees from the midsagittal axis. The resting motor thresholds were established using the criterion of lowest intensity of stimulation that allowed to induce peak-to-peak amplitude MEPs at rest of approximately 100 μV (in at least 8 of 10 consecutive trials) in the FDI muscle of the right hand (**Supplementary Figure 2**). In order to avoid any modification of MEPs amplitude due to background EMG activity, trials in which muscular pre-activation was greater than 100 μV within a 500 ms window preceding the TMS pulse were discarded. Then, the optimal scalp position (OSP) of the coil was defined as the position allowing to induce MEPs simultaneously in the 8 muscles involved in the reaching movements, which is possible because of the proximity of the representation area of the studied muscles. The OSP was obtained by moving the coil in approximately 0.5 cm steps around the subject's left M1. Throughout the experiment, the coil was manually maintained over the OSP using the Brainsight frameless stereotactic system (Rogue Research Inc., Montreal, Canada) to continuously monitor coil placement; coordinates of each stimulation relative to the hotspot were recorded for *post hoc* verification. The stimulus intensity was set at 120% of the resting motor threshold in order to obtain SP in the recorded muscles (see **Supplementary Figure 2**).

Analysis

Data analysis was carried out offline using custom written Matlab programs.

Movement onset was defined by the time at which the cursor tangential velocity exceeded 5% of the maximal tangential velocity (**Figure 2A**), and RT corresponded to the time between cue appearance and movement onset. Calculation of the initial deviation was based on Ludwig and Gilchrist (2002): a rotation was applied on the reach trajectory so that the straight line between start and endpoint always coincided with the horizontal axis, and the values on the ordinate indicate the perpendicular deviations from the straight line (**Figure 3A**). We then calculated the initial deviation (ID) as the angle between the horizontal axis and a fixed point in the movement trajectory obtained 100 ms after the movement onset.

Most of these movements were single-curved trajectories, whereby lateral deviations from target direction display a single peak. However, for some trials, the hand trajectory changed directions multiple times during the movement, often characterized by a double-peak curve of lateral deviations indicating movement corrections. A careful examination was conducted on each trial and when more than one local maxima (peak) was found on the trajectory, we classified the trial as "self-corrected" or vacillation (see **Supplementary Figure 4C** for examples).

For the measurement of the silent period duration, we considered the absolute silent period. Its beginning is defined as the first moment after MEP the EMG crossed the rest period ± 2 sem. It ends, similarly, at the first moment after the suppression of the ongoing EMG, when the EMG crossed the rest period ± 2 sem (see **Figure 4B**). A first automatic analysis is performed with a custom Matlab program and verified visually for each trial. The duration of the silent periods is not influenced by changes in

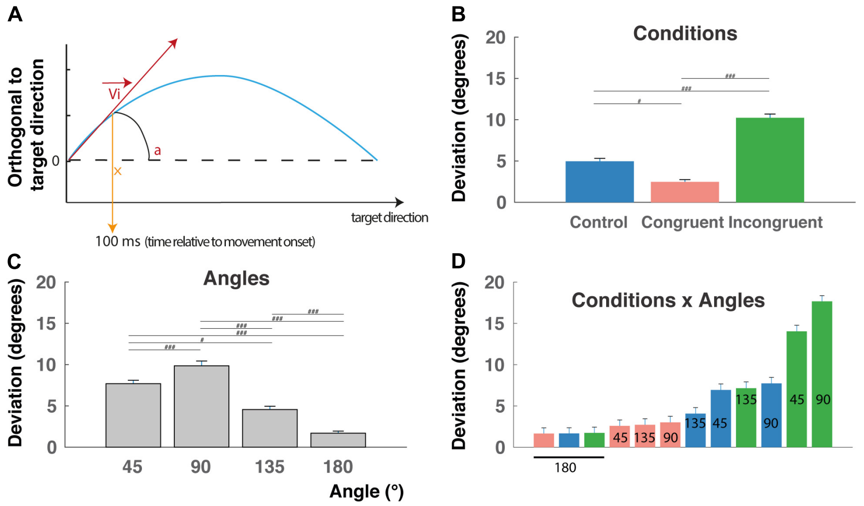

FIGURE 3 | Initial deviation (ID). **(A)** The initial deviation (ID) corresponds to the angular difference between the initial direction computed 100 ms after the movement onset and the overall direction determined as the center of the target location. It indicates the decision made early after movement onset. Blue line: reach trajectory. Red arrow: initial direction. **(B)** ID for incongruent trials are significantly longer than control and congruent trials RTs and congruent trials are faster than control trials ($^{\#\#\#}P < 0.0001$) indicating that the interference and congruency effects are found also after movement onset. **(C)** ID decrease with the angular distance between targets, except for the 90° angular separation. **(D)** Almost linear increase of RT when considered the (12) conditions x angles trial types and revealing a continuum in the competition level induced by these trials-types also after movement onset (but see text for peculiarity of the 90° and 180° angular distances). $^{\#}p < 0.01$.

contraction strength (Taylor et al., 1997), rendering unnecessary to normalize the SP to background EMG.

Because the use of a supra-motor threshold could have disturbed motor execution, movement times were not presented in detail in this paper, and we focused our behavioral analyses on RT and Initial deviation that both occurred before the TMS pulse.

Because the silent period is defined as a suppression of ongoing EMG activity, it can only be recorded when muscles are actually activated for a particular reaching movement. This activation was characterized when the EMG activity before at least 100 ms preceding the TMS pulse exceeded by ± 2SD the baseline EMG level recorded during the rest period (green dotted line; **Figure 4B**). As all muscles do not contribute to each reaching movement, this means that all muscles did not exhibit a SP for every reaching direction. Hence, we considered a muscle only if the SP were consistently found in at least 8 out of 10 times for this movement in the one-target condition. The SP duration for a movement direction corresponds to the mean of the SP actually recorded in each considered muscles.

ANOVAs and *t*-tests with Bonferroni-Dunn correction for *post hoc* analysis were used. We set the significance levels for the ANOVAs to correct for multiple comparisons and for the *post hoc* *t*-tests to $P < 0.05$. All data are given as means ± SE. For RTs and SPs, we also performed a one-way ANOVA, reporting the statistical size effect index f [see (Cohen, 1988) for more information] including the One-Target condition. Indeed, in the One-target condition the target location is identified unambiguously by its spatial location, while in the three cognitive conditions two potential targets (target and distractor) are simultaneously presented. Hence, the comparison between the One-target condition (no competition) and all other cognitive conditions (competition between representations of the alternative choices) is a good indicator of the very impact of competition on RTs or SPs. This One-target condition was excluded from the two-way ANOVA with Angle separation as a factor because no distractor (and consequently no angle) was used in this condition. Finally, the One-Target condition is not directly presented in the ID analyses because each trajectory in a particular direction was normalized relatively to the correspondent mean trajectory of the one-target trials.

RESULTS

Behavioral Results

Because of the extremely low error rate (<3%), only behavioral measures for correct trials were considered in the analyses. Regarding the behavioral analyses, we only analyzed in the following section the behavioral parameters sampled before the stimulation time, and consequently not affected by the TMS pulse. We are then able to pool RTs or initial deviations (IDs) analyses for trials *with* and *without* TMS. For the statistical analysis of RTs, IDs and silent periods (SPs), two factors were taken into account: *task conditions* (control, congruent, or incongruent) and *angular distance* between the target and distractor (45°, 90°, 135°, and 180°).

We first performed a one-way ANOVA on RTs in order to compare with the One-Target condition. This analysis showed a clear main effect of condition on RT ($F_{(3,12754)} = 1268.6$, $P < 0.0001$), $f = 0.18$ as confirmed by *post hoc* comparison showing that mean RT was significantly lower for the One-target condition (412 ± 1.7 ms) than the other three cognitive conditions, confirming a strong effect of competition on RTs. Moreover, we found, respectively increased RTs for incongruent

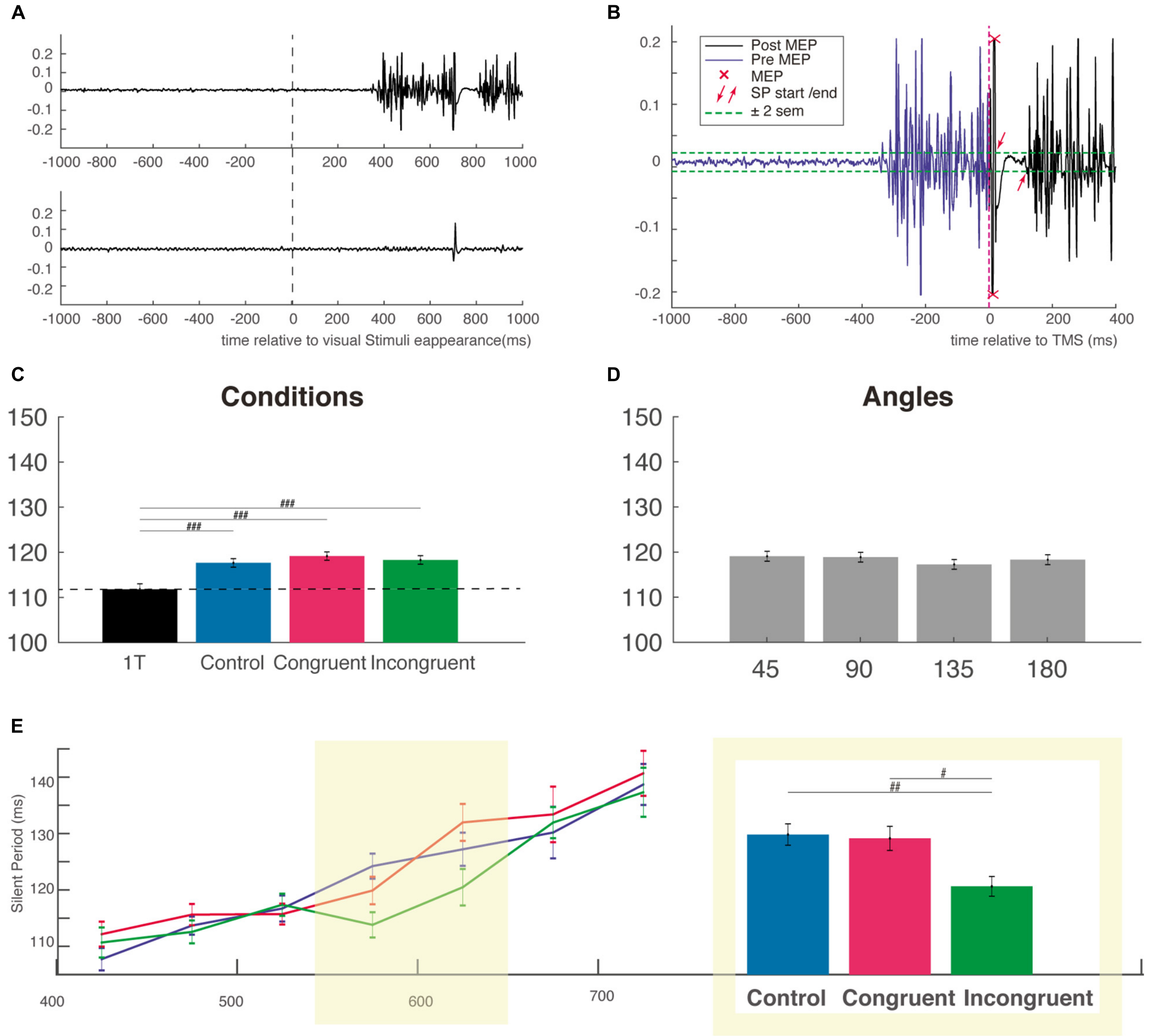

FIGURE 4 | Silent period duration (SP). **(A)** Typical EMG response in a muscle involved (top EMG trace) or not (bottom EMG trace) in a reaching trial. Activity is centered on the onset of visual stimuli **(B)** example of calculation of the SP for the EMG trace shown in panel **(A)** the SP was measured from offset of the MEP to the resumption of voluntary EMG activity. **(C)** The SP is not modulated by the cognitive condition but is shorter for the one-target condition, attesting the influence of the very competition between potential options. **(D)** SP duration as a function of the angular distance between the target and distractor. **(E)** Mean SP in each bin of RT as a function of cognitive condition (control, congruent, and incongruent) showing that SP generally increase with competition strength. The two bins centered, on the mean incongruent RT, is highlighted in yellow and the SP for this subgroup is presented in the adjacent inset (the same ordinate axis as for the main graph). MEP, motor evoked potential; sem, standard error of the mean. $^{\#}p < 0.01$; $^{\#\#}p < 0.001$; $^{\#\#\#}p < 0.0001$.

trials (574 ± 2 ms) and decreased RTs for control trials (541 ± 1.8 ms) as compared to congruent (524 ± 1.7 ms) trials, attesting the congruency and interference effect (**Figure 2B**, *t*-test, $P < 0.00001$). We also found a clear main effect of angular distance on RT ($F_{(3,9009)} = 32.97$, $P < 0.0001$), $f = 0.1$, as confirmed by *post hoc* comparison showing that mean RT was significantly lower for 45°, and increased until 180° (**Figure 2C**, 530 ± 2.4; 544.1 ± 2.3; 546.3 ± 2.3; 562 ± 2.5; *t*-test $p < 0.01$). Finally, a significant *Condition* X *Angle* interaction (**Figrue 2D**) was found ($F_{(6,9009)} = 3.71$, $P < 0.002$), $f = 0.05$, indicating a continuum of increasing RT from the congruent-45° trials to the incongruent-180° trials that could be due to gradual increases in the competition process between targets and distractors before movement onset. *Post hoc* tests are not described here in detail, because of the numerous significant differences between trial types (56 out of 66 tested comparisons).

This behavioral congruency effect and interference effect found in the RT are thought to reflect the competition between the two incompatible responses induced either by the color or by the shape of the cue. This hypothesis was further confirmed by a main effect of condition found on IDs (**Figure 3A**; $F_{(2,9009)} = 117.14$, $P < 0.0001$), $f = 0.16$, with *post hoc* comparisons indicating higher deviation toward the distractor for the incongruent condition (10.2 ± 0.4 mm), intermediate deviations for the control condition (4.9 ± 0.3 mm), and lower deviations for the congruent condition (2.5 ± 0.2 mm) (**Figure 3B**, $P < 0.00001$ for all t-tests). We also found a clear main effect of angular distance on IDs ($F_{(3,9009)} = 71.93$, $P < 0.0001$), $f = 0.15$, confirmed by *post hoc* comparisons showing that mean ID was significantly higher for 45° (7.7 ± 0.4) and decreases for 135° (4.6 ± 0.4 mm) and 180° (1.7 ± 0.2 mm) (**Figure 3B**, $P < 0.01$ for all t-tests), with a higher value for 90° (9.8 ± 0.6 mm), probably due to geometrical factors (see the section "Discussion"). Finally, a significant *Condition* X *Angle* interaction was found ($F_{(6,9009)} = 22.78$, $P < 0.0001$), $f = 0.12$, indicating a continuum of increasing ID from the congruent-45° trials to the incongruent-180° trials, and thereby could be a continuum in the competition process occurring after movement onset. Unsurprisingly, ID for a target localized at 180° of the distractor exhibited the lower IDs for geometrical reason (see the section "Discussion"). *Post hoc* interactions are not described here in detail, because of the numerous significant differences between trial types (51 out of 66 tested interactions).

The percentage of trials during which the hand trajectory changed course during the movement was calculated. In a significantly greater proportion of incongruent trials (19.3%), the hand trajectory changed course during the movement, indicating a self-correction, in comparison to control (11.6%) and congruent (6.7%) trials (X2 = 14.66, $p < 0.0001$; **Supplementary Figure 4**).

Silent Period Duration

The mean intensity of a single TMS pulse needed to evoke a MEP of 100 μV at rest in the FDI, considered as the resting motor threshold, was 51 ± 3% of the stimulator output for the experiment with the figure-of-eight coil and 47 ± 3% with the circular coil.

We next considered how the SP duration was influenced by the competition, the congruency and interference effect as well as by the angular distance between target and distractor. Using a one-way ANOVA on SP obtained in our different conditions (including the One-Target condition), we found a main effect of condition ($F_{(3,5724)} = 8.89$, $P < 0.00001$), $f = 0.07$, with a *post hoc* test indicating a significant difference only between the three cognitive condition and the One-Target condition (**Figure 4C**). This result indicates that there is a clear effect of competition on the SP duration, but that this effect is independent of the nature of the distractor.

We then used a two-way ANOVA with the factors *Condition* and *Angle* and failed to find a main effect for any of those two factors (respectively, $F_{(2,4711)} = 0.63$, $P = 0.56$, $f = 0.016$ and $F_{(3,4711)} = 0.56$, $P = 0.63$), $f = 0.02$; Mean SP were almost identical (∼118 ms) for every cognitive and angular condition (**Figures 4C,D**). Based on the idea that RT is a good indicator of the level of competition involved, we divided the SP distribution of each condition according to RT into 7 non-overlapping time bins of 50 ms sorted by ascending order (**Figure 4E**). This Bin size was obtained using the automatic binning algorithm provided by Matlab and the associated function "histogram" which is based on the Scott's rule (Scott, 1979). A two-way ANOVA with task conditions (control, congruent, or incongruent) and RT bins as factors was performed. The shorter and longer RT trials were excluded from this analysis (and not displayed on **Figure 4E** and on **Supplementary Figure 3C**) because of too small number to allow a comparison between the three conditions. This analysis revealed a main effect for bins ($F_{(6,4376)} = 25.84$, $P < 0.00001$), $f = 0.19$, but not for condition factor ($F_{(2,4376)} = 2.27$, $P = 0.1$), $f = 0.03$, indicating a gradual increase of the SP from the fastest to the slowest RT, consistent with an increased gabaergic activity of the cortico-spinal neurons activated during the voluntary movement. We then performed a one-way ANOVA with the factor condition (control, congruent, and incongruent) for each individual RT bin, and found a clear influence of cognitive condition for the two bins centered approximately on the mean RT of incongruent trials ($F_{(2,1113)} = 6.03$, $P < 0.001$), $f = 0.13$. This was confirmed by *post hoc* comparisons, which showed that SPs were significantly shorter in the incongruent condition (115.9 ± 1.8 ms) than in the congruent (124.6 ± 2 ms) and control conditions (125.3 ± 1.9 ms), indicating a reduction (or an inhibition) of cortical inhibition specifically for incongruent trials (**Figure 4E**, right inset). Importantly, a significant reduction of inhibition was also found for the SP recorded after stimulation with the figure-of-eight coil (i.e., for the earliest part of the SP) at roughly the same RT bins, attesting of the specificity of this cortical reduction in inhibition for incongruent trials with long RT (**Supplementary Figure 3C**). Critically, however, for this figure-of-eight set of data with shorter overall SPs, we did not find the linear increase from the faster to the slower RT bins (**Supplementary Figure 3C**), a result which could be interpreted in favor of a mainly spinal origin of this early SP. Finally, it is likely that in both experiments, the longer RT bins corresponded to outliers trials, with a mixed influence of task difficulty and decrease level of general attention over the course of almost 1,000 trials performed. We were therefore reluctant to interpret SP for those trials that were probably impacted by a lack of attention.

DISCUSSION

In order to better understand the neuronal bases of voluntary movement and its control, we designed a directional analog of the Stroop task (Stroop, 1935; MacLeod, 1991) allowing (1) to involve complex movements requiring several muscles, (2) to control the level of competition between simultaneous movement options, and (3) to clarify the functional role of inhibitory circuits in competition resolution, more particularly during the ongoing evolution of the decision.

Our DSLT task allowed us to generate the well-known three conditions of a classical Stroop task (control, congruent and incongruent), but also, to intermingle different motor context by varying both the orientation of the target and the relative position between the target and the distractor (**Figure 1**).

As expected, we found the classical results described in every conflict task, with longer RT for incongruent condition and a shorter RT for congruent condition relative to control condition (**Figure 2A**), which confirms the existence of both *behavioral congruency and interference effects* (MacLeod, 1991). As previously observed, the color dimension provided salient but irrelevant information which strongly influences the decision (Michelet et al., 2016). Moreover, the angular distance was also found to influence significantly the reaction times, with RT increasing with angular distance from 45 to 180° (**Figure 2B**), in line with the trivial idea that it is more difficult to process simultaneously information that are not close to each other. However, this is probably not a consequence of a facility to move the eyes from one potential target to the other as proposed by a study indicating that a closer distance do not imply purely attentional effects (Bock and Eversheim, 2000). Rather, we found that these results fit well with a model of interaction within a population of motor neurons, which predicts that the strength of the competition between two targets should be greater when they are far apart from each other than when they are close together (Cisek, 2006; Cisek, 2012), in agreement with *the affordance competition hypothesis* (Cisek and Pastor-Bernier, 2014). The combination of cognitive conditions and angular distances provided 12 different types of trials that could be ordered according to a continuum of increasing RT, which would be proportional to the level of competition or task difficulty (**Figure 2C**). Because the time of movement onset is given by the RT, this continuum of increasing RT clearly suggests that the decision to move is a function of a response activation (or decision) variable that depends on the gradual accumulation of evidence over time as predicted by several accumulator models (Gold and Shadlen, 2007; Thura, 2016). Hence it is likely that most of the competition resolution operates before movement execution, a process that engage several brain structures from prefrontal areas (Michelet et al., 2016) to the primary motor cortex (Michelet et al., 2010). However, it has been proposed that decision could still evolve after action onset (Tipper et al., 2000; Cisek, 2006; Resulaj et al., 2009; Cisek, 2012; Lepora and Pezzulo, 2015; Michalski et al., 2020). The analyses of the initial deviation (ID) indicate clearly that the decision process is not ended at the time of movement onset, and that decision variables still inform the executive brain regions during movement execution. Indeed, the deviations of reaching trajectories were significantly impacted by the cognitive conditions (**Figure 3**), and we found for the ID the same *congruency and interference effects* as described for RT. Regarding the angular distance analysis, the initial deviation is more pronounced for an angular separation of 90° between target and distractor, consistent with the vector geometry of reaching in a 2D plane. For the same reason, it was also expected that the initial deviation is less important in the 180° angle separation. At first sight, this later result could seem at odd with the stronger impact found on RT for angular separation of 180°. Our interpretation is that this is in accordance with previous works clearly showing that decisions take also biomechanical costs into account when choosing between multiple actions, and that these biomechanical costs bias movement choice before movement onset (Cos et al., 2011). Relative to the one-Target condition, we can then conclude that the movement trajectory is deviated toward the distractor in every condition (control, congruent, or incongruent), indicating that the representation of the task-irrelevant information (the distractor) is not totally suppressed at the time of movement onset. This is in agreement with the idea that several plans of action are prepared before actually choosing one of them, and that these potential actions are still present and competing after movement onset. In other words, when a competition exists between multiple potential targets, the unselected action program is not completely suppressed at movement onset (Cisek, 2012).

