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**NEUROECONOMICS PROCESSES UNDERLYING
DECISION-MAKING IN JOINT VS INDIVIDUAL ACTIONS:
a behavioral and EEG study on non-human primates**

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Abstract

A hallmark of the successful evolution of our species could reside in the ability to optimize collective behavior in order to achieve goals otherwise unattainable by acting alone. Inter-individual motor coordination can be considered as a key feature of sharing actions with others. As much as advantageous though, acting together can also be costly since it requires special cognitive and motor skills. We know that non-human primates are able to coordinate their actions in a dyadic context by dynamically adapting their motor behavior in a way that favors inter-individual synchronization. However, this type of behavioral adaptation has been proved to entail a cost, which is evident in a reduction of successful monkeys' performance when sharing actions for a common goal. In the recent years, the existence of internal models of the own and the other's action has been hypothesized by several authors, but how these models are formed and coded at the neural level is still object of study. The currently most accredited hypothesis is that acting with others requires the ability to integrate one's own and others' action representations in a dyadic motor plan. In order to better understand the behavioral and neural underpinnings of sharing actions, we conducted three experiments.

In the first part of this work (*Experiment 1*) we investigated whether, how and under which task conditions monkeys can improve their performance in a joint action task. To address these questions, we have investigated the influence of a pre-instructing "social cue" providing anticipatory information about action context (individual or joint). Our findings suggest that pre-instructing the action context increase the chances of dyadic success by establishing an optimal "kinematic setting" that ultimately facilitates inter-individual motor coordination. Moreover, we speculate that such joint performance improvement can be ascribe to a successful resort to a "we-representation", possible only when the joint action is pre-cued.

In the second part of this thesis (*Experiment 2*) we aimed at investigating monkeys' ability to estimate the cost of acting together and to use this information to decide between acting alone or jointly with a partner. To this aim we trained two monkeys to choose between two possible goals, each associated to different action types (solo or together) and payoffs. Our findings suggest that their economic choice was not merely dictated by the reward offered but also by the action cost, whereby motor inter-individual coordination was evaluated as more demanding than individual action.

In the third and final part (*Experiment 3*) we conducted dual neural recordings using electroencephalography (EEG) while the monkeys were working on the same task adopted in *Experiment 2*. Preliminary results demonstrate that monkeys' response evoked by the two offers was modulated by the action type chosen or expected to be chosen by the partner. This provides, for the first time, evidence of the feasibility of studying neural correlates underlying value-based decision making in non-human primates by mean of EEG methods.

Introduction

The ability to optimize collective behavior, in order to achieve goals otherwise unattainable by a single individual is considered one of the highest evolutionary achievements of our species. In this context, inter-individual motor coordination represents a key feature of sharing actions with others. As much as advantageous, though, it can be also costly since it requires cognitive and motor skills that go beyond what is necessary to carry out an individual action.

Previous work from our lab (Visco-comandini et al. 2015, Ferrari-Toniolo et al. 2019a) has demonstrated that non-human primates are able to coordinate their actions in a dyadic context, by dynamically adapting their motor behavior in a way that boosts inter-individual synchronization. However, this type of behavioral adaptation has been proved to entail a cost, evident in a reduction of monkeys' performance when acting jointly to achieve a common goal.

Our knowledge on the neural underpinnings of sharing actions is still poor and patchy. The existence of internal models of one's own and the other's action has been in fact hypothesized by several authors. But how these models are formed and coded at the neural level has yet to be clarified. While some initial approaches suggested an interpretation of individual action as supported by the same network subtending action observation (Wolpert et al. 2003, Rizzolatti & Sinigaglia, 2010), recent evidence started to point towards a more complex model of action representation based on the proofed segregation of behavioral and neural substrate of observing others' action compared to acting with them (Sacheli et al. 2018). The currently most accredited hypothesis is that acting with others requires the ability to integrate own and other's action representations in a dyadic motor plan (Keller et al. 2016, Pesquita et al. 2018; Sacheli et al. 2018).

In order to better understand the behavioral and neural underpinnings of sharing actions, we conducted three experiments that will be presented in three separate sections of the current manuscript.

In the first part of this work (*Experiment 1*) we investigated whether and how monkeys can improve their performance in a joint action task, when given the time to prepare for it. We trained three couples of monkeys to perform an isometric center-out task requiring each

individual animal to either work individually or together with a partner while applying force in one out of eight possible directions. Two versions of this task were adapted. In the first one, the force direction and the type of action (alone or together) were cued simultaneously. In the latter, the type of action was pre-instructed during a dedicated delay time while the information about the force direction was provided afterwards. Manipulating the presence or absence of a pre-instruction about the future action condition (Solo or Together), allowed us to investigate on the existence of a “we-representation” in macaque monkeys. We found that pre-instructing about the action context increased the chances of dyadic success, thanks to an optimal “kinematic setting” that ultimately facilitates inter-individual motor coordination. Our results offer also empirical evidence in macaques of a “We-representation” during collective behavior, that once is cued in advance has an overall beneficial effect on joint performance.

In the second part of this thesis (*Experiment 2*) we aimed at investigating the ability of the monkeys to estimate the perceived cost of coordinating actions in the context of economic decisions. Two rhesus monkeys were trained to choose between acting individually (SOLO) or jointly (TOGETHER), depending on the reward offered to each option. In the TOGETHER condition, the two animals had to coordinate their actions to reach a common target, while in the SOLO condition one of them could reach a target alone. The two monkeys were instructed to take turns in choosing between the SOLO and TOGETHER targets. Additionally, control trials were presented, in an intermingled fashion, in which the monkeys had to choose between two SOLO or two TOGETHER targets were presented. Target preference in these control conditions was purely dictated by the payoff value. On the other hand, when the monkeys had to choose between action types (SOLO vs TOGETHER), the economic choice was subdued to the cost of motor inter-individual coordination – which was paid evidently with a decrease of joint performance and a re-adaptation in motor behavior. These results showed that non-human primates can estimate this cost and use it to decide whether to act jointly with others.

In the third and last part (*Experiment 3*) we tested our monkeys on a task similar to the one used in *Experiment 2* while simultaneously recording their neural activity by mean of electroencephalography techniques (EEG). Preliminary results demonstrate that the monkeys’ evoked response, as recorded while they were seemingly weighing the two offers, was modulated by the cognitive key-features of the task. In fact, the action type (individual or joint) was coded in a way that reflected the action engagement (having to act or to