Because in every cognitive condition a clear influence of the competing response for the distractor is still present at least 100 ms after the start of the movement, a continuing process is probably still needed to finally reach the correct target. This process could involve the inhibition of the distractor, the enhancement of the activity related to the chosen target, or both. Although conflict resolution has been proposed to occur through cortical amplification of task-relevant information (Egner and Hirsch, 2005), it remains that "Response inhibition is the most basic form of behavioral control" (Stuphorn, 2015), and should still be considered. The continuum found in RT and ID for our 12 conditions (**Figures 2C**, **3C**) confirms that this task is well suited to assess the involvement of inhibitory process in response competition because it allows to compare SP durations among a wide range of competition level.

Based on the report that RT and ID reflect, respectively, the pre- and post-movement competition between options, we tried to corelate these results with measures of SP that is known to provide a quantitative assessment of inhibitory processes. This SP could be separated into an early component thought to reflect spinal inhibition, and a late component determining the duration of the whole SP, involving inhibitory effects at cortical level (Ziemann et al., 1993; Chen et al., 1999). However, it has also been proposed that the SP is exclusively of cortical origin (Schnitzler and Benecke, 1994). In any case, it seems that SP is proportional to the amount of inhibitory inputs onto the M1 projection neurons (Taylor et al., 1997). Because the reaching movements are subserved by the activity of a population of neurons in the primary motor cortex, each of them being involved in several movement directions (Georgopoulos et al., 1986), we computed the SP for the 8 recorded muscles in order to reflect global (population level) inhibition during arm reaching movements (see **Supplementary Figure 2**). This is further recommended (1) because inhibitory influences responsible for the SP are widely distributed across muscles, irrespectively of their agonist or antagonistic role (Ho et al., 1998); (2) because agonist and antagonist could nevertheless be simultaneously activated (Latash, 2018).

Using the focal figure of 8 coil, we found relatively short SP (around 60 ms; see **Supplementary Figure 2**), indicating either an insufficient intensity of TMS pulse, or a spinal contribution to the recorded SP (Säisänen et al., 2008). With such coil, the area of stimulation is probably too focal and covers small surface of the M1 upper-limb area and may thus mostly reflect spinal mechanisms (Säisänen et al., 2008). Using the circular coil, allowing to use stronger stimulus intensity targeting a broader cortical region we recorded SP duration longer than 100 ms, and therefore more likely to depend on cortical GABAergic inhibition (Chen et al., 1999; Orth and Rothwell, 2004). This result is also in accordance with the well documented effect of simulation intensity on the SP duration (Taylor et al., 1997; Säisänen et al., 2008).

We first studied the SP as a function of cognitive conditions and angular distances. We found a significant difference between the One-Target and the cognitive conditions, indicating that the very presence of a competition modulate the SP duration. However, we failed to find an overall difference between the three cognitive conditions (**Figure 4C**).

We then speculate that if the SP is directly related to the competition, it should be positively correlated with the RT, irrespective of the cognitive condition. We then compare the SP for seven successive RT bins, thereby matching the RT for each condition (**Figure 4E**). The interaction between condition and RT bins is not significant, as well as the main effect of condition. However, we found a significant main effect of RT bins, with a positive correlation between RT and SP duration, suggesting that situations involving more competition also involves more inhibition. This is consistent with several experimental and theoretical observations, described below, which all lead to sustain our proposal.

This is firstly consistent with the accumulator models postulating that selection between multiple options operates through biased competition involving a mutual inhibition process between different brain regions or within M1. Indeed, we have previously shown that in parallel with the growing agonist activity for the target related movement, the activity related to the alternative movement toward the distractor is gradually inhibited during the RT period (Michelet et al., 2010). The increased inhibition found in the present experiment is consistent with this previous finding, and indicate with a direct measure of the inhibitory process that the inhibition could last after movement onset. Critically, a significant proportion of corticospinal neurons become active after EMG onset (Cheney and Fetz, 1980) and could directly benefit from this late process. Secondly, this is consistent with the proposal that selective inhibition build up progressively (Ridderinkhof et al., 2004), which implies that the strength of the inhibition should be greater for longer RT. This is even more likely because the SP was measured here just few milliseconds after movement onset, and consequently before the whole system returned to a baseline level of activation. In this respect, the SP is considered as a continuation of the mechanisms that led to initial choice (van den Berg et al., 2016).

Third, the build-up of the SP is consistent with a pharmacological experiment effect showing a GABAb agonist (Baclofen) dose-dependent increased duration of the SP (Siebner et al., 1998), thereby confirming the hypothesis of a gradual increase of the inhibitory processes.

However, at the neuronal level, a specificity emerges from the conflict situation beyond the strict competition: while a global increase of the inhibitory processes is found, correlatively with the increasing difficulty of the task, a drop in the inhibitory processes become visible for (late) incongruent trials (**Figure 4E**). This is consistent with previous report indicating that in difficult tasks, online error correction latencies (i.e., correction during ongoing movements) increases as the RT increases (Rabbitt and Vyas). This result is also in accordance with the activation-suppression hypothesis (Ridderinkhof et al., 2004), which predicts that long delay could imply a strong inhibition of both congruent and incongruent stimuli, which could impede the ability to finally choose any option. This hypothesis is strengthened by the broad tuning in population coding of the primary motor cortex, implying that the same neurons could be involved in different reaching movements. Indeed, the inhibition of the movement toward the distractor could hence possibly affect neurons involved in both reaching actions (i.e., toward target and distractor). In this context, a dampening of the inhibition could momentarily impede the process of action selection, and allow other processes to bias decision through vacillation between the two options, also providing more time to complete the decision process. This result is in accordance with the seemingly paradoxical increase of motor variability that were previously found to improve learning performance (Wu et al., 2014). Furthermore, and considering the gabaergic origin of the SP, it is noteworthy that an administration of baclofen (GABAb agonist) also increases behavioral flexibility (Beas et al., 2016).

We hence propose that this transient reduction of GABAergic inhibition could serve as an adaptive process to let the system free of changing its mind until the last moment before reaching the target. This result is consistent with previous work demonstrating that under conflicting or uncertain conditions, the motor system adapts quickly to a changing and unpredictable context by equalizing the preparation of alternative responses (Bosc et al., 2021). In accordance with this hypothesis, the reach kinematics indicate a larger proportion of trajectories with a change of direction for these trials, confirming a greater disposition to vacillation or changing mind strategy (**Supplementary Figure 4**).

We could link this effect to an uncertainty that increases as time elapses, and a more likely influence of upstream brain structures to influence this process. This is partly confirmed by the fact that in incongruent trials, the reaching movement is first directed toward a position intermediate between the target and the distractor. Vacillation here resemble the exploration mode favored by an increased baseline release of noradrenaline making neurons more responsive to any stimulus, thereby allowing a broad scan of possible options (Aston-Jones and Cohen, 2005). Interestingly, anterior midcingulate (aMCC) inputs are supposed to drive these exploration mode (Aston-Jones and Cohen, 2005), and this brain regions send also direct inputs to both the spinal cord and M1, which could explain, respectively the decrease of the early (**Supplementary Figure 3**) and late (**Figure 4**) SP. Previous results in monkeys, in a conflict task where vacillation or self-corrected movements were found, indicated that the timing of aMCC activation for incongruent trails is compatible with the timing of the SP reduction (Michelet et al., 2016).

The present experiment used a wide range of movement directions and angles between target and distractor that have somehow limited the number of trials for each condition and consequently the power of our statistical analysis. Moreover, we have explored the validity of two types of coils, which have also limited the number of subjects we were able to consider simultaneously. In future experiments following this pilot study, we will focus our analysis on fewer movement directions, using exclusively the circular coil. Such evolution of our experimental protocol would allow to directly test, with more participants, the interaction between M1 and other frontal areas (PMd, SMA) using the dual-coil TMS technic during movement execution.

Indeed, other regions of the frontal cortex are also likely to participate in the inhibition of M1, such as pre-SMA (Duque et al., 2013; Quoilin et al., 2021), or the Pre-motor cortex (Parmigiani et al., 2015; Parmigiani et al., 2018) in line with the idea that inhibition is a fundamental function of the frontal cortex (but see Neige et al., 2021 for a comprehensive review). This idea is also well in line with the fact that there are several possibilities of inhibition within M1 (Sanger et al., 2001), potentially implemented by different brain regions, either cortical or subcortical. For instance, one such candidate is the subthalamic nucleus, a basal ganglia region well known to be involved in the inhibition of competing motor representation, acting as a brake on the cortico-striatal system (Cavanagh et al., 2011), thereby preventing premature responding (Frank, 2006; Cavanagh et al., 2011; Mirabella et al., 2012; Zavala et al., 2015; Wessel et al., 2019) to facilitate decision making under conflict (Cavanagh et al., 2011; Mirabella et al., 2012; Zavala et al., 2015).

Overall, this pilot study provides evidence that a subtle imbalance of the GABAergic inhibitory processes participates, even after movement onset, to the conflict-resolution. This process could complete the repertoire of adaptive strategies allowing before (Frank, 2006; Cavanagh et al., 2011; Mirabella et al., 2012; Duque et al., 2013; Klein et al., 2014), during and after (Bosc et al., 2021) movement control over competition and more specifically conflict situations.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the CPP N° 2013A01444936. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

TM conceived and designed the experiments. NL and MG programmed the software. BR and AD collected the data. BR, AR, and TM conducted the data analyses and wrote the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnhum.2021.736732/full#supplementary-material

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Action Intentions, Predictive Processing, and Mind Reading: Turning Goalkeepers Into Penalty Killers

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The key to action control is one's ability to adequately predict the consequences of one's actions. Predictive processing theories assume that forward models enable rapid "preplay" to assess the match between predicted and intended action effects. Here we propose the novel hypothesis that "reading" another's action intentions requires a rich forward model of that agent's action. Such a forward model can be obtained and enriched through learning by either practice or simulation. Based on this notion, we ran a series of studies on soccer goalkeepers and novices, who predicted the intended direction of penalties being kicked at them in a computerized penalty-reading task. In line with hypotheses, extensive practice in penalty *kicking* improved performance in penalty reading among goalkeepers who had extensive prior experience in penalty blocking but not in penalty kicking. A robust benefit in penalty reading did not result from practice in kinesthetic motor *imagery* of penalty kicking in novice participants. To test whether goalkeepers actually use such penalty-kicking imagery in penalty reading, we trained a machine-learning classifier on multivariate fMRI activity patterns to distinguish motor-imagery-related from attention-related strategies during a penalty-imagery training task. We then applied that classifier to fMRI data related to a separate penalty-reading task and showed that 2/3 of all correctly read penalty kicks were classified as engaging the motor-imagery circuit rather than merely the attention circuit. This study provides initial evidence that, in order to read our opponent's action intention, it helps to observe their action kinematics, and use our own forward model to predict the sensory consequences of "our" penalty kick if we were to produce these action kinematics ourselves. In sum, it takes practice as a penalty kicker to become a penalty killer.

Keywords: action intention, predictive processing, mind reading, body language, goalkeeper or goalie

INTRODUCTION

Action control has two faces. Not only do we need to coordinate perception and action in order to pursue our motives and accomplish our goals: we also need to coordinate our actions with those of others. Key to the latter is the ability to "read" the actions of others and the intentions behind them. We derive from predictive processing theory the notion that in order to read someone else's action intention, one needs to have a rich kinesthetic experience with that action oneself (kinesthetic experience refers to what a movement feels like in your own body). In a series of studies, we test the novel and nontrivial hypothesis that penalty-reading performance in soccer improves after practice in penalty-*kicking*.

In a first experiment, we test the hypothesis that the more kinesthetic experience a goalkeeper has in penalty-*kicking*, the more effectively s/he can predict the shooter's aim, thus improving her/his chances to prevent the shooter from scoring a goal. A second experiment tests the hypothesis that similar benefits can be obtained by motor imagery, that is, by vividly mimicking and experiencing the shooter's movement in one's mind. In a third experiment, we train a machine-learning pattern classifier on fMRI data to test (using cross-classification) whether motor-imagery brain networks are engaged in successful penalty reading.

Penalty Killers

Soccer is one of the most popular sports world-wide. When the stakes are high, such as in knock-out games in the UEFA Champions League or the FIFA World Championship tournament, penalty shout-outs are decisive in 25% of major tournaments matches (Jordet et al., 2007). A fast and well-aimed penalty kick almost never fails. More often than not, however, the results are driven by penalty-shooters who choke under the pressure, or by goalkeepers who distinguish themselves as penalty killers.

Penalty-blocking skills involve both speed and accuracy, which engage in a trade-off: the later the goalkeeper initiates her/his dive, the more information s/he can process about the movement of the shooter and the speed and trajectory of the ball. Hence, the longer s/he waits, the greater the likelihood that s/he will choose the correct direction, but also the greater the likelihood that s/he will be too late. As it turns out, goalkeepers who excel at penalty blocking tend to wait long (Memmert et al., 2013).

Once the shooter has hit the ball, the goalkeeper can use information about the ball's speed, direction, and rotation to predict at 98% accuracy where it will land. However, waiting and then responding is barely an option: the time it takes for a well-hit ball to cross the goal line and the time it takes for the goalkeeper to respond and arrive are on average close to equal (∼600 ms; Franks and Harvey, 1997). Responding after the ball has been hit literally leaves the goalkeeper with too little time to arrive before the ball crosses the goal line (Glencross and Cibich, 1977; Chiappori et al., 2002). Thus, by the nature of the game, goalkeepers are not terribly successful at penalty blocking. In the German *Bundesliga*, they block 18.8% of all penalty kicks (Dohmen, 2008).

Goalkeepers may focus on training reaction speed, but the gain is only marginal. Instead, or in addition, goalkeepers may try and push their luck. One way to do so is by guessing: a risky decision ahead of time to dive left, or right, or to stay in the center, regardless of the shooter's action (Bar-Eli et al., 2007). Another, more informed way is to use intel about shooter statistics: many penalty shooters have a "favorite angle", and goalkeepers who have access to this information may take their chances by betting on it. Or else they may *pretend* to know the kicker's favorite angle, and thus try and intimidate their opponent (who is probably already quite nervous). Other psychological tricks that goalkeepers often entertain include making oneself as tall as possible, trying to engage their opponent in a staring game, distracting them by stalling, by objecting to the ball position, by moving their arms up and down during the pre-shot duration, or by positioning slightly off-center, thus tempting the shooter to aim for the "open" side (Masters et al., 2007; Wood and Wilson, 2010; Weigelt et al., 2012; Memmert et al., 2020).

"Reading" The Body Language of Penalty Kicks

Alternative, more cognitive ways to improve penalty-blocking success involve attempting to "read" the penalty: assessing the shooter's kinematic body and movement parameters to predict the direction and speed of the kick (Savelsbergh et al., 2002; Williams, 2009; Dicks et al., 2010; Piras and Vickers, 2011). Penalty-reading skills may well be trainable, and hence of great interest to goalkeepers, coaches, and researchers alike. Thus, goalkeepers should learn to acquire as much information as possible from the run-up and kicking movement of the penalty-shooter in order to improve their blocking performance (Dicks et al., 2010; Memmert et al., 2013).

Optimal visual search helps promote penalty-saving success by having the goalkeeper focus on the speed and direction of the run-up, the position, and orientation of the supporting leg and foot, or the orientation of the torso of the shooter (Savelsbergh et al., 2002; Van Kampen, 2010). Already 100 ms before the shooter hits the ball, these combined kinematic properties are ∼85% informative about the direction of the immanent kick. The supporting leg is positioned approximately 250 ms before ball contact, and its orientation is by itself about 80% informative (Franks and Harvey, 1997; Savelsbergh et al., 2002). Experts not only are faster at detecting the relevant information for efficient perception-action coordination (Savelsbergh et al., 2002; Yarrow et al., 2009); they also tend to focus more selectively on the legs, whereas novices also inspect hips, torso, and even arms (Memmert et al., 2013). A proper and timely focus can be learned through training and can help improve penalty-blocking performance by giving the goalkeeper a head start (Savelsbergh et al., 2010b).

Here we go off the beaten path in studying alternative ways of reading the body language of penalty kicks. We will focus on the possibility to *simulate* the observed kinematics as if we engage in that action ourselves, in order to *forward-model the anticipated* *effects* of "our" action, and then use that *to infer the motive* of the other agent's action: the intended direction of the penalty kick ("if I were moving like this, then I"d intend to kick the ball in the left lower corner"). Forward modeling is key to modern theories of active inference and predictive processing (e.g., Wolpert et al., 2003; Friston et al., 2011; Clark, 2013), and will be discussed in more detail below.

Darts players can predict where a dart will land on a dartboard by studying the movement kinematics of the thrower, the more accurately so as they are more experienced themselves (Knoblich and Flach, 2001). Likewise, professional basketball players are more accurate at predicting whether a shot at the basket goes in or out (when watching videos that stop at the time the ball is released) than professional coaches, commentators, and journalists (Aglioti et al., 2008). While all of them presumably have similarly extensive experiences in watching such shots, only the players have extensive hands-on experience and hence rich forward models of kicking.

di Pellegrino et al. (1992) observed that so-called mirror neurons fire both when executing a deliberate action and when observing that same action. Mirror neurons help interpret and understand the actions of another individual but also help prime the motor system for one's own incipient action (Iacoboni et al., 2005; Costantini et al., 2011). Seeing other people's body movements unconsciously activates motor representations in the observer's brain (Fadiga et al., 1995; Rizzolatti et al., 2009). This so-called motor resonance (Gallese, 2001) suggests that individuals subconsciously simulate someone else's action. Note that the activity of the motor system is not *exactly* identical between observing and executing an action—if this were the case, then a person would move every time they observed another person acting (Babiloni et al., 2016, 2017). Brain regions rich in mirror neurons show increased activation when anticipating the opponent's movements in soccer (Bishop et al., 2013).

Mirroring a movement is not always adequate, however: if someone hands you a coffee mug by holding its ear, one needs to *complement* rather than mirror the other's action (Sebanz et al., 2006; Sartori et al., 2012). An observed action must first be read and comprehended in order to infer its intent (s/he aims to hand me the coffee); next, the observed action should be linked to appropriate complementary actions (to grasp the mug I should open my hand, as s/he holds it by the ear) (Sartori and Betti, 2015). In such situations, unconscious motor resonance reflects not only the imitative kinematics of the observed actions but also the predicted kinesthetic effects of our response (Sartori et al., 2015).

Penalty situations likewise entail complementary actions. The goalkeeper needs to infer, based on observations of the kicker's run-up and shooting kinematics, the orientation of the supporting leg, etc.), the intention of the shooter (which angle will s/he take), and then act accordingly. Generalizing from the darts and basketball examples, we may argue that for goalkeepers to read the body language of penalty kicks, they should be experts in kicking penalties themselves—an entirely novel conjecture.

Predictive Processing

Crucial to the theory's credit (and wider applicability in elite and amateur sports) will be an empirical demonstration not only of the predicted effect but also of the neurocognitive mechanisms through which reading the shooter's actions promote successful penalty-blocking. Compatible with the darts and basketball findings, a view on reading others' action intentions in terms of predictive processing was proposed by Ridderinkhof and Brass (2015). These authors derived predictions about penalty-blocking skills from a specific instantiation of predictive processing theory, the *Impetus, Motivation, and Prediction in Perception-Action Coordination Theory* (IMPPACT; Ridderinkhof, 2014).

Predictive processing theories such as IMPPACT refer to the brain metaphorically as a "prediction pump", constantly predicting the effects of one's actions in order to optimize the selection of actions appropriate for obtaining present goals. Such predictions are made using forward models: rapid computational algorithms that predict the consequences of one's actions (as perceived through exteroceptive senses, such as our eyes; or through interoceptive senses, such as proprioception: "how does the movement feel"). The forward model stores the link between the specific kinematic parameters of the action, the specific kinesthetic experience associated with that action, and the specific effects of that action in the world. Information stored in forward models emanates from prediction errors, which arise from the discrepancy between the *desired* consequences of one's action on the one hand, and either the *observed* or the *predicted* consequences on the other. By testing model predictions and minimizing prediction errors, the forward model becomes more and more accurate. By practicing or simulating the action over and over, in a variety of circumstances, one's forward model is gradually augmented, so that it provides an increasingly rich and accurate repertoire in predicting the consequences of one's movements (Wolpert et al., 2003) across a variety of situations—such as in penalty-kicking and penalty-blocking.

In movement-reading, we apply forward models to predict the consequences of actions executed by others rather than oneself. The richer one's forward model, the better one will be able to "inverse model", and hence predict, the effects of the corresponding action executed by someone else (Kilner et al., 2007; Ridderinkhof, 2017). A rich forward model is built on extensive kinesthetic experience; thus, for goalkeepers aiming to block a penalty, IMPPACT suggests that the more kinesthetic experience a goalkeeper has in penalty-*kicking*, the more effectively s/he can inverse model and predict the shooter's aim, thus improving her/his chances to prevent the shooter from scoring a goal (Ridderinkhof and Brass, 2015). Here we will test this proposal empirically, in a sample of experienced goalkeepers.

Pre-Play: Kinesthetic Motor Imagery

The notion of forward modeling of the proprioceptive consequences of one's action bears resemblance to the notions of *kinesthetic motor imagery* (KMI). In KMI, one performs and experiences a movement in one's mind, vividly but without moving (Moran et al., 2012). One pre-plays the movement, as it were. Practicing through mental pre-play can help improve a movement (and hence learning to perform it optimally; Ziessler and Nattkemper, 2002; Ridderinkhof, 2014). KMI engages a first-person perspective (rather than the third-person perspective in visual motor imagery): an act is "seen" through the person's own eyes and "felt" through the person's own interoceptive senses. Gymnastic athletes report realistic kinesthetic sensations during KMI of a complex gymnastics exercise, the so-called Yurchenko jump (Calmels et al., 2018). We conjecture that the more vivid one's KMI, the more one's forward model can gain in precision. The present study will put this further proposal to the test by giving participants experience in observing and pre-playing penalties to see if their penalty-reading skill improves.

The notion that kinesthetic experience can be acquired through KMI relies on the assumption of functional equivalence: physical movements and their mental (imagined) counterpart engage similar neural circuits and neurophysiological processes (Decety and Jeannerod, 1996), and hence largely activate the same brain areas (Ridderinkhof and Brass, 2015). Neural activation during KMI resembles the preparatory planning phase that precedes movement (Jeannerod, 2006), but also goes beyond mere preparatory planning, as demonstrated by the finding that KMI engendered activation in the contralateral primary motor cortex just as actual movements did (Stinear et al., 2006).

fMRI and lesion studies have produced a fair picture of the network of brain regions recruited by actual movement execution and mental pre-play of the same movement (an overview of these networks is depicted in **Figure 1**; details are beyond the present scope). As reviewed in Ridderinkhof and Brass (2015), these networks largely overlap, with the differences between play and pre-play characterized by spatial gradients (visualized in **Figure 1**) rather than the recruitment of entirely different regions (for the details, which go beyond the present scope, we refer the reader to our previous review.)

Multivariate pattern analysis (MVPA) is an increasingly popular analysis technique to quantify the involvement of cortical networks in particular perceptual or cognitive processes. Here, we use MVPA of fMRI data to test whether the individual motor-imagery brain networks are engaged in successful penalty reading. We first train a classifier to discern, separately for each individual, the circuitry unique to motor imagery from the circuitry involved in viewing penalties for individual participants in general. Subsequently, we test if individuals use their motor imagery circuitry to successfully read penalty kicks and predict their direction. This will be the aim of the third experiment reported here.

EXPERIMENT 1: PRACTICING PENALTY KICKING

Deriving from a set of assumptions embodied in the IMPPACT theory, here we test the hypothesis that goalkeepers, in order to improve their penalty-reading skill and hence their penalty-blocking performance, should develop kinematic and kinesthetic experience in penalty-*kicking*.

In a sample of experienced goalkeepers, playing in high-level amateur competitions, we create three groups: one group of goalkeepers who practice in penalty-kicking; another who practice in penalty-blocking (in conventional ways); and finally a control group of goalkeepers who practice in non-penalty-related soccer skills, under otherwise comparable circumstances. The main aim of having the control group is to establish the baseline improvement from pre-test to post-test in performance in the penalty-reading task. Beyond such practice effects (or their counterparts: effects of fatigue or boredom), such a control group also helps rule out interpretations of training improvements in terms of the effects of motivation, attention, expectation, and the like.

Goalkeepers who practice penalties should improve more than those in the control group. Goalkeepers in the penalty-blocking group may obviously improve because of training penalty-blocking itself (building on their prior experience). Goalkeepers in the penalty-kicking group may improve because the enrichment of their forward model of penalty kicking will allow a more optimal reading of the body language and intention of the penalty shooter. The latter prediction is, to our knowledge, unique to IMPPACT (although other varieties of predictive processing theory can readily be extended to include such assumptions). Since the penalty-blocking group builds on prior experience and hence had less room for improvement, we might expect the penalty-kicking group to improve most. Nonetheless, any observation of improvement in the penalty-kicking group (compared to the control group) would already satisfy our theoretical prediction.

Conceivably, individuals with greater interoceptive awareness of their bodily senses (Khalsa and Lapidus, 2016) may benefit from the richer kinesthetic experience and hence more effective forward and inverse modeling. Thus, we include an interoceptive awareness scale to examine whether higher scores come with greater penalty-reading success.

Methods

Participants

Goalkeepers were recruited via high-level amateur soccer clubs and goalkeeper training centers in the Netherlands. Inclusion criteria were an age of 16 or older and a minimum of 3 years of active experience as a goalkeeper in an amateur or (semi-) professional soccer team participating in a competition of the Royal Dutch Soccer Association (KNVB) in the period immediately preceding the experiment. Exclusion criteria were more-than-minimal prior experience in kicking penalties (i.e., at least monthly during the past year). Our remaining sample consisted of 51 male goalkeepers with a mean age of 22.8 years (range 16–60 years). Participants could win one of five vouchers of 25€ each assigned through a lottery in return for their participation. They provided informed consent before participation. All procedures were approved by the university ERB (nr. 2017-DP-8029) and complied with relevant laws and institutional guidelines.

Design

Using a pre-test/post-test non-equivalent group design, participants were assigned pseudo-randomly to three groups, with the restriction that goalkeepers from the same soccer club or

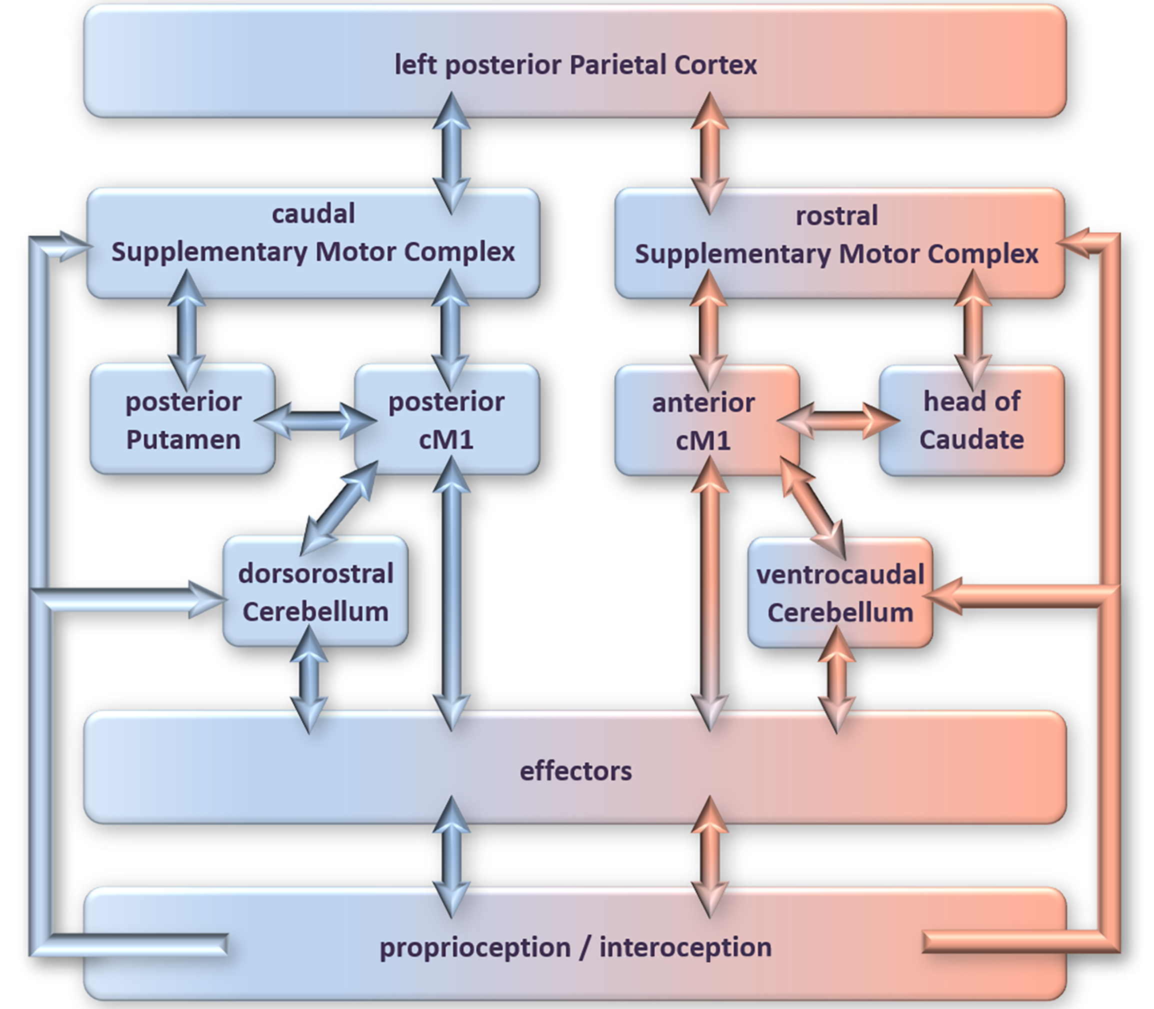

FIGURE 1 | The neural circuitry involved in overt motor performance (blue/left side of figure) compared to motor imagery (rose/right side of figure/nodes). Adopted from Ridderinkhof and Brass (2015); for details please refer to that article.

training center formed duo's in two of the groups (see below). In the penalty-blocker (PB) group, goalkeepers practiced blocking penalties in the conventional way (as detailed further under *Procedures*). In the penalty-shooter (PK) group, goalkeepers practiced *kicking* penalties instead of blocking them. In the control (C) group, participants ran a series of 80 meters, and practiced keeping the ball in the air (using all body parts except their arms and hands, and without holding the ball in any way), for as long as possible.

In the PB and PK groups, goalkeepers were matched in pairs. They performed individually but formed duo's to facilitate procedures. One of the two goalkeepers always kicked the penalty shots (and never blocked them, consistently throughout the experiment), while the other always blocked them (and never kicked them). Goalkeepers were assigned to duo's pseudo-randomly, such that both goalkeepers in a pair played at the same club and trained together, or at least trained an equal amount of time in the same environment. Matching was based on level of goalkeeping experience, ranking within the team (first or second goalkeeper), and age, as much as possible.

Materials

Training

During PB and PK training, a standard full-sized soccer goal (7.32 m wide × 2.44 m wide) was used and penalties were shot from the standard distance of 11 meters from the goal. All three groups practiced with a standard size soccer ball on a regular training field, with all participants wearing their typical training gear.

Penalty-Reading Task. Goalkeepers performed a computer task twice on a 15-inch laptop to assess penalty-anticipation skills. Video clips showed a soccer player running up to the ball to shoot a penalty from the 11-meters dot on a regular soccer pitch (kickers were youth players of PSV Eindhoven Football Club; materials were adapted from Savelsbergh et al., 2010a). Penalties were videotaped from the goal-line, thus rendering a goalkeeper's first-person perspective. At the moment the shooter's foot touched the ball, the clip was arrested, and (with a fade-out time of 0.5 s) the screen turned green (the same color as the grass of the soccer pitch). The time between the start and "arrest" of the clip varied between 1.2 and 1.5 s. Participants were asked to predict the direction of the ball by pushing one of four buttons, arranged in a spatially compatible fashion. Each button (keyboard letters E/I/C/N) referred to one of four possible sections in the goal shown on the screen, divided into right/left, and low/high. Thirty unique video clips, with 15 different penalty kickers, were shown in randomized order. Each test consisted of six practice trials and 60 test trials. Instructions emphasized accuracy, but also stressed speed of responding (since in real-life penalty-blocking, diving in the correct direction won't save a goal if the dive is too late). Accuracy is defined as the percentage of responses in which the selected button corresponded with the actual penalty direction "behind the video". Reaction time was measured at each trial as the interval (in milliseconds) between the moment the shooter touched the ball and the moment the participant hit the button. After every block of trials, accuracy was displayed on the screen. *Presentation* software was used to show the video clips, record the responses, and control the experiment. The task was based on materials and prior experience with a similar task in previous research (Savelsbergh et al., 2002).

Penalty-Kicking Experience Questionnaire. Participants filled out a questionnaire that asked for goalkeeper experience (0–1 year, 1–3 years, 3–5 years, >5 years), experience in penalty kicking (yes/no), and if yes, at which frequency (a few times a year, every month, every 2 weeks, or every week).

Interoceptive Awareness Questionnaire. Participants also filled out a brief self-developed questionnaire on interoceptive awareness. They rated 10 statements on a 7-point Likert scale from never to always. Example statements are "when I move, I can focus my attention on how that movement feels physically", "when I see someone moving, I can feel in my own body how that movement feels", and "I notice changes in my body, such as breathing faster or slower, or a change in my heart rate". These statements were selected and compiled from existing questionnaires on interoception; our selection has not been validated or tested for reliability as such.

Procedure

The experimenters visited the goalkeepers at their clubs/training centers. After a brief introduction, the goalkeepers were seated individually in a silent room, where they first provided informed consent. They filled out the questionnaires and then were administered the penalty-reading task as a pre-test. This part of the session took ∼25 min, including ∼15 min for the penalty-reading task. Participants were then provided with standardized instructions on the training to be carried out. The instruction emphasized taking their time, and focusing on how it feels to kick/block a penalty or how the movements to keep the ball in the air feel. In the PK/PB groups, the goalkeeper duo's kicked/blocked penalties in the conventional way. They were instructed to take a moment before each penalty to plan their kick/save, and after each kick/save to recall how well it went and, especially, how it felt in their body. After a series of 10 kicks/saves there was a 1-min break. The training entailed four series of 10 penalties and lasted ∼20 min in total. Goalkeepers in the control group were instructed to run 80 meters, fast but not at full sprint speed, and then try and keep the ball in the air as long as possible during 1 min. After a 1-min break, the next series of 80 meters running and 1 min of keep-the-ball-in-the-air started. There were four series, lasting ∼20 min in total. To stir up motivation, participants in each group kept article records of their performance during each 1-min break (these data were not analyzed). After the training, the penalty-reading task was administered again as a post-test. Finally, the goalkeepers were debriefed. All procedures involved the continuous presence of an experimenter. The entire session lasted approximately 1 h.

Statistical Analysis

In the data obtained from the penalty-reading task, trials where participants gave no response at all were discarded from analysis (<1%). Reaction times could in principle be negative since participants were encouraged to respond as soon as they thought they knew the direction of the kick; sometimes this was already before the ball was kicked, which in theory is possible (indeed, goalkeepers don't always wait).

Accuracy scores and average reaction times were analyzed (separately) using analysis of variance (ANOVA), with interoceptive awareness as a covariate in a follow-up ANCOVA. Group was entered as a between-subjects variable (control, PB, PK) while Time was entered as a within-subjects variable (pre, post). Bayes Factors (BF) were calculated to assess how much more probable the observed data under H_0 was than under H_A. That is, we report BF_{01}, not BF_{10}. In case of a significant interaction, paired-samples *t*-tests were used to examine pre-post differences per group.

Results

Accuracy

Accuracy averaged 51.3%, which is well above chance level (25%), indicating that participants were reasonably well able to predict penalty direction from the video clips. Groups did not differ in penalty-reading accuracy ($F_{(2,48)} = 1.00$, $p = 0.375$, $\eta^2 = 0.040$, $BF = 2.445$). Accuracy improved from pre- (50.1%) to post-training (52.5%) tests ($F_{(1,48)} = 11.20$, $p = 0.002$, $\eta^2 = 0.189$, $BF = 0.138$). Most important, the effect of training differed between training groups ($F_{(2,48)} = 3.99$, $p = 0.025$, $\eta^2 = 0.143$; the BF for the full model of both main effects and the interaction term equalled 0.133, signaling that the probability of these data was considerably lower under H_0 than under H_A). As depicted in **Figure 2**, accuracy improved for both the PB and PK groups, but not for the control group. This interaction pattern survived after partialing out covariance with interoceptive awareness ($F_{(2,48)} = 4.19$, $p = 0.021$, $\eta^2 = 0.151$), indicating that it was not produced by group differences in interoceptive skill.

When zooming in *post hoc* on pre-post differences per group, we observed that both the PB and PK groups improved from pre- to post-test ($t_{(16)} = -3.29$, $p = 0.005$; and $t_{(14)} = -3.21$, $p = 0.006$, respectively), whereas the control group did not ($t_{(18)}$ = 0.25, p = 0.803). The improvement in accuracy was numerically greater for the PK than the PB group (4.5 vs. 3.4%, but this difference did not obtain statistical significance in an independent-samples t-test ($t_{(30)} = -0.69$, p = 0.498).

Response Speed

Response speed averaged 664 ms. Groups did not differ in penalty-reading speed ($F_{(2,49)}$ = 1.93, p = 0.156, η^2 = 0.073, BF = 1.238). Reaction time improved from pre- (691 ms) to post-training (636 ms) tests ($F_{(1,49)}$ = 4.81, p = 0.033, η^2 = 0.089, BF = 1.858). Most important, the effect of training did not differ between training groups ($F_{(2,49)}$ = 1.49, p = 0.235, η^2 = 0.057; the BF for the full model of both main effects and the interaction term equalled 1.135, signaling that the probability of these data was considerably higher under H_0 than under H_A). This interaction pattern was not altered after partialing out covariance with interoceptive awareness ($F_{(2,49)}$ = 1.66, p = 0.201, η^2 = 0.065).

Discussion

Practicing in penalties improved penalty-reading accuracy. Not surprisingly, this held for practicing in penalty-blocking: practicing one's physical penalty-blocking skill could well be expected to generalize to improved penalty-reading skill in "virtual space", even though the former includes features that are not entailed in the latter (such as the actual dive, which can fail even if it is in the correct direction, and which feels more real).

What is less trivial, and confirms our hypothesis, is that practicing in penalty-*kicking* improved penalty-reading accuracy as well. This can clearly not be explained by experiencing penalty-blocking situations *per se*. It might potentially be explained by increased experience in the specific penalty-reading task that we used, but this account fails to receive support by the finding that penalty-reading accuracy did *not* increase in the control group. A remaining difference between control and penalty groups is that the latter underwent "general practice" in penalty situations, which might benefit their penalty-reading skill even for goalkeepers who practiced kicking rather than blocking. However, we fail to see a possible mechanism behind such an effect, especially given that goalkeepers in the control and PK conditions alike already have quite abundant experience with penalty situations in general. Thus, we conclude that the hypothesis derived from the IMPPACT model in terms of forward modeling is much more specific and at this point cannot be discarded.

The improvement in accuracy in the PK group was 4.5%, which may seem small, but is meaningful nonetheless: a small increase in penalty-reading accuracy (after merely 20 min of training) may well instantiate the difference between winning and losing a match.

Obviously, small sample sizes are always a hazard, as they are here. For example, it cannot be excluded that the finding that goalkeepers in the PK group scored relatively low at pre-test might be a consequence of sampling error. Pre-test accuracy differed between groups, ranging from 43.3–60.0% in the control group to 40.0–59.2% in the PB group and 33.3–59.2% in the PK group. The latter group scored lowest at pre-test and improved the most. However, when, by way of an exploratory analysis, we remove the only two participants who scored below 40% at pre-test (both scoring 33.3%, both in the PK group) from the analysis, the patterns remain very much the same, with the interaction effect remaining highly comparable both qualitatively as quantitatively, even though the accuracy at pre-test has now become quite similar across groups. Thus, this specific alternative account in terms of sample error does not seem to be supported by the data, although obviously, the sample size remains small, and the present finding stands to await independent replication.

Practicing exerted a considerable improvement in penalty-reading speed (55 ms) in the same direction as it did for accuracy; however, this effect was not modulated by training condition, and hence cannot be attributed specifically to forward modeling or any other specific factor. Although practice in the penalty-reading task did not improve accuracy in the control group, it did improve speed, so it would seem that this was a mere practice effect.

The observed patterns of findings were not modulated by interoceptive awareness scores, which ran counter to our intuition. Our instrument to measure interoceptive awareness was based on existing instruments, but it was brief and selective, and at any rate, not yet validated. Thus, future studies may aim to replicate the present findings with more optimal measures of interoceptive awareness.

Our sample was relatively homogeneous in terms of goalkeeping experience. Future studies might include players that differ in level and years of experience to see if these moderate the observed effects.

In conclusion, this experiment provides initial evidence that practicing penalty-kicking improves penalty-reading accuracy. The assumption that the improvement in penalty-reading skill, as ensuing from enriched forward models of penalty-kicking, actually involves pre-play was tested in the next experiment.

EXPERIMENT 2: KINESTHETIC MOTOR IMAGERY OF PENALTY KICKING

The notion of forward modeling of the proprioceptive consequences of one's action is thought to invoke kinesthetic motor imagery or rapid pre-play. It has been argued and shown that mental action simulation alone can aid in learning a specific motor skill (Ziessler and Nattkemper, 2002; Ziessler et al., 2004). Here we assess the power of pre-play by giving participants experience in observing and pre-playing penalties to see if their penalty-reading skill improves.

A sample of novices was divided into two groups: one group that practices in KMI of penalty-kicking; and one that practices in KMI of penalty-blocking. The groups are exactly comparable in all other respects, including materials and instructions other than the focus on penalty kickers and goalkeepers. A separate control group was omitted since the previous experiment had already demonstrated that mere effects of practice, expectation, and motivation on performance in the penalty-reading task were negligible.

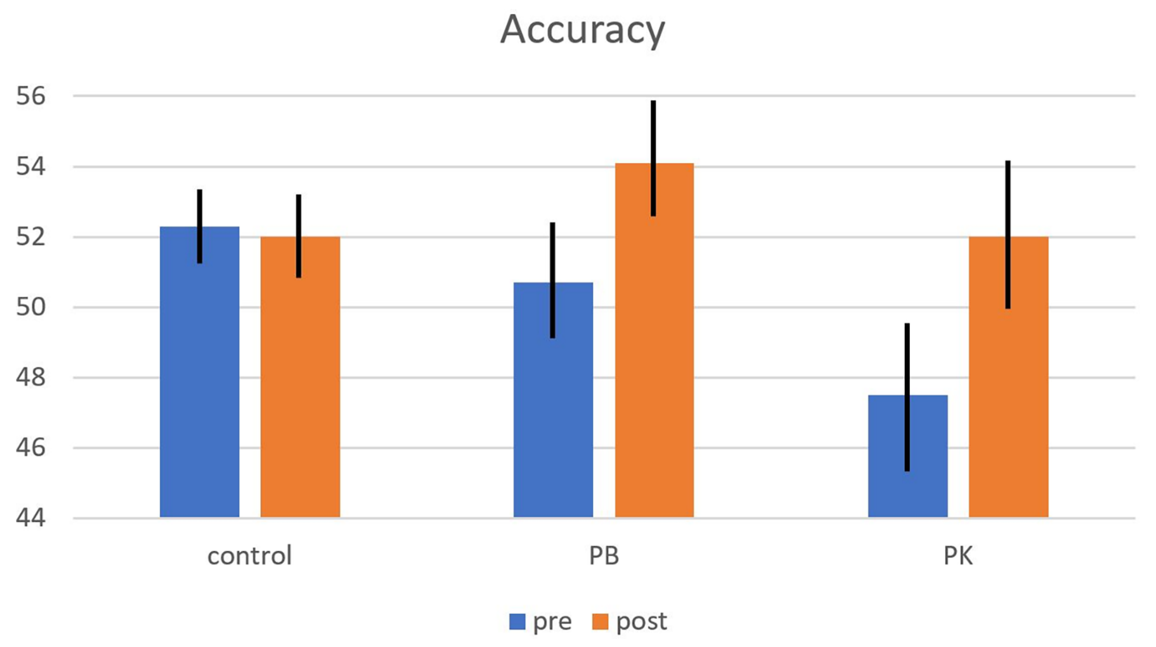

FIGURE 2 | Interaction of the effects of Group (X-axis) and Time (separate bars/violins) on penalty reading accuracy (Y-axis) in a bar graph (left panel) and a violin plot (right panel). Accuracy improved from pre- to post-test for both the PB and PK training groups, but not for the control group. Error bars (left panel) represent 1 standard error to the mean.

Goalkeepers in the penalty-kicking group may improve because KMI of the movements of the penalty kicker enriches their forward model of penalty kicking, which should allow for more optimal reading of the intention of the penalty kicker. The latter prediction is, again, to our knowledge, unique to IMPPACT. Goalkeepers in the penalty-blocking group may improve as well, either because KMI may enrich their forward model of penalty blocking, which might benefit the speed and accuracy of their response to penalties fired at them, or because of more generic experience with penalty-blocking situations. While we might expect the penalty-kicking group to improve most, observing that this group improved at all would already satisfy our theoretical prediction.

KMI might be likened to empathic perspective-taking, often described as "understanding another's point of view". Shared representations in the perception and action of motor behavior correspond to shared representations between understanding and experiencing the state of another (Preston, 2007), presuming a kind of bodily merging of the self with the other (Erle and Topolinski, 2015). Conceivably, then, individuals with higher dispositional empathy may be more proficient at KMI and at action-intention reading. Thus, we include an empathy scale to examine whether higher scores come with greater penalty-reading success.

Methods

Participants

Participants were first-year Psychology students at the University of Amsterdam who participated in return for course credits. They ranged in age from 18 to 35 years. Exclusion criteria were prior experience as a field player or goalkeeper in a regular soccer team, either anytime in the past 2 years, or for a total of more than 1 year in the farther past. Our remaining sample consisted of 55 participants (33 females) with a mean age of 21, 7 years (range 18–29 years). They provided informed consent before participation. All procedures were approved by the university ERB (nr. 2017-DP-7945) and complied with relevant laws and institutional guidelines.

Design

Using a pre-test post-test non-equivalent group design, participants were assigned pseudo-randomly to one of two groups, with the restriction that groups of up to four participants who participated simultaneously were always assigned to one and the same group, so as to prevent them from entertaining hypotheses about which of the training regimes might work best. Participants in the penalty-blocker (PB) group practiced KMI of blocking penalties, while participants in the penalty-kicker (PK) group practiced KMI of *kicking* penalties (as detailed further under *Procedures*).

Materials

Penalty-Reading Task

This task was identical to the one described under Experiment 1.

Penalty-Kicking Experience Questionnaire

Participants filled out a questionnaire that asked for soccer field player and goalkeeper experience (0–1 year, 1–3 years, 3–5 years, >5 years), experience in penalty kicking (yes/no), and if yes, at which frequency (a few times a year, every month, every 2 weeks, or every week).

Empathy Questionnaire

Participants also filled out the Dutch translation of the *Basic Empathy Scale* (Jolliffe and Farrington, 2006; Van Langen et al., unpublished manuscript). They rated 20 statements on a 5-point Likert scale from "entirely disagreed" to "entirely agreed". Example statements are "I feel sad when I see people cry, " "I get carried away easily by the feelings of others, " and "I have a hard time grasping when my friends are happy." Reliability coefficients for the subscales ranged from $\alpha = 0.72–0.81$.

KMI Training Materials

During the training, participants watched a series of 75 unique video clips, each showing a penalty kick. The video clips show penalties that have taken place in actual matches and feature professional soccer players. Fragments were clipped from YouTube footage of penalty shoot-outs from European Champions League matches or from UEFA European Championship or FIFA World Championship tournament matches. Each clip was filmed from behind the penalty shooter, such that both the shooter, the goalkeeper, and the goal were in full view. The ball was at the 11-meters spot; the goalkeeper was at the goal-line. Each video clip lasted between 1.2 and 1.5 s and was shown twice in succession. Clips were separated by a black screen for 1 s. The duration of one block of clips was 10 min. Participants were instructed to imagine, as lively as possible, the bodily feeling of the movements of the goalkeeper (in the PB group) or of the penalty kicker (in the PK group) during each of the penalties. Informal pilot work had indicated that KMI was much facilitated by the immediate repetition of each fragment.

Procedure

The experiment took place in the labs of the University of Amsterdam. Groups of up to four participants were instructed together but performed the tasks in separate cubicles. After a brief general explanation they provided informed consent, and then were administered the penalty-reading task as a pre-test, which took about 15 min. Next, they received instructions for the KMI training, and then took two blocks of the training, separated by a few minutes rest. The training lasted for 21 min. They were then administered the penalty-reading task again, as a post-test, which again took about 15 min. Finally, they filled out the empathy questionnaire, followed by debriefing. The entire session lasted approximately 1 h.

Statistical Analysis

In the data obtained from the penalty-reading task, trials where participants gave no response at all were discarded from analysis (<1%).

Accuracy scores and average reaction times were analyzed (separately) using analysis of variance (ANOVA), with empathy scores as a covariate in a follow-up ANCOVA. Group was entered as a between-subjects variable (PB, PK) while Time was entered as a within-subjects variable (pre, post). Bayes Factors (BF) were calculated to assess how much more probable the observed data under H_0 was than under H_A.

Results

Two participants scored at chance level after training (23.3% and 26.7%), whereas all others scored (well) over 30%. Two other participants were excessively slow in responding (>1,500 ms), whereas all others scored 1,138 ms or below. These four participants (all from the PB group) were removed from the sample, although we verified that the results presented below were not influenced qualitatively by their removal.

Accuracy

Accuracy averaged 43.8%, which is well above chance level (25%), indicating that participants were reasonably well able to predict penalty direction from the video clips. Groups did not differ in penalty-reading accuracy ($F_{(1,49)} = 2.87$, $p = 0.097$, $\eta^2 = 0.055$, $BF = 1.006$). Accuracy improved slightly from pre- (43.5%) to post-training (44.0%) tests, but this effect was not statistically robust ($F_{(1,49)} = 0.23$, $p = 0.632$, $\eta^2 = 0.005$, $BF = 4.406$). Most important, the effect of training did not differ between training groups ($F_{(1,49)} = 0.02$, $p = 0.902$, $\eta^2 = 0.000$; the BF for the full model of both main effects and the interaction term equalled 14.624, signaling that the probability of these data was far higher under H_0 than under H_A). This interaction pattern did not change after partialing out covariance with empathy scores.

Response Speed

Response speed averaged 711 ms. Groups did not differ in penalty-reading speed ($F_{(1,49)} = 0.04$, $p = 0.835$, $\eta^2 = 0.001$, $BF = 2.024$). Reaction time improved from pre- (723 ms) to post-training (699 ms) tests, but this effect was not statistically robust ($F_{(1,49)} = 1.22$, $p = 0.274$, $\eta^2 = 0.024$, $BF = 2.908$). The effect of training id not differ between training groups ($F_{(1,49)} = 0.28$, $p = 0.596$, $\eta^2 = 0.006$; the BF for the full model of both main effects and the interaction term equalled 18.166, signaling that the probability of these data was far higher under H_0 than under H_A). Partialing out covariance with empathy id not alter this interaction pattern.

Discussion

Practicing in kinesthetic motor imagery of penalties failed to improve penalty-reading accuracy, in either the penalty-blocking or the penalty-kicking condition, thus disconfirming our predictions. Our KMI sessions appeared to lack the power to produce the improvements in penalty anticipation that we observed after practice in physical penalty kicking in Experiment 1. This finding falsifies part of the predictions derived from the IMPPACT theory: KMI of penalty kicking failed to strengthen and enrich the forward model of penalty kicking enough for the observer to improve in reading an opponent's penalty kick.

A number of observations may limit this straightforward falsification. First, the fact that practice in KMI of penalty *blocking* also failed to produce improvements may suggest that our KMI sessions were not successful in instilling *any* effects, at least in the present samples. A more successful implementation of KMI might still produce the expected effects; this remains to be tested. Second, and relatedly, the present sample consisted of novices with little experience in penalty kicking or blocking. Stronger effects might be obtained by testing goalkeepers, as in

Experiment 1. Note that both accuracy and response speed were considerably poorer among the novices in Experiment 2 than in the goalkeepers in Experiment 1. For instance, experienced players may have a more refined notion of what aspects of movement to imagine. Third, as noted before, sample sizes were relatively small, amplifying the risk of false negative findings. However, our finding was not a case of a sizable effect that failed to reach statistical robustness; rather, in the present samples the effect was just negligible.

The video clips used for KMI training showed the shooter from behind, whereas those used for the penalty-reading task showed the shooter from the front. This difference in viewpoint might limit the effect of training. Yet, we opted for this difference for two reasons. First, if the same point of view were used for both the imagery training and the penalty-reading task, then the two would become more visually similar, such that penalty-reading performance might benefit simply from rehearsing similar material rather than from practice in motor imagery. And second, for the motor-imagery training materials, the movements of both the goalkeeper and the shooter should be in full view, in order that the same clips can be used both for motor imagery of the goalkeeper and for imagery of the shooter; this is difficult to accomplish from behind the goal (and virtually no footage is available from that viewpoint).

Individuals may vary considerably in terms of the vividness of their KMI, both in general (as a dispositional trait) and in the present set-up (as a situational state). Possibly, for some individuals in the present experiment, the vividness of KMI was limited, which would also limit the chances of finding *any* effect of KMI practice. Future studies may incorporate instruments to measure KMI skills.

Vivid KMI may depend in part on prior actual (physical) experience with the skill being practiced (Ridderinkhof, 2014). Thus, perhaps KMI should build on physical training rather than being administered separately. A replication (with larger samples) might focus on *combining* physical and virtual training, and might compare novices to experienced goalkeepers to examine if and when KMI might contribute to performance beyond physical training.

The effects of KMI were not modulated by empathy, which is no surprise given the lack of effect of KMI. Potential relationships between KMI efficacy and empathy remain to be explored further.

The finding that practice in KMI of penalty-kicking and penalty-blocking did not improve penalty-reading skills does not exclude the possibility that KMI *is* used during penalty reading in the first place. This possibility was tested in a further experiment, described next.

EXPERIMENT 3: AN MVPA-BASED ANALYSIS OF PRE-PLAY IN READING PENALTY KICKS

Multi-variate pattern analysis (MVPA) of fMRI data is a technique that can quantify the difference between multivariate patterns of neural activity associated with different classes of cognitive, affective, or behavioral factors (Haxby, 2012). MVPA has become popular because of its sensitivity to slight differences in activity patterns that univariate techniques have more difficulty detecting (Haynes and Rees, 2006). In MVPA, a machine-learning classifier algorithm is trained on data from a subset of the experiment and then tested on the remaining subset of data. During training, the classifier is informed about the condition from which the test trials came, so that it can learn which patterns of activation across voxels distinguish the conditions. Learning is successful if classification performance transfers with greater-than-chance accuracy from the training set to the testing set. Thus, through its ability to "decode" information in the test set, MVPA constitutes a test of the difference between multivariate neural representations (Snoek et al., 2019).

An emerging trend in such machine-learning classifiers is cross-classification, which capitalizes on its power to provide evidence for *similarity* among neural patterns. When a classifier is trained on data from one cognitive task and tested on data from another, conclusions can be drawn about the role of specific clusters of voxels in the brain in cognitive processes that generalize across those two tasks (Kaplan et al., 2015). MVPA cross-classification (MVPA-CC) has proven useful in establishing correspondences among neural patterns across a variety of cognitive domains, including neural overlap between self-focused emotion imagery and other-focused emotion understanding (Oosterwijk et al., 2017) in our lab.

Here we apply MVPA-CC to the question whether the neural circuits engaged in KMI are also engaged in reading the body language of penalty-kicking. We will first train a classifier to discern, separately on half of each individual's data, the circuits unique to motor imagery from the circuits involved in attention to kinematic features of penalties (Note that such attentive viewing occurs in KMI as well; we are interested in the circuitry that *distinguishes* "pure" KMI circuitry from the more generic circuitry.). We then test the trained classifier on the remaining half the data per individual, to see if classification accuracy is above chance. Subsequently, we will use cross-classification to test if individuals use their motor imagery circuitry to successfully read penalty kicks and predict their direction. We hypothesize that successfully read penalties (in which direction was correctly anticipated) are associated with activation of voxels that were identified in the KMI task.

Methods

Participants

Participants were students at the University of Amsterdam who were rewarded €25 in return for their participation. All participants in the experiment reported no known medical or psychological problems, right-hand dominance, not taking medication, no psychiatric disorders or neurological history, and normal color or corrected-to-normal vision acuity, and no head injury. Exclusion criteria were general MRI contraindication (e.g., claustrophobia, metal implants, possible metal scraps), prior experience as a field player or goalkeeper in a regular soccer team, either anytime in the past 2 years, or for a total of more than 1 year in the farther past; or a self-reported history of neurological or psychiatric disorders. Our remaining sample consisted of 35 participants (19 females) ranging in age between 22 and 38 years. Participants provided informed consent before participation. All procedures were approved by the university ERB (nr. 2016-DP-7251), and complied with relevant laws and institutional guidelines.

Materials

The *penalty-kicking experience questionnaire* was identical to the one described under Experiment 1.

The *penalty-reading task* was identical to the one described under Experiment 1, with the exception of timing. Clips were separated by intervals of on average 5 s (2–8 s, jittered in steps of 0.1 s), with a break of on average 5.5 s (3–8 s, jittered in steps of 0.1 s) after every series of 3 clips. These mini-blocks of three jittered trials and a jittered break served to prevent saturation of the BOLD signal.

KMI Training Materials

Each video clip lasted between 1.2 and 1.5 s and was shown twice in succession. Clips were separated by a black screen for 1 s. The duration of one block of clips was 10 min. Participants were instructed to imagine, as lively as possible, the bodily feeling of the movements of the goalkeeper (in the PB group) or of the penalty kicker (in the PK group) during each of the penalties. Informal pilot work had indicated that KMI was much facilitated by the immediate repetition of each fragment.

The *video training materials* consisted of the same fragments as described under Experiment 2. Video clips lasted between 1.2 and 1.5 s and were separated by intervals of on average 5 s (2–8 s, jittered in steps of 0.1 s), with a break of on average 5.5 s (3–8 s, jittered in steps of 0.1 s) after every series of three clips. In between clips, rather than a black screen, the goal area was blurred (including the goalkeeper, the penalty kicker, and the advertisement billboard surrounding the goal). All video clips in a block of four mini-blocks were viewed under the same instructions, twice under "attention" instructions (ATT) and twice under "imagery" instructions (IMG) (as described under *Procedures* below). A brief cue indicating the task instruction ("ATTENTION" or "IMAGERY") was shown during 5 s, followed by the first clip after an interval of 5.5 s (3–8 s, jittered in steps of 0.1 s). The two instructions were given in AABB order to half of the participants, and in BBAA order for the other half, such that participant received two blocks of four mini-blocks each under one instruction, and then two blocks of four mini-blocks each under the other instruction.

Procedure

The experiment took place in the labs of the University of Amsterdam Spinoza Center for neuroimaging. All participants were supervised individually by experimenters outside and inside the scanner rooms. After a brief general explanation, they first filled out the standard MR-screening questionnaire and, if passed, they provided informed consent.

Penalty-Reading Task Outside the Scanner

Participants started the experiment by performing a practice session of the penalty-reading task, so they would be well prepared by the time they performed the same task inside the MR scanner.

Video-Training Outside the Scanner

Next, they started training with the video materials; half of them practiced first with the "attention" instructions and then with the "imagery" instructions' the other half took the reverse order.

The attention training worked as follows. The participant watched the clips from penalty kicks (from CL or WC tournaments) and was instructed to try and learn to anticipate the direction in which the penalty shooter would kick, by discovering which features of the shooter's movement are most predictive. They were instructed to attend to the length, angle, and speed of the run-up; the orientation of the torso, arms, and supporting leg during kicking; the degree and angle of moving the kicking leg, the orientation of the kicking foot, the side (inside or front) of the foot used for kicking, the side (lower or middle) of the ball where it is hit, and the like. They were asked to picture themselves being the goalkeeper, trying to "read" the shooter's aim: which of these aspects of the shooter's movements are best imagined in order to infer and predict the penalty direction?

The imagery training worked as follows. The participant again was instructed to try and learn to anticipate the direction in which the penalty shooter would kick, by imagining as vividly as possible what it feels like to take penalties in various directions, given the way the penalty shooter moves. They were instructed to imagine feeling the movement of their torso, arms, supporting leg, and kicking leg during the run-up and especially during kicking; to imagine feeling the strength and speed of the movement; and to imagine feeling their body posture, balance, muscle tension, adrenalin rush, breath, or heartrate. They were asked to picture themselves being the goalkeeper, trying to "read" the shooter's aim: which of these aspects are best attended to in order to infer and predict the penalty direction?

During either video training, incidentally (after every fourth mini-block) a text *"press a button to continue"* would appear, upon which they should push any button as fast as possible. This was a phony task, since other than that the participant did not have to actually do anything (other than stick to instructions); the phony response merely allowed us to verify that the participant was still attentive.

Imaging was conducted with a Phillips 3T Intera MR scanner using a 32-channel SENSE head coil at the Spinoza Centre for Neuroimaging at the Amsterdam University Medical Center. For anatomical referencing, a high-resolution 6-min T1-weighted structural scan was acquired first for each participant (T1 turbo field echo, TR 8.2 s, TE 3.8 ms, 220 slices, slice thickness 1 mm, voxel size 1 × 1 × 1 mm, FOV 240 × 188 mm, flip angle 8°). During the Video-training and penalty-reading tasks inside the scanner, the blood oxygen dependent (BOLD) signal was measured with a T2*single shot echo planar imaging (EPI) sequence (TR 2.0 s, TE 27.6 ms, 37 slices, slice thickness 3 mm, voxel size 3 × 3 × 3 mm, interslice gap 0.3 mm, FOV 240 × 121 mm, flip angle 76.1°).

After the participant was positioned in the MR scanner, an anatomical scan of 10 min was taken.

Penalty-Reading Task and Video-Training Inside the Scanner

The video training and penalty-reading task were performed as described under *Materials*. Participants were asked explicitly not to move during the session, other than when asked to respond, and then only with the muscles pertinent to that response. Responses were issued by pressing the left and right index and middle finger to indicate the left and right bottom or upper corner respectively on hand-held scanner-compatible button-boxes.

Data Analysis

MRI Preprocessing

Results included in this manuscript come from preprocessing performed using *FMRIPREP* version 0.6.2 (Esteban et al., 2019), a *Nipype* (Gorgolewski et al., 2011) based tool. Each T1-weighted volume was corrected for bias field using *N4BiasFieldCorrection* v2.1.0 (Tustison et al., 2010) and skullstripped using *antsBrainExtraction.sh* v2.1.0 (using the OASIS template). The skullstripped T1-weighted volume was co-registered to skullstripped ICBM 152 Nonlinear Asymmetrical template version 2009c (Fonov et al., 2009) using nonlinear transformation implemented in *ANTs* v2.1.0 (Avants et al., 2008).

Functional data were motion-corrected using *MCFLIRT* v5.0.9 (Jenkinson et al., 2002). This was followed by co-registration to the corresponding T1-weighted volume using boundary-based registration 9 degrees of freedom—implemented in FSL (Greve and Fischl, 2009). Motion correcting transformations, T1 weighted transformation, and MNI template warp were applied in a single step using *antsApplyTransformations* v2.1.0 with Lanczos interpolation. The time series were subsequently high-pass filtered using FSL with a threshold of 100 s and each volume was spatially smoothed using FSL with an FWHM of 5 mm.

Three tissue classes were extracted from T1-weighted images using *FSL FAST* v5.0.9 (Zhang et al., 2001). Voxels from cerebrospinal fluid and white matter were used to create a mask which in turn is used to extract physiological noise regressors using aCompCor (Behzadi et al., 2007). Mask was eroded and limited to subcortical regions; to limit overlap with gray matter, six principal components were estimated. Frame-wise displacement (Power et al., 2014) was calculated for each functional run using Nipype implementation. For more details of the pipeline see https://fmriprep.readthedocs.io/en/0.6.2/workflows.html.

First-level (participant-specific) single-trial models were estimated using *FSL FEAT* (Woolrich et al., 2001). Each model contained separate predictors for each trial (lasting for the duration of the video) convolved with a double-gamma HRF, as well as time series from the six motion realignment parameters and a single global signal (i.e., average time series across all voxels) time series. The resulting whole-brain z-statistic maps of all trials (i.e., 60 per run) were subsequently used in the MVPA analyses.

Model Training

For each participant, a support-vector classifier with a linear kernel and default hyperparameters as implemented in the Python package *scikit-learn* (Pedregosa et al., 2011) was iteratively trained on 90% of the trials to distinguish the task condition: either attention (ATT) or imagery (IMG). The classifier was then evaluated on the remaining 10% of the ATT and IMG trials (i.e., 10-fold cross-validation). Because the data was balanced in terms of class frequency, model performance was summarized as the average accuracy across 10 folds. This average accuracy was statistically tested against chance level (i.e., an accuracy of 50%) using a permutation analysis (Ojala and Garriga, 2010) with 1,000 iterations in which the classifier was trained and evaluated on shuffled target labels.

Importantly, because the voxel time series may still contain low-frequency drift, trials from the same task may be temporally correlated, violating the independence assumption of cross-validation and thus likely yielding inflated accuracy scores. This issue is, notably, not present in the cross-classification analysis, because the trials from the two tasks (ATT/IMG and penalty-reading) are in fact independent.

To visualize the voxels that are most important in the classification analysis, we averaged (across folds) the classifier weights for each participant and computed for each voxel a two-sample t-test (against a population value of 0) of the fold-average classification weights across participants.

Model Cross-Classification

For the cross-classification analysis, we evaluated the classifier (as specified in the previous section) trained on the ATT and IMG trials on the trials from the penalty-reading task, again for each participant separately. Thus, each trial in the penalty-reading task was classified as either ATT or IMG. See **Figure 3** for a visualization of the training and cross-classification procedure.

We then computed, per participant, the proportion of ATT and IMG predictions for the "blocked" (i.e., accurately anticipated) trials from the penalty-reading task. This is equivalent to the classifier's *recall* score when the correctly anticipated trials are regarded as the positive class. If the engagement of the motor imagery circuitry would contribute to successfully blocking a penalty, we would expect a relatively high proportion (i.e., >50%) of IMG predictions for these trials. Similar, to the permutation analysis described in the previous section, we ran a permutation analysis for the cross-classification models by training the models, for each participant separately, on shuffled target labels and evaluating them again on the trials from the penalty-reading task. Finally, statistical significance on the group-level statistics was computed using a two-sample t-test against 50% (chance level) of the proportion of IMG predictions for the successfully blocked penalty trials across participants.

Results

Training Task

The classifier was able to correctly classify the trials from the training task significantly above chance-level (i.e., 50%) for all participants ($p < 0.001$), with an average (across participants) accuracy score of 94% (*SD*: 0.045). However, as discussed previously, the magnitude of the results is likely inflated due to a likely violation of independence across trials from the same condition. Regardless, the spatial pattern of classifier weights (see **Figure 4**) show to-be expected regions associated with the attention condition (primarily occipital and parietal cortex) and the motor imagery condition (such as the supplementary motor complex, the caudate nucleus, and the cerebellum).

Penalty-Reading Task

The participant-specific analyses showed that the proportion of IMG predictions for the correctly anticipated trials was significantly higher than chance in twenty out of the total number of 35 participants (i.e., 57%; see also **Supplementary Figure 1**). At the group-level, in line with our expectations, the proportion of successfully blocked trials predicted as motor imagery was, on average across participants, 62.2% (*SD*: 0.246), which was significantly above chance ($t_{(34)}$ = 2.925, $p = 0.006$).

Discussion

Using MVPA, a classifier was trained to discern the circuits unique to motor imagery from the circuits involved in attention to kinematic features of penalties. When applied to the untrained subset of the data, the classifier correctly categorized the trials as belonging to the imagery or attention instructions at high accuracy. We then employed MVPA-CC and observed that individuals use their motor imagery circuitry in roughly two-thirds of all successfully read penalty kicks, which was significantly above chance. The predictive clusters in the motor-imagery circuitry corresponded roughly to at least some of the regions of the motor-imagery network depicted in **Figure 1** (e.g., the supplementary motor complex, the caudate nucleus, and the cerebellum). Thus, we established that KMI is used (at least part of the time) to successfully anticipate the direction of the opponent's penalty kick. Consistent with the predictions derived from IMPPACT, we conclude that pre-play in the form of KMI is used in reading other people's body language to infer their action intention. By inference, we assume that reading others' action intentions invokes "inverse modeling", which requires the presence of a forward model that can be enriched using KMI.

A number of factors may potentially limit the straightforwardness of these conclusions. First, despite instructions and design features, we can't know what participants are actually doing when viewing the training fragments. For instance, it may be possible that they distribute attention across all possible kinematic parameters in the attention condition, whereas they focused specifically on one parameter (such as the orientation of the supporting leg) in the KMI condition. Although such scenarios cannot be excluded, they seem unlikely, as (in this example) there should be a specific neural circuitry that is engaged specifically in focusing on the kinematic parameter of the orientation of the supporting leg, substantially more than on all other kinematic parameters together. While not impossible, we are not aware of data implying such specific sensitivity to specific motion parameters.

Second, there is no real way of knowing whether the participants actually moved muscles during motor imagery while keeping their heads still. If so, the neural activity related to the muscle contractions might be what the pattern classifier picked up on; in fact, this may have contributed to the relatively high accuracy of classification. However, this would not likely explain the successful cross-classification unless participants contracted the exact same muscles during the video training and the penalty anticipation task.

Third, in recent years we have seen a rapid increase in the preferred number of participants in fMRI research. While 35 was considered adequate when we initiated this study, this number may already be on the small side compared to present standards. Thus, it will be useful to try and replicate this study with a larger sample.

Forth, the design for the fMRI study in Experiment 3 was constructed such that the attention and imagery trials were grouped in separate fMRI runs. As mentioned, this design most likely induced temporal correlations across single trials within a particular condition, increasing their neural pattern similarity. This in turn might incur dependence across trials, which likely inflated accuracy scores for the model performance. To avoid this issue, future research should make sure that trials (or, equivalently, trial blocks) from different conditions are properly randomized across fMRI acquisition runs (for details, see Mumford et al., 2014). However, because the training and test task (i.e., the penalty-reading task) were independent, this issue of temporal correlations across trials is not applicable to the cross-classification analysis.

Notwithstanding these minor limitations, we believe that the current findings constitute reasonably strong evidence in favor of the notion that pre-play is used in reading other people's body language to infer their action intention. The present demonstration further underlines the notion that MVPA and especially cross-classification comprises a sensitive tool to uncover the hidden mechanisms underlying complex cognitive processes represented in distributed cortical networks.

GENERAL DISCUSSION

Key to the coordination of our actions with those of others is the ability to "read" the actions of others and the intentions behind them. Based on predictive processing theory, we hypothesized that in order to read someone else's action intention, one needs to have a rich kinesthetic experience with that action oneself. We applied this conjecture to the special case of penalty-reading. In a series of studies, we tested the nontrivial prediction that penalty-reading performance in soccer

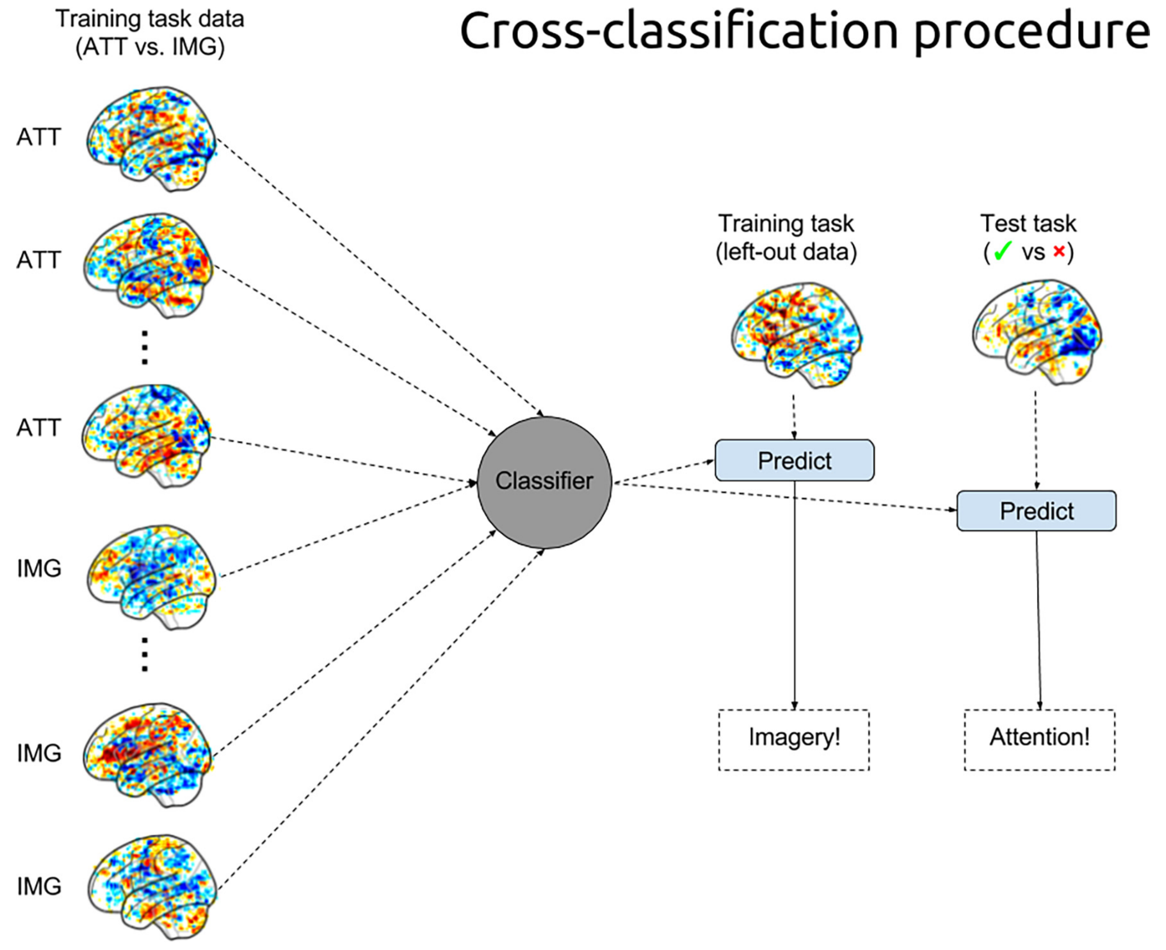

FIGURE 3 | MVPA training and cross-classification procedures. The pattern classifier was trained on 90% of the data of each participant in the training task to distinguish attention (ATT) trials from imagery (IMG) trials and was used to predict (and evaluate) the remaining trials from the training task as well as to predict the trials from the test task (i.e., the cross-classification of the penalty-reading task).

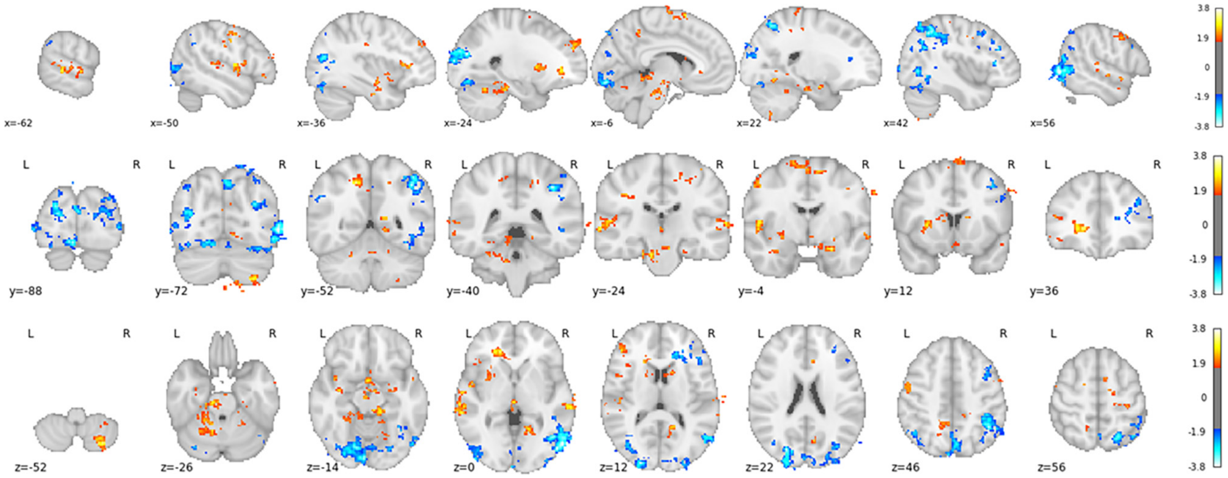

FIGURE 4 | T-value map of classifier weights, computed using a one-sample *t*-test against 0, thresholded at $t > 1.7$ and only showing clusters with more than 200 voxels. Clusters in yellow/red and blue are associated with imagery and attention predictions, respectively.

improves after practicing the kinematics and/or kinesthetics of penalty-*kicking*.

Summary of Findings

In Experiment 1, we developed a direct test of the hypothesis that the more kinesthetic experience a goalkeeper has in penalty-*kicking*, the more effectively s/he can predict the shooter's aim, thus improving her/his chances to prevent the shooter from scoring a goal. We observed that not only practicing in penalty-blocking but also practice in penalty-kicking improved penalty-reading accuracy, which cannot be explained by experiencing penalty-blocking situations *per se*. Future studies might include players that differ in level and years of experience to see if these moderate the observed effects.

In Experiment 2, we examined whether similar benefits can be obtained by motor imagery, that is, by vividly mimicking and experiencing the shooter's movement in one's mind. As it turned out, practicing kinesthetic motor imagery of penalties failed to improve penalty-reading accuracy, in either the penalty-blocking or the penalty-kicking condition, thus disconfirming our predictions. KMI of penalty kicking apparently failed to strengthen and enrich the forward model of penalty kicking enough for the observer to improve in reading an opponent's penalty kick. A number of observations urged for caution in accepting this falsification as conclusive, however. First, our implementation of KMI might not have been sufficiently powerful; the fact that practice in KMI of penalty *blocking* also failed to produce improvements may suggest that our KMI sessions were not successful in instilling *any* effects, at least in the present samples. Possibly, for some individuals in the present experiment, the vividness of KMI was limited, which would also limit the chances of finding *any* effect of KMI practice. Second, both accuracy and response speed were considerably poorer among the novice participants with little experience in penalty kicking or blocking in Experiment 2 than in the experienced goalkeepers in Experiment 1. Stronger effects might be obtained by testing the KMI experiment with goalkeepers. Finally, perhaps KMI should build on physical training rather than being administered separately. A replication (with larger samples) might focus on combining physical and virtual training to examine if and when KMI might contribute to performance beyond physical training.

The finding that practice in KMI of penalty-kicking and penalty-blocking did not improve penalty-reading skilsl does not exclude the possibility that KMI *is* used during penalty reading in the first place. This possibility was tested in Experiment 3, in which we trained a machine-learning pattern classifier on fMRI data to test (using MVPA-cross-classification) whether motor-imagery brain networks are engaged in successful penalty reading. We observed that individuals use their motor imagery circuitry in roughly two-thirds of all successfully "read" penalty kicks. Thus, KMI was used (at least part of the time) to successfully anticipate the direction of the opponent's penalty kick. Although the fMRI design likely induced temporal correlations across single trials within a particular condition, which may have inflated accuracy scores for the model performance, this issue of temporal correlations across trials is not applicable to the cross-classification analysis, since the training and test task (i.e., the penalty-reading task) were independent. The findings suggest that pre-play is used in reading other people's body language to infer their action intention.

Implications

The results from Experiment 1 revealed that, after merely 20 min of training, practice in penalty-kicking improved the accuracy of penalty-reading by 4.5%. Given that professional goalkeepers in the German *Bundesliga* block 18.8% of all penalty kicks (Dohmen, 2008), an increase of 4.5% would be massive, and may well imply the difference between winning and losing a match (or a tournament, for that matter). Although the goalkeepers tested in this experiment were experienced high-level amateurs, it remains to be established, of course, whether the improvements extend beyond the experimental setting and if professionals in national soccer competitions also benefit as much. Yet, this is a most encouraging result, opening the stage for expanding goalkeeper training strategies to increased experience in penalty-kicking. Responding after the penalty ball has been hit leaves the goalkeeper with too little time to arrive before the ball crosses the goal line (Glencross and Cibich, 1977; Chiappori et al., 2002); reading the shooter's movements during the run-up and during the kick may give the goalkeeper a head-start and an increase in their probability of blocking the penalty.

Improved performance by attempting to "read" the penalty through an assessment of the shooter's kinematic body and movement parameters is consistent with the predictions derived from IMPPACT (Ridderinkhof, 2014) that build on the notion of forward modeling, which is key to modern theories of active inference and predictive processing (e.g., Wolpert et al., 2003; Friston et al., 2011; Clark, 2013). Note that the central notion of deciphering others' action intentions was formulated already 100 years ago by Edward Kempf: "*understanding the behavior of others — that is, by miniature tonal forms of reflex reproduction of the movements of others — the proprioceptors, giving the appropriate kinesthetic sensations, enable the personality to become aware of the significance of the posture and movements or behavior of others*" (Kempf, 1921, p.22). This skill of "reading" action intentions is of obvious evolutionary-adaptive value to social animals: in fighting, courting, and all kinds of joint and complementary action, animals need to be able to read other animals' body language. The goalkeeper needs to infer, based on observations of the kicker's run-up and shooting kinematics, the orientation of the supporting leg, etc., the intention of the shooter (which angle will s/he take), and then act accordingly (cf. Kilner et al., 2007; Ridderinkhof, 2017). The present results are consistent with the novel hypothesis that for goalkeepers to read the body language of penalty kicks, they should be experts in kicking penalties themselves. The more experience a goalkeeper has in penalty-kicking, the more effectively s/he can inverse model and predict the shooter's aim, thus improving her/his chances to prevent the shooter from scoring a goal.

The present data did not support the notion, building on the above conjecture, that kinesthetic motor imagery of penalty-kicking might suffice to bring about an improvement in penalty-reading. Neural activation observed during KMI has been found to display a reasonable correspondence with activation during the preparatory planning phase that precedes movement (Jeannerod, 2006), but also goes beyond mere preparatory planning, as demonstrated by the finding that KMI engendered activation in the contralateral primary motor cortex just as actual movements did (Stinear et al., 2006). Still, our instantiation of KMI lacked the power to induce a training benefit, at least in novices. Combining physical and KMI practice may perhaps result in more optimal benefits.

Although practice in KMI of penalty-kicking was not found to help improve penalty-reading skills, this does not imply that KMI is not used at all during penalty reading in the first place. Based on an MVPA-cross-classification procedure, we could demonstrate that in fact pre-play in the form of KMI was used (at least part of the time) for reading the opponent's body language to infer their action intention and successfully anticipate the direction of the opponent's penalty kick. By inference, we may speculate that reading others' action intentions invokes inversing the forward model, which requires the presence of a rich forward model in the first place.

In Conclusion

The key to action control is one's ability to adequately predict the consequences of one's actions. Reading another's action intentions requires a rich forward model of that agent's action; we showed that goalkeepers who had extensive prior experience in penalty blocking but not in penalty kicking can enrich their forward model of penalty kicking and use that to predict the direction of an imminent penalty kick. MVPA-cross-classification showed that 2/3 of all correctly read penalty kicks were classified as specifically engaging the circuitry involved in motor imagery of penalty kicking. In sum, this study provides initial evidence that it takes practice as a penalty kicker to become a penalty killer.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Ethics Review Board of the University of Amsterdam, Faculty of Societal and Behavioral Sciences. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

KR and AC performed the experiments. KR performed the data analysis of experiments 1 and 2. LS performed the data analysis of experiment 3. JC and AC developed scanning procedures for experiment 3. GS and AC prepared the video materials for the penalty-reading task. KR, LS, JC, GS, and AC wrote the text of the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIALS

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/103389/fnhum.2021.789817/full#supplementary-material.

SUPPLEMENTARY FIGURE 1 | Observed scores (red vertical line) and distribution of permuted scores (blue histogram) for each participant-specific IMG/ATT model cross-validated to the trials from the penalty-reading task. Scores (x-axis) represent the proportion of correctly anticipated trials predicted as IMG (or, equivalently, the *recall* score).

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Inhibitory Control and the Structural Parcelation of the Right Inferior Frontal Gyrus

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The right inferior frontal gyrus (rIFG) has most strongly, although not exclusively, been associated with response inhibition, not least based on covariations of behavioral performance measures and local gray matter characteristics. However, the white matter microstructure of the rIFG as well as its connectivity has been less in focus, especially when it comes to the consideration of potential subdivisions within this area. The present study reconstructed the structural connections of the three main subregions of the rIFG (i.e., pars opercularis, pars triangularis, and pars orbitalis) using diffusion tensor imaging, and further assessed their associations with behavioral measures of inhibitory control. The results revealed a marked heterogeneity of the three subregions with respect to the pattern and extent of their connections, with the pars orbitalis showing the most widespread inter-regional connectivity, while the pars opercularis showed the lowest number of interconnected regions. When relating behavioral performance measures of a stop signal task to brain structure, the data indicated an association between the dorsal opercular connectivity and the go reaction time and the stopping accuracy.

Keywords: structural parcelation, right inferior frontal gyrus, inhibitory control, response execution, response inhibition

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INTRODUCTION

The right inferior frontal gyrus (rIFG) is considered a key node for the inhibition of premature or no longer appropriate motor responses, which is one of the core aspects of behavioral flexibility and control (Swann et al., 2012; Aron et al., 2014, 2016). The IFG represents a structurally diverse area in the prefrontal cortex that usually is divided into three sub-regions based on its cytoarchitecture: the pars opercularis, pars triangularis, and pars orbitalis. Given that variability in the structural architecture of the brain often relates to specific aspects of behavior (Johansen-Berg, 2010), it is likely that the rIFG exhibits a richer functional diversity than often posited. A recent meta-analysis identified different functional clusters of the rIFG to be involved in distinct large-scale networks; only the posterior part (roughly corresponding to the pars opercularis) seemed to be involved in motor control, and was further divided into dorsal and ventral regions associated with response initiation and general inhibition, respectively (Hartwigsen et al., 2019). However, a structural connectivity map of rIFG subregions that would support this functional parcelation is lacking.

The rIFG has been suggested to be part of a right-lateralized fronto-basal ganglia network (Chambers et al., 2009; Jahanshahi et al., 2015), that instantiates inhibition of the motor cortex jointly with the pre-supplementary motor area (preSMA), the basal ganglia, and thalamic nuclei (Aron et al., 2014). Structural and functional connections have been established between the IFG, the preSMA (Swann et al., 2012), subthalamic nucleus (STN), and striatum (Isaacs et al., 2018). While the specific roles of the rIFG and the preSMA for response inhibition are not fully understood, increased fractional anisotropy (FA) in the pars opercularis has been negatively associated with inhibitory performance in a stopping task (i.e., shorter stop signal reaction times), while the reverse association has been reported for the preSMA (Xu et al., 2016). However, the relationship between rIFG and preSMA during inhibitory control is still unclear. It is therefore of fundamental importance to map the structural architecture of those regions that facilitate stopping of behavior in order to fully understand the functionality of the stopping network.

The stop signal task (SST) is one of the most widely used paradigms to study response inhibition, and is often considered the most direct measure of reactive inhibition (van Belle et al., 2014), due to the possibility of calculating the stop signal reaction time (Logan et al., 1984). Yet, the SST additionally provides behavioral measures related to motor preparation under cognitive control, such as the trade-off between fast responding and accurate stopping, captured complementarily by the go reaction times (goRTs) and the stopping accuracy. This is important, because functional studies show that different rIFG subregions are involved in motor initiation as well as proactive and reactive inhibition (Hartwigsen et al., 2019; Messel et al., 2019). However, the interpretation of goRTs produced under the SST as task-general marker of motor preparation has been challenged. For instance, SST goRTs have been found to slow down with increasing probability of a stop signal (Zandbelt and Vink, 2010), which has been taken as evidence for a braking mechanism that proactively restrains responses (proactive inhibitory control) (Zandbelt and Vink, 2010; Albares et al., 2014). Thus, motor initiation in the SST seems to be influenced by other cognitive mechanisms, such as strategic slowing in order to balance performance speed and accuracy (Leotti and Wager, 2010). Correspondingly, it has been found that activations associated with go responses in the SST overlap with those related to outright stopping (e.g., the preSMA and striatum, Forstmann et al., 2008). It has also been reported that the IFG and preSMA are involved during unconsciously initiated response slowing in tasks other than the SST (van Gaal et al., 2010).

Contrasting the SST with a response choice task represents the ideal tool to study the associations of rIFG subdivisions with respect to their potential involvement in response generation and inhibition. We therefore investigated the associations of rIFG subregions with response initiation (responding without stopping constraints in a pure response choice task), response initiation under proactive inhibitory control (goRT in SST), as well as response inhibition under reactive inhibitory control (stop signal reaction time and accuracy in the SST).

The primary aim of the present study was to map the structural connections of the three subregions of the rIFG: the pars opercularis, pars triangularis and pars orbitalis. Further, we extended the abovementioned literature by investigating the white matter fiber pathways connecting the dorsal and ventral region of the pars opercularis to regions critical for motor control. We expected that the dorsal and ventral connections would show differential functional associations such that connections from the dorsal part would be associated with response initiation irrespective of the task context (that is, we expect associations with the go reaction times both in the response task and in the SST), while those of the ventral part would show associations with measures of response inhibition (i.e., stop signal reaction time).

MATERIALS AND METHODS

Participants

Thirty-one participants took part in the experiment (14 females, mean age = 26.35, range = 20–36 years). One participant was excluded from behavioral and connectivity analyses due to technical issues that caused partial data loss. Five participants were excluded from the behavioral analyses: two participants were excluded due to technical issues with the response device, two more did not complete the behavioral tasks, and one participant was excluded due to an interruption in the middle of the experiment, leading to non-convergence of the stop signal delays (SSD). This resulted in 30 participants for the structural connectivity analyses and 25 participants for the analysis of brain-behavior associations. All participants were right-handed, had normal or corrected to normal vision and reported no history of psychiatric or neurological disorders, migraine, or loss of consciousness. The experiment was approved by the internal review board of the Department of Psychology, University of Oslo. All participants gave informed consent and received a gift card of 300 NOK for participation.

Image Acquisition

All magnetic resonance imaging (MRI) sequences were run on a 3.0 Tesla Philips Ingenia whole-body scanner (Philips Medical Systems, Best, Netherlands) with a 32-channel head coil. Diffusion-weighted imaging (DWI) was performed using a single-shot EPI sequence, one b0 image, and diffusion weighting was conducted across 32 non-collinear directions with a b-value = 1000 s/mm^2, flip angle = 90°, repetition time (TR) = 13.45 s, echo time (TE) = 62 ms, field of view (FOV) = 224 × 224 × 120, Matrix = 96 × 94 × 60. The acquired voxels of size 2.33 mm × 2.38 mm × 2.0 mm were reconstructed to 2.0 mm isotropic voxels. T1 images were acquired using the following parameters: TE = 2.3, TR = 5.1, FOV = 256 × 256 × 184, Matrix = 256 × 254 × 184, voxel size = 1.0 mm × 1.0 mm × 1.0 mm.

Data Processing

All processing and transformation steps were conducted in ExploreDTI v.4.8.6 (Leemans et al., 2009). All images were inspected for artifacts and excessive head movements, corrected for eddy current-induced distortions and head motions with a non-diffusion weighted image as reference. Plugin options for artifact correction in ExploreDTI were used, including one for EPI correction (Leemans and Jones, 2009; Irfanoglu et al., 2012). Specifically, as part of the initial quality assessment, all diffusion-weighted images were loaded to ExploreDTI and looped for each subject using the "loop" function in the "QA DWIs" tool. For the automatic processing steps, we utilized each participant's high-resolution T1-weighted image to cope with distortions induced during DWI. Here, all corrections were included in one interpolation step (i.e., subject motion and echo current induced distortions), in which the T1 image was used to unwarp deformations. To further improve the correction procedure, the registration was constrained along the phase encoding direction. Tensor estimation was performed using a linear estimation approach, which is the default estimation approach in the ExploreDTI toolbox (Tax et al., 2015). Finally, the diffusion weighted images were aligned with the T1 image, and correspondingly resampled to 1mm isotropic voxels, and overlayed with the T1 image for final inspection of the outputs (see **Supplementary Figure 1** for sample participant).

Brain Atlas and Tractography

A standardized brain atlas consisting of the Automated Anatomical Labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002) and a bilateral binarized mask of the STN (Forstmann et al., 2012) were used to outline 92 brain regions across both hemispheres. The AAL atlas does not separate the preSMA and SMA proper region, and there are short frontal tracts that connects the IFG to both the preSMA and SMA proper region (Catani et al., 2012), without a clear separation between the two regions. Thus, we further used the AAL region for the SMA to increase the reliability of the tracts across participants to prevent the possibility for the same tract ending in the preSMA region in some participant, while in the SMA proper in other participants (potentially at the expense of decreased regional specificity of the connections). Here, the preSMA and SMA proper will collectively make up a region that will be referred to as SMA complex (SMAc). Further, a whole brain deterministic tractography with every voxel as seed point was completed with the following parameters: seed point resolution = 1 mm isotropic and angle threshold = 45°, FA threshold = 0.2, fiber length range = 50–500 mm, step size = 1. The "From atlas template/labels" tool in ExploreDTI was used to register an atlas template to the corrected data for each participant, which resulted in 92*92 connectivity matrices for every participant. From these connectivity matrices, the passing and ending tracts of the three subregions of the rIFG were extracted. An ending connection was determined between two regions if the reconstructed fiber pathway originated in one of the regions and terminated in the other (i.e., the "END" option in ExploreDTI). A connection was deemed a passing pathway if the reconstructed tract passed through the regions (i.e., the "PASS" option in ExploreDTI). We reran the same procedure after parcelating the pars opercularis into a dorsal and ventral region based on a halfway split along its longest extent. Specifically, a new connectivity matrix was created including the parcelated dorsal and ventral pars opercularis, as well as the regions of interest that had previously shown reconstructed connections with the right pars opercularis. Then, we extracted the connectivity profile seeding from the dorsal and ventral part of the pars opercularis, respectively. It is important to note that the results derived from the connectivity matrices should not be interpretated as true measure of fiber pathways in the brain, but are reconstructed streamlines from the deterministic tractography procedure (henceforth referred to as reconstructed connections).

Tasks and Procedure

All participants were measured on two separate days (with a median interval of 1 day). Session one consisted of three MRI sequences, including a T1, DWI and resting-state fMRI measurement. Session two consisted of a concurrent measurement of electroencephalography (EEG), single-pulse transcranial magnetic stimulation (TMS), and electromyography (EMG) during two separate computer-based experiments: the delayed response task (DRT) and the stop signal task (SST). As this study focused on the associations of white-matter structure with behavior, the acquired EEG, EMG, and TMS data will not further be regarded here.

The experimental tasks were developed as in-house MATLAB scripts (The MathWorks, Inc., Massachusetts, United States) using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007). Participants sat in a chair at a viewing distance of 1 m from the monitor and responded on separate response devices with their left and right index fingers. The screen resolution was 1280*1024 with a refresh rate of 60 Hz. The experimental tasks consisted of a cued DRT of 3 blocks and a cued SST of 12 blocks. Each block took approximately 6 min to complete with the possibility to take breaks of self-determined durations in-between each block and task (total time = 92,4 min + pauses). Trials containing TMS pulses were excluded from the analyses. The DRT data consisted of 96 non-TMS pulse trials with 72 go-trials and 24 catch trials, while the SST consisted of 432 non-TMS pulse trials with 288 go-trials and 144 stop trials. The go and stop stimuli were presented as circles colored either blue or orange. The colors of the stimuli were counterbalanced for the go and stop signal; the color of the go signal remained the same for the DRT and SST throughout the experiment.

The cued DRT started with a fixation cross randomly jittered between 1,800 and 2,300 ms. After this, a cue (i.e., a right or left leaning bracket) was presented that indicated which finger to prepare for a response (e.g., right leaning bracket = right index finger). The inclusion of these valid cues eliminated the decision making phase after the detection of the go signal (as the decision about which hand to use is shifted to the cue-delay period), and thus allows for the investigation of response initiation without confounding response conflict. The cue duration was fixed at 900 ms. The go signal (a circle next to the bracket) appeared after the cue and was present for 800 ms or until a response was made. A go signal was omitted in 9% of the trials to diminish premature responding. The SST was similar in all aspects of the task but two: (i) the inclusion of a stop signal in a minority of the trials, and (ii) that no go signals were omitted. Stop signals appeared in 33% of the trials and were presented after a stop signal delay (SSD) that was adjusted following a tracking procedure. The SSD was initially set to 250 ms for both hands and was subsequently adjusted based on the performance in the preceding trial. The SSD was increased by 33 ms if the previous stop signal trial was successful, and decreased by 33 ms after unsuccessful stop trials. The minimum and maximum SSD were set to 80 and 800 ms, respectively. All stimuli included in the tasks were visual, including the stop signal in the SST.

Instructions

For the DRT, participants were told to respond as fast as possible to the circle appearing next to the cue. For the SST, the participants were told that the task was similar to the DRT, but that a stop signal would be shown on a minority of the trials to which they should try to withhold their response. They were further instructed to be as fast and accurate as possible and that mistakes were to be expected during the task. In go trials, feedback ("too late") was presented if no response was produced within 800 ms after the go signal. The participants were also shown feedback after each block. If the average goRT of the preceding block was above 600 ms, the participants were instructed to be faster. However, if the average accuracy was below 45%, they were instructed to be more accurate. If the participants' performance was within these thresholds, they were presented with the feedback "Well done."

Derivation of Dependent Variables and Statistical Analyses

To quantify white matter microstructure, we extracted the FA values of the tracts of interest from the whole brain tractography analyses. Further, the average FA across the brain for each participant was derived by calculating the mean value of the FA for all passing and ending tracts across the brain and averaging these into a single global FA value. Specifically, this was derived from the FA values across the reconstructed connections corresponding to the 92*92 connectivity matrices (only cortical and subcortical regions as per the AAL atlas described above). Two regions were deemed connected if it showed any number of streamlines between the two regions. To test if the rIFG subregions differed in their number of binary connections to other brain regions, we ran paired *t*-tests between the total number of binary connections each subregion exhibited for each participant. Here, we define the number of interconnected regions as node degree, or more specifically the out-degree (the number of out-going edges or connections, differentiating for passing and terminating tracts) Thus, the paired *t*-tests include the node degree for each of the three rIFG subregions to test differences between the number of interconnected regions. Note that this was derived from a connectivity matrix that only included real value entries if a tract was identified during tractography with the parameters outlined above, with zeros for the regions for which tracts could not be identified. This allowed us to quantify the number of cortical regions that were connected to each rIFG subregion by simply counting the non-zero entries for each participant. As false positives and false negatives could influence reconstructed brain networks (de Reus and van den Heuvel, 2013), we also confirmed the results from the paired *t*-test after using a group detection threshold (i.e., only including the binary connections that were present in at least 80% of the individuals). The results from the paired *t*-tests using the 80% detection threshold can be found in **Supplementary Note 2**.

The following behavioral measures were extracted from the DRT and SST: Go-accuracy, goRT, probability of choice errors, omissions, and premature responses (responses given after the cue, but before go signal onset). For the SST, we also calculated the stopping accuracy, unsuccessful stop RT, stop signal delay, and stop signal reaction time (SSRT). The SSRTs were estimated based on the integration method (Verbruggen and Logan, 2009). Specifically, the goRT distribution for each participant was extracted that included premature responses and go errors, and the omissions were replaced by the maximum go RT (Verbruggen et al., 2019). The SSRT was calculated by subtracting the mean SSD from the n_{th} value in the sorted goRT distribution, where n corresponds to the probability of responding in the stop trials multiplied with the number of values in the go RT distribution. All behavioral measures are reported as an average of both hands. The association between the goRT and SSRT in the SST was calculated as a parametric bivariate correlation. All statistical analyses assessing behavioral and brain-behavior associations were carried out with IBM SPSS Statistics for Windows, Version 25.0.

Brain-Behavior Analyses

The goRT, SSRT, and stopping accuracy were used as dependent variables, and the global FA and parameters of the tracts from the dorsal and ventral part of the pars opercularis and to the target region SMAc were used as predictor variables in the regression analyses. First, the global FA may be associated with general cognitive ability, thus we expected correlations with all of the behavioral measures (i.e., DRT and SST goRT, SSRT, and stopping accuracy). For this reason, the global FA was also included in the regression analyses to account for global inter-individual differences in white matter microstructure of the brain. We specifically focused on the pars opercularis as it has been considered the key node of inhibitory control (Aron et al., 2014; Hartwigsen et al., 2019). For visualizations and brain-behavior analyses, we used tracts that were present in at least 80% of the participants for generalizability and reliability.

RESULTS

Structural Connectivity Maps of the Three Right Inferior Frontal Gyrus Subregions

The structural connections of the rIFG sub-regions are visualized in **Figure 1**, and the mean node degree of passing and ending tracts for each subregion is depicted in **Figure 2**. In total, the three subregions showed extensive inter-regional connectivity that covered all four lobes in the right hemisphere, as well as several structures within the basal ganglia. The pars

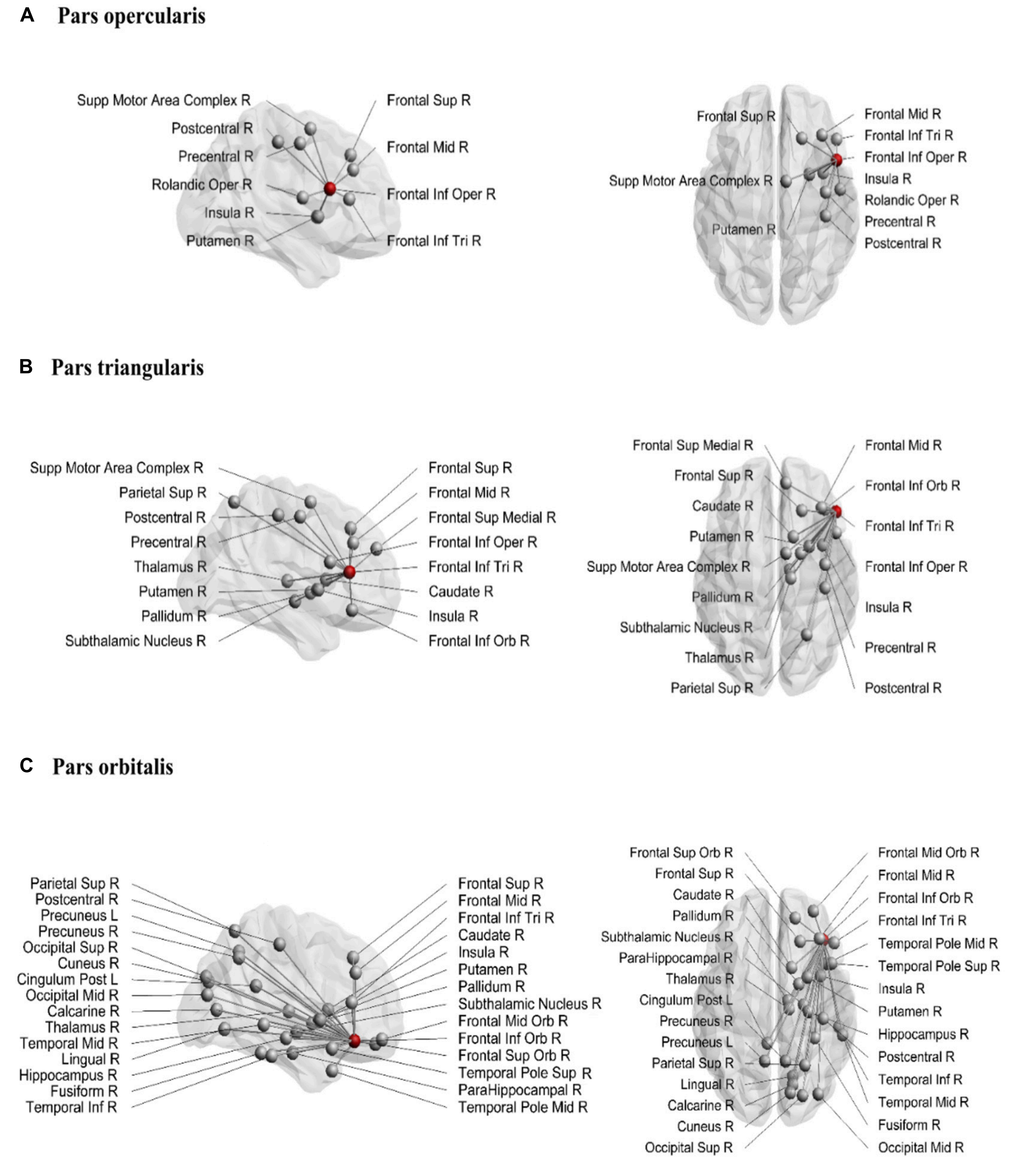

FIGURE 1 | Structural connections from pars opercularis **(A)**, pars triangularis **(B)**, and pars orbitalis **(C)**. The seeding region is marked as a red node. Sup, superior**;** Inf, inferior**;** Mid, middle**;** Supp, supplementary**;** Oper, opercularis**;** Tri, triangularis**;** Orb, orbitalis**;** R, right**;** L, left.

opercularis (**Figure 1A**) exhibited a similar connectivity pattern as the pars triangularis, albeit with fewer interconnected regions (**Figure 1B**), while the connectivity fingerprint of the pars orbitalis (**Figure 1C**) exhibited a more widespread network that also reached peripheral regions such as the occipital cortex (see **Supplementary Figure 2** for a sample participant). The data may suggest a posterior to anterior gradient with increasing connectivity from the opercularis, via the triangularis, to the orbitalis. To quantitatively test this observation, we computed pair-wise *t*-tests between these regions with the node degree estimated for each subject as dependent variable (**Figure 2**). These tests were run separately for both passing and terminating projections. For the terminating reconstructed connections, the results revealed a significantly lower node degree for the pars opercularis compared to the pars triangularis [$t(29) = -6.67$, $p < 0.001$] and the pars orbitalis [$t(29) = -9.04$, $p < 0.001$], while the pars triangularis showed a lower node degree compared to the pars orbitalis [$t(29) = -3.98$, $p < 0.001$]. A similar pattern emerged for passing connections, where the pars opercularis exhibited a lower node degree compared to the pars triangularis

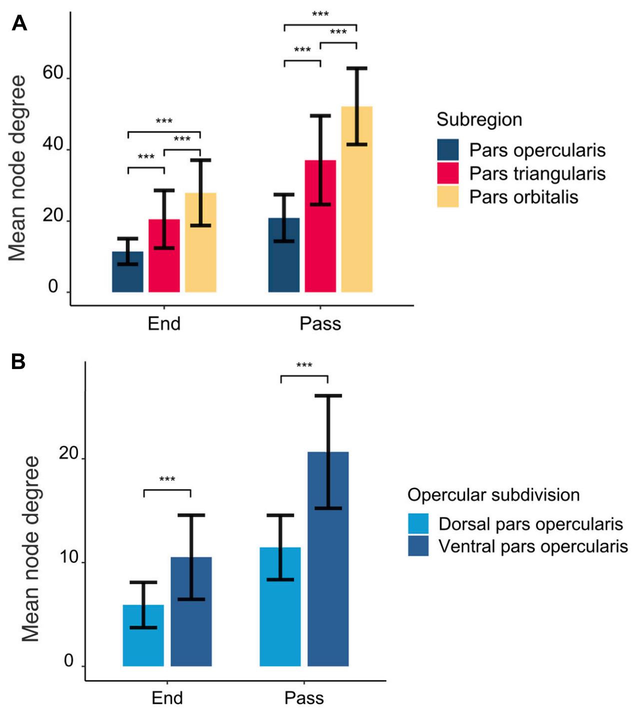

FIGURE 2 | The mean number of interconnected regions seeding from the rIFG subregions **(A)** and opercular subdivisions **(B)**. End and pass represent whether the tracts were part of an ending or passing fiber pathway. The error bars represent standard deviations. The asterisks above the bars mark statistical significance level at $p < 0.001$.

[$t(29) = -8.46$, $p < 0.001$] and the pars orbitalis [$t(29) = -14.38$, $p < 0.001$], while the pars triangularis showed a lower node degree compared to the pars orbitalis [$t(29) = -6.59$, $p < 0.001$].

Structural Connectivity Maps of the Dorsal and Ventral Pars Opercularis

The structural connections of the dorsal and ventral pars opercularis are visually presented in **Figure 3**. While the connectivity patterns of these two subregions show considerable overlap, the ventral part of the pars opercularis exhibited a higher node degree as indicated via significant paired t-tests for both ending [$t(29) = -6.49$, $p < 0.001$] and passing [$t(29) = -9.20$, $p < 0.001$] tracts. Connectivity differences emerged such that the dorsal opercularis showed a connection to mid-frontal cortex, whereas the ventral opercularis showed connections to postcentral cortex, rolandic operculum, insula, and putamen.

IFG Connectivity Within the Stopping Network

We conducted a connectivity analysis that specifically focused on differential connectivity patterns of the three IFG subregions with the other brain areas considered part of the stopping network: the SMAc, insula, caudate, putamen, and the STN. Connections to the stopping network were deemed to be reliably present if they were identified in at least 80% of the participants. **Figure 4** depicts the frequencies of these connections and **Figure 5** depicts the connections. The pars opercularis showed reliable connections to the SMAc, insula, and putamen. The pars triangularis showed reliable connections to the SMAc, insula, putamen, caudate, and the STN. The pars orbitalis exhibited reliable connections to the insula, putamen, caudate, and STN. Thus, the three rIFG subregions showed a differential connectivity within the stopping network, with connectivity in pars opercularis being limited to the cortical areas and putamen, while the other two regions showed additional subcortical basal ganglia connections.

Behavioral Results

Descriptive statistics of the behavioral measures obtained from the DRT and SST are presented in **Table 1**. Across participants, the average accuracy ($\geq$ 95% in both tasks) indicated good task performance. The average stop accuracy was 48%, which indicated successful SSD tracking, and all participants showed faster unsuccessful stop RTs than go RTs. The goRTs were shorter in the DRT than in the SST [$t(24) = -9.18$, $p < 0.001$] and did not correlate with each other ($r = 0.081$, $p = 0.700$). The average SSRT was 209 ms and did not correlate significantly with the mean goRT in the SST ($r = -0.30$, $p = 0.15$). However, stopping accuracy showed a significant association with goRT ($r = 0.57$, $p = 0.003$) and SSRT ($r = -0.60$, $p < 0.001$) in the SST.

Global and Tract-Specific Associations With Behavior

First, we tested whether the global FA was predictive of task performance, and found that the global FA value was not significantly correlated with the DRT goRT ($r = 0.091$, $p = 0.664$), but that it exhibited significant correlations with the SST goRT ($r = 0.434$, $p = 0.030$), SSRT ($r = -0.414$, $p = 0.040$) and stopping accuracy ($r = 0.479$, $p = 0.015$). Note that under conservative control for Type I error, these correlations would not survive correction for multiple comparisons in our sample. However, we consider the effect sizes and the consistencies across different behavioral measures sufficient to warrant the inclusion of the global FA in the regression models.

We then focused more specifically on key regions of the stopping network. Given the putative interactions of the pars opercularis and the SMAc in the stopping literature and their role in motor and inhibitory control, we computed a linear regression analysis using the FA of the dorsal pars opercularis-SMAc and the ventral pars opercularis-SMAc tracts as predictors of DRT goRT, SST goRT, SSRT, and stopping accuracy (**Table 2**). The global FA was added as a covariate, given the aforementioned associations of global FA with task performance measure, to further test the regional specificity of the described effects. The full model was only significant for the SST goRT and accuracy with the dorsal pars opercularis-SMAc tract as a significant predictor. The associations were also found to be significant with age and sex included as covariate instead of the global FA value (**Supplementary Note 1**). **Figure 6** depicts the associations between the goRT in the DRT and the SST and stopping accuracy with the dOp-SMAc tract.

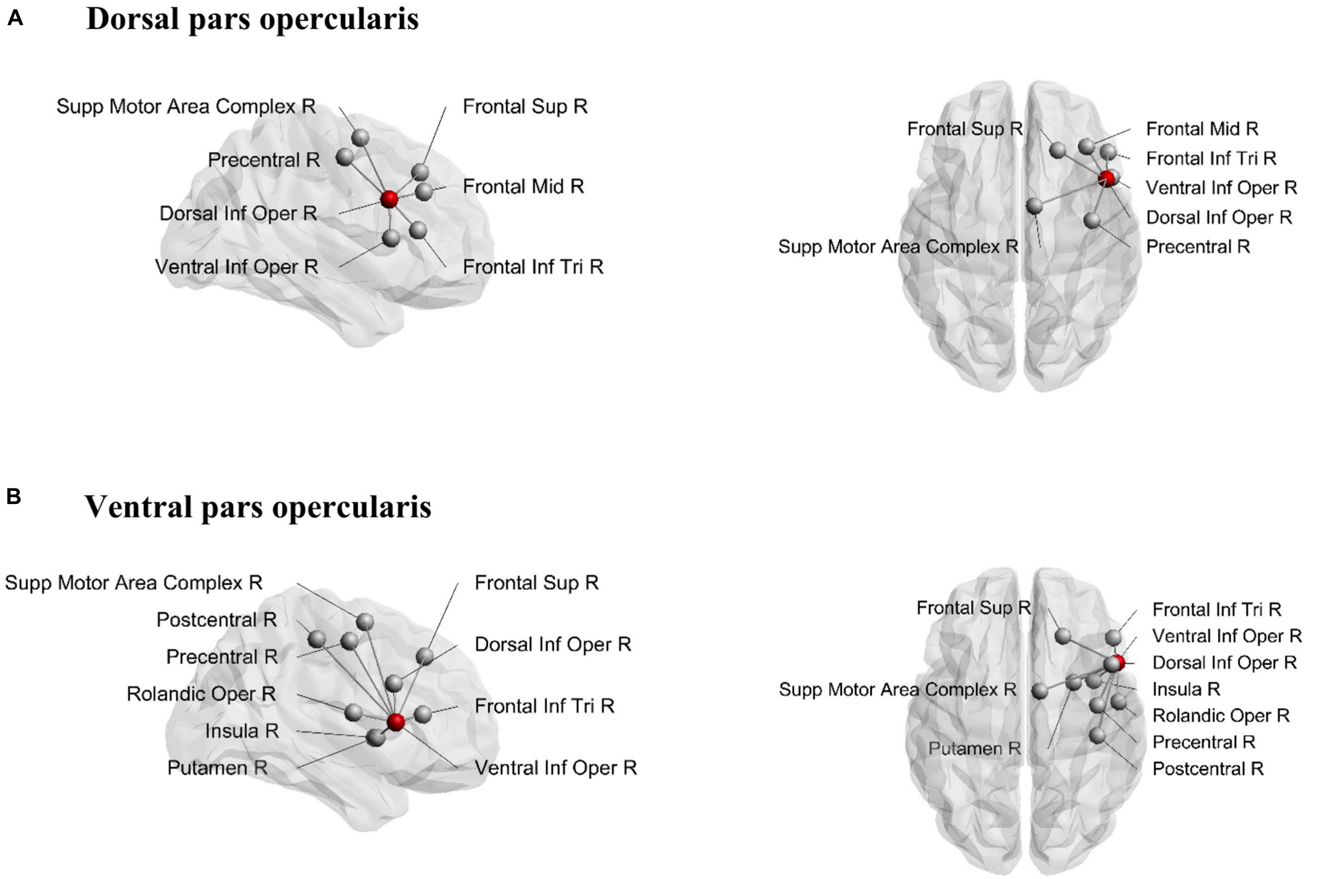

FIGURE 3 | Structural connections from dorsal pars opercularis **(A)** and ventral pars opercularis **(B)**. Seeding region is marked as a red node. Sup, superior; Inf, inferior; Mid, middle; Supp, supplementary; Oper, opercularis; Tri, triangularis; R, right.

DISCUSSION

Our primary objective was to investigate the white matter fiber pathways of three rIFG sub-regions (i.e., pars opercularis, pars triangularis, and pars orbitalis) using diffusion weighted imaging and deterministic tractography. The three subregions showed substantial differences in their connectivity patterns, as well as a posterior to anterior gradient in node degrees. In addition, the pars opercularis was segmented into a dorsal and ventral region, both of which were shown to have connections to SMAc. However, only the fractional anisotropy of the dOp-SMAc tract was a significant predictor of task behavior, namely for the goRT and stopping accuracy in the SST.

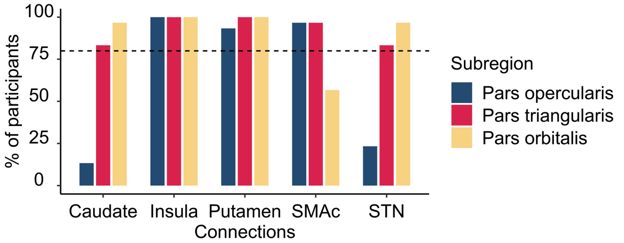

FIGURE 4 | Histogram illustrating the percentage of participants having connections from the rIFG subregions to the regions within the stopping network. The vertical dashed line refers to the inclusion threshold of 80% for a reliable connection. SMAc, supplementary motor area complex; STN, subthalamic nucleus.

Hartwigsen et al. (2019) identified functionally diverse subregions in the rIFG, following a posterior-to-anterior axis, where the posterior part was associated with motor functioning and the anterior part was related to abstract cognitive functions. In relation to this, we found evidence for a posterior-to-anterior division of structural connections within the rIFG. That is, the pars orbitalis showed the highest number of interconnected regions, followed by the pars triangularis, while the pars opercularis exhibited the lowest number of interconnected regions. Moreover, the connectivity fingerprints of the pars opercularis and pars triangularis were largely restricted to central and frontal regions, while the pars orbitalis showed the most widespread inter-regional connectivity pattern among the three rIFG sub-regions. This is interesting as the pars orbitalis has been associated with abstract cognitive functions (Hartwigsen et al., 2019), whereas the current study indicates that it also shows a widespread connectivity pattern reaching regions across all four

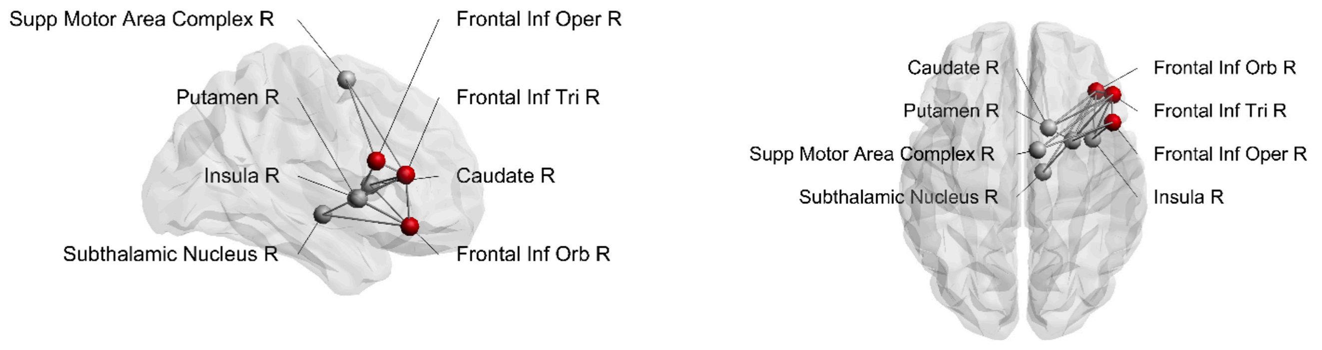

FIGURE 5 | Structural connections from rIFG subregions to the stopping network. Seeding region is marked as a red node. Inf, inferior; Supp, supplementary; Oper, opercularis; Tri, triangularis; Orb, orbitalis; R, right.

lobes in the right hemisphere. Speculatively, it might be that the widespread connections of the pars orbitalis serve its involvement in complex cognitive functioning, such as abstract thinking and social cognition. This is in contrast to the posterior part of the rIFG, which has been proposed to be crucial for inhibitory control (Aron et al., 2014), with a further subdivision of a dorsal region involved in motor execution and a ventral region involved in motor inhibition (Hartwigsen et al., 2019). In the current study, the segmentation of the pars opercularis into a dorsal and ventral region revealed some marked differences where the ventral part of the pars opercularis showed a higher inter-regional connectivity compared to the dorsal part. In addition, both regions exhibited connections to the SMAc, an important region within the stopping network. Altogether, in line with previous evidence suggesting a functional divergence in the rIFG along its posterior-to-anterior axis, our results showed increased node degrees along the posterior-to-anterior axis as well, possibly reflecting a structurally diverse rIFG.

We also identified several connections of the rIFG subregions to other parts of the stopping network. The pars opercularis showed reliable connections to the SMAc, insula, and putamen. Surprisingly, we did not find evidence for a reliable connection from the pars opercularis to the STN. This is in contrast to previous research that has shown this connection (Isaacs et al., 2018), albeit with data acquired with ultra-high field MRI and probabilistic tractography. However, the current results do show a reliable connection from both the pars triangularis and pars orbitalis to the STN. This might indicate that a connection between the pars opercularis and the STN consists of a tract with a complex architecture, which is harder to reconstruct with the conservative tractography technique used in the present study. It is interesting to note, however, that the pars triangularis was the only rIFG subregion that showed

TABLE 1 | Behavioral characteristics.

	DRT	SST
Go accuracy, %	96 (3.92)	95 (2.7)
Choice errors, %	0.38 (0.74)	0.24 (0.34)
Go omissions, %	1.48 (1.73)	3.15 (1.62)
Premature responses, %	1.89 (3.35)	1.21 (1.68)
Go RT, ms	320 (53)	475 (70)
Stop accuracy, %	–	48 (3.83)
Unsuccessful stop RT, ms	–	409 (74)
Stop signal delay, ms	–	293 (91)
Stop signal reaction time, ms	–	209 (26)

Go RT, mean reaction time on go trials; ms, milliseconds, standard deviations are presented in the brackets.

TABLE 2 | Summary of multiple regression analyses (*N* = 20).

	B	*SE B*	β	*t*	*P*
SST go reaction time (R^2 = 0.485, adjusted R^2 = 0.394, *F* = 5.336, *p* = 0.009)					
Intercept	−658.553	436.643		−1.508	0.150
Global FA	2142.835	1170.607	0.372	1.831	0.085
dOp-SMAc	2150.711	810.318	0.793	2.654	0.017
vOp-SMAc	−1568.957	875.468	−0.527	−1.792	0.091
SST stop signal reaction time (R^2 = 0.221, adjusted R^2 = 0.084, *F* = 1.611, *p* = 0.224)					
Intercept	537.138	209.253		2.567	0.020
Global FA	−575.825	560.993	−0.257	−1.026	0.319
dOp-SMAc	−487.667	388.331	−0.461	−1.256	0.226
vOp-SMAc	273.082	419.553	0.235	0.651	0.524
SST stop accuracy,% (R^2 = 0.495, adjusted R^2 = 0.405, *F* = 5.547, *p* = 0.008)					
Intercept	−20.243	26.058		−0.777	0.448
Global FA	111.247	69.860	0.321	1.592	0.130
dOp-SMAc	128.572	48.359	0.787	2.659	0.017
vOp-SMAc	−75.158	52.247	−0.419	−1.439	0.168
DRT go reaction time (R^2 = 0.037, adjusted R^2 = −0.133, *F* = 0.217, *p* = 0.883)					
Intercept	176.723	528.020		0.335	0.742
Global FA	458.469	1415.582	0.090	0.324	0.750
dOp-SMAc	623.966	979.895	0.260	0.637	0.533
vOp-SMAc	−732.951	1058.679	−0.278	−0.692	0.498

SST, stop signal task; DRT, delayed response task; dOp, dorsal pars opercularis; vOp, ventral pars opercularis; SMAc, supplementary motor area complex. All predictors had tolerance > 0.1 and variation inflation factor < 0.3.

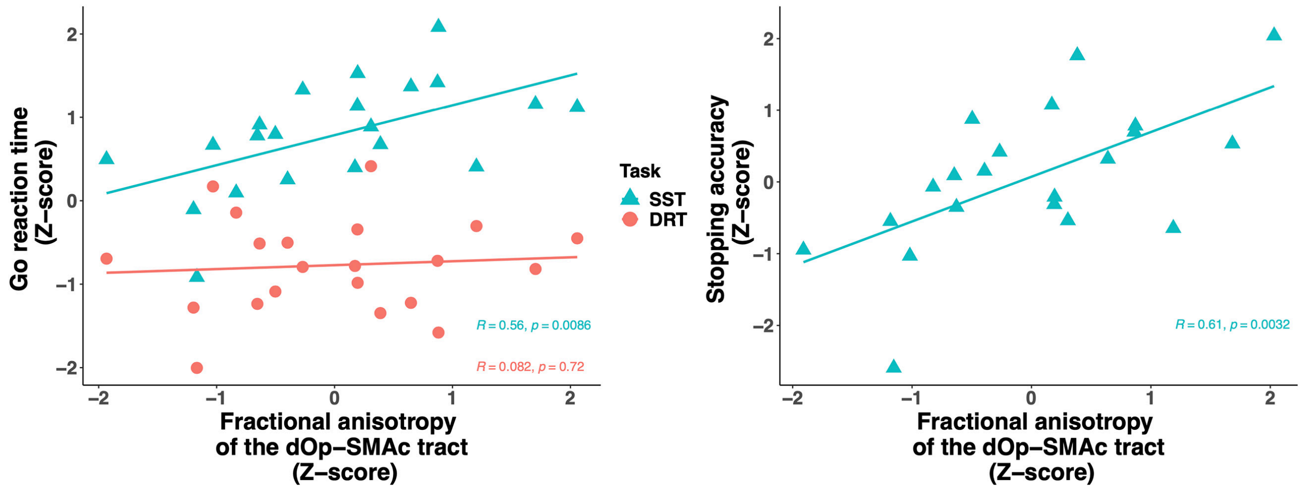

FIGURE 6 | Scatter plot of the fractional anisotropy of the dOp-SMAc tract predicting go reaction time in the stop signal task and the delayed response task (left) and stopping accuracy (right). All variables were z-scored based on the raw values. Go reaction time was scaled across the delayed response task and the stop signal task. dOp, dorsal pars opercularis; SMAc, supplementary motor area complex.

a reliable connection to the SMAc, insula, putamen, caudate and STN. Given the overlapping connectivity fingerprints of the pars opercularis and pars triangularis, the combination of these regions might be a more suitable connectivity hub for inhibitory control compared to pars opercularis alone. Altogether, the results show connections between rIFG subregions and other regions that were also found in a meta-analysis on functional MRI during inhibitory control, and which included the insula, SMAc, middle frontal gyrus, striatum, and posterior parietal area (Cai et al., 2019).

Furthermore, Hartwigsen et al. (2019) suggested that the posterior part of the rIFG could be segmented into a dorsal and ventral region and that these regions are associated with motor initiation and inhibition, respectively. However, it is unclear whether the dorsal part relates to the cognitive effort necessary to execute correct responses in demanding tasks, or whether it relates to motor execution proper. In the current study, both the dorsal and ventral regions of the pars opercuarlis showed connections to the SMAc, a connection that has been suggested to be important for inhibitory control (Aron et al., 2007; Swann et al., 2012). Thus, it is interesting that our results revealed a significant positive relationship between the dorsal pars opercularis-SMAc and the goRT from the SST, while the ventral pars opercularis-SMAc showed a (non-significant but considerable) negative relationship with the goRT. We also observed the same pattern for the stopping accuracy, showing that increased connectivity strength in the dorsal pars opercularis-SMAc is related to increased reaction time and stopping accuracy. This is interesting in context of previous research that showed increased fractional anisotropy in the pars opercularis to be negatively associated with the SSRT, while increased fractional anisotropy in the preSMA was positively associated with the SSRT (Xu et al., 2016). Moreover, the dorsal pars opercularis-SMAc tract was a significant predictor of goRT in the SST and not the DRT, and the goRTs from the DRT and SST did not correlate. This suggests that the goRTs obtained from the SST are influenced by other cognitive control mechanisms than motor generation alone. This supports a role of the dorsal opercularis in cognitively demanding motor initiation or the balancing of response speed and accuracy as opposed to plain motor generation in itself. The observed pattern thus supports the hypothesis of different functional roles of the dorsal and ventral parts of the opercularis.

In conclusion, the results indicate that the three sub-regions of the rIFG exhibit heterogeneity in terms of their connectivity, which is supported by the difference in the intra and inter-individual amount of tracts across the sub-regions. The overall pattern followed a posterior to anterior gradient with increasing node degrees from the pars opercularis, via the pars triangularis and to the pars orbitalis. Although, the pars orbitalis showed the most widespread connectivity, all three rIFG subregions showed several connections to regions implicated in inhibitory control. The segmentation of the dorsal and ventral pars opercularis showed that both regions had reliable connections to the SMAc, but only the ventral part was connected to the insula and putamen. We believe that the results from the current study provide novel insights into connectivity differences between the rIFG subregions. As always, some caution is warranted as quantitative differences in streamlines can also be caused by other microstructural differences (e.g., branching, length, and curvature of tracts; Jones et al., 2013). Finally, the go reaction times from the SST were considerably longer compared to that of the DRT, likely due to demand for increased cognitive control. Thus, associations between measures of motor initiation in a more cognitive demanding task (i.e., reaction time in the SST) and brain structure may reflect multiple aspects of action generation, including motor preparation, uncertainty estimation, and movement invigoration. Taken together, the brain-behavior associations partly supported a functional differentiation between the dorsal and ventral pars opercularis, possibly implicating them in response execution under increased cognitive control and inhibition, respectively.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The study was reviewed and approved by the Internal Review Board of the Department of Psychology, University of Oslo. The participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct, and intellectual contribution to the work, and approved it for publication.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnhum.2022.787079/full#supplementary-material

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The Role of Motor Inhibition During Covert Speech Production

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Covert speech is accompanied by a subjective multisensory experience with auditory and kinaesthetic components. An influential hypothesis states that these sensory percepts result from a simulation of the corresponding motor action that relies on the same internal models recruited for the control of overt speech. This simulationist view raises the question of how it is possible to imagine speech without executing it. In this perspective, we discuss the possible role(s) played by motor inhibition during covert speech production. We suggest that considering covert speech as an inhibited form of overt speech maps naturally to the purported progressive internalization of overt speech during childhood. We further argue that the role of motor inhibition may differ widely across different forms of covert speech (e.g., condensed vs. expanded covert speech) and that considering this variety helps reconciling seemingly contradictory findings from the neuroimaging literature.

Keywords: covert speech, inner speech, motor imagery, motor simulation, motor control, motor inhibition

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1. INTRODUCTION

The ability to mentally examine our verbal thoughts is central to our subjective experience. This covert (internal) production of speech typically accompanies everyday activities such as problem solving (Sokolov, 1972; Baldo et al., 2005), future planning (D'Argembeau et al., 2011), reading (e.g., Lœvenbruck et al., 2005; Perrone-Bertolotti et al., 2012), or writing (Frith, 1979). Because *overt* speech production results from sequences of motor commands that are assembled to reach a given communication goal, it belongs to the broader category of motor actions (Jeannerod, 2006a). Therefore, a parallel can be drawn between covert speech, also known as *inner speech* or *speech imagery* (for reviews, see Perrone-Bertolotti et al., 2014; Alderson-Day and Fernyhough, 2015; Lœvenbruck et al., 2018), and other imagined actions (i.e., motor imagery). The motor simulation theory of motor imagery (Jeannerod, 1994, 2001, 2006b) postulates a continuum between the covert and the overt execution of an action, and that action representations can operate off-line via a simulation mechanism.

However, the proposal that overt and covert actions share common processes and neural circuits is faced with a serious problem. If the neural circuits used for the control of overt actions are also used for covert actions, how can covert actions not lead to execution? This puzzle was coined as *the problem of inhibition of execution* by Jeannerod (2001). In this perspective, we examine some theoretical and experimental consequences that emerge from considering covert speech as inhibited overt speech. First, we explore the role and plausible neural implementation of inhibitory mechanisms during covert speech production. Second, we relate the maturation of inhibitory control during childhood with the progressive internalization of overt speech. Third, we consider how inhibitory mechanisms may play different roles across different forms of covert speech. By bridging recent results from the covert speech, motor imagery, and motor inhibition literature, we highlight some novel and possibly fruitful lines of research.

2. COVERT SPEECH PRODUCTION AS INHIBITED OVERT SPEECH PRODUCTION

2.1. Cognitive and Neural Mechanisms Supporting Motor Inhibition

First and foremost, we need to make a distinction between at least two different types of inhibition. First, cognitive inhibition, defined as the stopping or overriding of a mental process, with or without intention (MacLeod, 2007). Second, the inhibition of physical response, or motor inhibition, defined broadly as the withholding, suppression, or overriding of an inappropriate, prepotent, or unwanted motor response (Aron, 2007; O'Shea and Moran, 2018). Here, we are concerned with the latter. Ridderinkhof et al. (2014) further described the concept of response inhibition on three continuous dimensions: intentionality, premeditation, and specificity. Inhibition can be employed with more or less intentionality, planned ahead or employed in the moment, and applied to a specific action and effector, or more globally, to all actions, and/or effectors.

Within Ridderinkhof et al.'s classification of response inhibitions, we hypothesize that covert speech involves an intentional (we know we want to produce these actions covertly rather than overtly) but implicit/automatic (we do not explicitly think about not producing movements) and planned ahead form of response inhibition. The distinction between implicit and explicit inhibition seems important to highlight. The type of motor inhibition that may be at play during motor imagery is still different from the "proactive inhibition" in the motor inhibition literature. Indeed, in behavioral tasks aiming to assess proactive inhibition, participants are instructed not to execute an action. In contrast, while doing motor imagery, participants are asked to imagine the action, which indirectly implies that it should not be executed overtly (Guillot et al., 2012). Moreover, the type of motor inhibition that is implemented during covert speech necessarily has to be planned ahead, otherwise speech acts would sometimes be (at least partially) executed. Finally, the level at which motor inhibition may be applied can be inferred from the example of hand movements. Rieger et al. (2017) used an action mode (overt vs. covert) switching paradigm, to show that the motor imagery of hand movements is accompanied by both global and effector-specific inhibition (these results were also replicated in Scheil and Liefooghe, 2018; Bart et al., 2021a,b,c). Here, we hypothesize that inhibition during covert speech may similarly apply both globally and in an effector-specific manner.

Based on evidence from electrophysiological, neuroimaging, and clinical studies, Guillot et al. (2012) suggested several possible routes whereby motor commands can be inhibited during motor imagery. First, cerebral regions such as the pre-supplementary motor area (pre-SMA) (Kasess et al., 2008) or the right inferior frontal gyrus (rIFG) may weaken the motor commands that are emitted during motor imagery (e.g., Angelini et al., 2015, 2016). More precisely, the pre-SMA and the rIFG may work together to intercept the action process via the basal ganglia (subthalamic nucleus), hence suppressing the output from the basal ganglia which in turn might inhibit the primary motor cortex (Aron, 2011). Second, motor imagery has been shown to be associated with modulations of short-interval intracortical inhibition within the primary motor cortex itself (Neige et al., 2020). Third, downstream regions in the cerebellum (e.g., Lotze et al., 1999), in the brainstem (e.g., Jeannerod, 2001, 2006a), or at the spinal level may contribute to motor inhibition at a later stage.

In addition to these three possible routes, another possibility highlighted by Guillot et al. (2012) is that motor inhibition can be integrated within the representation of the action to be produced internally, so that only subthreshold motor commands may be involved during motor imagery (hereafter referred to as the "subliminal level hypothesis," see also Glover et al., 2020; Bach et al., 2021). It has been suggested that during covert speech production, motor commands would be "simply specified in subthreshold way, requiring no active inhibition" (Geva, 2018). However, stating that covert speech (or motor imagery, more generally) only involves subthreshold activity (and therefore is not accompanied by the emission of motor commands that are inhibited) simply shifts the problem from "how and where motor commands are subsequently inhibited" to "how and where the magnitude of activity in the motor system is planned or monitored" (see also Scheil and Liefooghe, 2018). In other words, we still need to explain how (in a mechanistic and/or developmental way) this activity is maintained at a subthreshold level. In this section, we provided empirical arguments in favor of the "active inhibition hypothesis." Proponents of the "subliminal level hypothesis" need to clarify how this activity is maintained at a subthreshold level during covert speech production, thus preventing execution.

The putative involvement and functional role of (cortical and subcortical) inhibitory mechanisms during covert speech could be assessed in several ways. First, it could be assessed by experimentally manipulating the activity of the inhibitory network responsible for preventing execution during motor imagery. For instance, transcranial magnetic stimulation (TMS) could be used to interrupt these inhibitory mechanisms and thus trigger execution during motor imagery. Second, it could be assessed by looking at covert speech production in patients with acquired (focal) brain damage. For instance, Schwoebel et al. (2002) observed that bilateral parietal lesions can lead patients to execute actions when they asked to imagine them, suggesting a failure of inhibitory mechanisms. Third, the role of inhibitory mechanisms during covert verbal actions could be examined in populations with well-identified inhibitory deficits. For instance, Tourette syndrome is a childhood-onset neurological disorder affecting approximately 1% of children and characterized by chronic motor and phonic tics (Jackson et al., 2015). Verbal tics can consist of repeating sounds, words, or utterances (palilalia), producing inappropriate or obscene utterances (coprolalia), or the repetition of another's words (echolalia). In their review, Jackson et al. (2015) suggested that increased control over motor outputs, acquired by repeatedly trying to suppress tics, is brought about by local increases in GABAergic "tonic" inhibition within regions such as the SMA, leading to localized reductions in the gain of motor excitability. For these reasons, comparing the neural implementation of inhibitory mechanisms during covert speech in patients with Tourette syndrome and healthy controls may shed light on the role and flexibility of these mechanisms.

2.2. Covert Speech Development: Learning Not to Produce Speech

Watson (1919) suggested that thought was rooted in overt speech. In his terminology, thought referred to covert speech. Hence, his view was that covert speech matures from overt speech. Vygotsky (1934) further elaborated the idea that covert speech is internalized during childhood from private egocentric speech, that is, from self-addressed overt speech. Fernyhough (2004) extended these ideas by proposing four levels of internalization: external dialogue, private speech, expanded inner speech, and condensed inner speech. These levels represent stages of development but also define movements between levels, that is, how a speaker may transform overt speech to covert speech, and conversely. The level at which speech is expressed may depend on inhibitory control applied at different levels in the production flow, such as the formulation or the articulatory planning level (Grandchamp et al., 2019). Therefore, producing covert speech crucially depends on successfully inhibiting speech production at several levels.

Here, we hypothesize that the progressive internalization of speech during childhood may be related to the development of inhibitory abilities. This hypothesis could be tested in several ways. First, the relation between speech internalization and inhibitory abilities could be assessed during development at the critical ages (i.e., between 6 and 8 years). We would expect the ability to imagine actions, and speech specifically, to be positively correlated with motor inhibition at this age. Wang et al. (2021) provided correlational evidence that motor imagery (assessed in a hand laterality judgement task) and motor inhibition performance (assessed in a stop-signal task) improve together between 7 and 11 years old, and that these two abilities correlate at 7 years old but did not correlate at 11 years old. This suggests that inhibitory control may play a more prominent role when speech is being internalized, but its role may weaken with expertise. This would be consistent with results from training studies suggesting that, with growing expertise, mental imagery increasingly relies on memory-based processes (e.g., Jolicoeur, 1985; Tarr and Pinker, 1989).

Second, the hypothesized co-development of motor imagery and response inhibition abilities could be tested by examining how novel actions are internalized in adults. Consider for instance how the act of producing speech can be paralleled with the act of playing a music instrument (e.g., the piano). Both actions consist in the coordination of complex movements that result in some modifications of the environment, that in turn generate sensory feedback (e.g., kinaesthetic, auditory) for the agent. This analogy suggests that we might be able to study the development of internal models responsible for the sensory experience accompanying imagined actions in the adult mind (e.g., when an individual is learning either a novel music instrument or a new language with speech sounds that are not present in his/her native language). By examining the development of novel imagined actions in the adult mind and by using motor interference (e.g., articulatory suppression) procedures, we might gain new insights about the internalization of speech during childhood[1].

2.3. Does Covert Speech Always Involve Motor Inhibition?

The production of covert speech is often, although not always and not for everyone, accompanied by the feeling of *hearing* speech (Hurlburt, 2011). However, covert speech may also be accompanied by the feeling of *producing* speech. These two facets of covert speech are characterized by different phenomenological experiences. In this section, we discuss how these two forms of covert speech may require motor inhibition to a different extent.

The dual stream prediction model (Tian and Poeppel, 2012, 2013; Tian et al., 2016) describes two neural pathways that may provide the auditory content of covert speech. First, the simulation-estimation prediction stream implements a motor-to-sensory transformation via motor simulation, that is, by simulating speech movements and the perceptual changes that would be associated with these movements (see also Lœvenbruck et al., 2018, for a similar proposal). This stream includes cerebral areas involved in speech motor preparation such as the supplementary motor area, the inferior frontal gyrus, the premotor cortex, and the insula, as well as brain areas involved in somatosensory estimation and perception such as primary and secondary somatosensory regions, the parietal operculum, and the supramarginal gyrus (Tian et al., 2016). Second, the memory-retrieval prediction stream provides auditory percepts by "reconstructing stored perceptual information in modality-specific cortices" (Tian et al., 2016). This mechanism provides sensory percepts without the need for computing the predicted sensory consequences of (non executed) motor commands. Auditory percepts may be retrieved from various memory sources, relying (amongst others) on the hippocampal formation (Tian et al., 2016), or from a broad fronto-temporo-parietal lexico-semantic network (for more details, see Tian et al., 2016).

The balance between the mechanisms of simulation and memory retrieval may depend on the circumstances promoting covert speech or, in the lab, on the precise instructions given to participants, which may cue them to produce different forms of covert speech. For instance, either one of these two streams may be preferentially recruited depending on whether participants are instructed to "imagine speaking" or to "imagine hearing" (see also the distinction between the "inner ear" and the "inner voice," e.g., Smith et al., 1992). In line with this hypothesis, Tian et al. (2016) have shown that inner speaking recruits

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[1] We should keep in mind the obvious limitation that the child mind is not equivalent to the adult mind, nor is it equivalent to a smaller version of the adult mind. Nevertheless, examining the development of novel imagined actions in adults avoids the contamination of the process of interest (imagined action) by developmental confounds.

BOX 1 | Memoization

Memoization is a programming technique used to speed-up algorithms or programs. It avoids redundant computation by storing computational results and reusing them later (Dasgupta and Gershman, 2021). When calling a function (where a function can be a motor primitive), the function call is intercepted by a *memoizer* that inspects the previous calls of a function and its outputs. If a function has already been called with the same input, then the previously computed output is retrieved and reused.

In the context of covert speech, memoization can be postulated as the process by which covert speech percepts produced by motor simulation are stored for later retrieval and use without invoking the motor simulation mechanism.

brain regions in the simulation stream more strongly than inner hearing, which conversely recruits more strongly brain regions in the memory-retrieval stream. Ma and Tian (2019) have shown that inner speaking and inner hearing have distinct magnetoencephalographic (MEG) correlates and distinct effects on a subsequent phonetic categorization task (discriminating /ba/ vs. /da/).

In line with Tian and Poeppel (2012), we suggest that the balance between these two mechanisms may also depend on a participant's situational (e.g., surrounding noise) and individual (e.g., expertise) characteristics. We further suggest that a common currency to determine the recruitment of either one of these mechanisms is the computational cost of (or equivalently, the computational resources available for) each alternative. To clarify, we borrow the concept of memoization as applied to cognition and mental imagery by Dasgupta and Gershman (2021) (cf. **Box 1**). In these authors' view, memory can be considered as a computational resource that facilitates computational reuse through memoization. In the context of motor and speech imagery, memoization can be seen in the increasing reliance on memory in the course of learning.

In other words, situational (extrinsic) and individual (intrinsic) characteristics jointly determine the computational cost of (or equivalently, the available computational resources for) the task, which in turn determines the balance between the simulation and association mechanisms. For instance, we hypothesize that novel and/or difficult tasks (which are both computationally more expensive, ceteris paribus) may rely more on the simulation mechanism, whereas well known and/or easy tasks may rely more on associative mechanisms. This idea is supported by several studies showing a greater increase in facial EMG activity during the reading of difficult text or while performing difficult mental arithmetic tasks, compared to easier tasks (e.g., Faaborg-Andersen et al., 1958; Sokolov, 1972), suggesting a greater involvement of the speech motor system. Alternatively, these results may suggest a lesser involvement of inhibitory mechanisms (see also the discussion in Nalborczyk, 2019, 2020). This is congruent with the increased reliance on associative mechanisms with greater expertise, as discussed previously.

To sum up, whereas inner speaking may involve active inhibition of motor commands, inner hearing may not. These disparities between inner speaking and inner hearing may explain the variety of neural correlates reported for covert speech production (as reviewed for instance in Geva, 2018). More generally, different forms of covert speech may vary in condensation (from thinking without words to thinking in words), dialogicality (whether covert speech features monologes or dialogues), or intentionality (for more details, see Grandchamp et al., 2019) and may thus require inhibitory control to a different extent, from no inhibition at all for condensed forms of covert speech to active inhibition of motor commands for fully expanded forms of covert speech.

3. CONCLUSIONS

We explored some of the theoretical and experimental consequences that emerge from considering covert speech production as an inhibited form of overt speech production. To this end, we connected results from the motor imagery, motor inhibition, and covert speech domains. Regarding the role and implementation of general-purpose inhibitory mechanisms during the production of covert speech, we suggested that these may be similar to the inhibitory network responsible for proactive response inhibition and we summarized some propositions from this literature. We related the development of response inhibition abilities in childhood development with the purported internalization of private speech around the same period. From the response inhibition perspective, the internalization of speech from overt to covert speech may essentially be considered as "learning not to execute speech."

Regarding the neural origin of the sensory experience of covert speech, we discussed the dual stream prediction model (Tian and Poeppel, 2012, 2013; Tian et al., 2016), which suggests that these sensory percepts may be provided either by a motor-simulation process or by a memory-retrieval process. We suggested that the balance between these two mechanisms may be determined by task instructions, which may prompt different forms of covert speech, and also by the computational cost of the task. More precisely, novel or more difficult tasks are expected to rely more on the motor-simulation mechanisms whereas well-known and/or easy tasks may rely more on a "memoized version" of the motor simulation: the memory-retrieval prediction stream. Whereas the former mechanism should involve active inhibitory mechanisms, the latter should not, as there should be no (or less) motor commands to inhibit.

These propositions pave the way for several lines of research that should consolidate our understanding of the relations between overt and covert speech production. Several outstanding questions remain. Amongst others, further research should aim at testing whether and how the development of inhibitory control relates with the progressive internalization of speech during childhood. Do individual and situational constraints shape the role of motor inhibition during covert speech production? Is covert speech affected by poor or degraded inhibitory control? Can we experimentally force the externalization of speech in adults, for example through neurostimulation? The use of neurostimulation and the comparison between healthy controls and patients with well-identified inhibitory deficits could help refine the involvement of these inhibitory mechanisms during covert speech production, which may lead to applied outcomes in the care of motor and verbal tics.

DATA AVAILABILITY STATEMENT

No data were used in this paper. However, the source code is available at https://osf.io/dsfgb/.

AUTHOR CONTRIBUTIONS

All authors: conceptualization and writing—review and editing. LN, ML, F-XA: funding acquisition. UD, ML, AG, and F-XA: supervision. LN: writing—original draft. All authors contributed to the article and approved the submitted version.

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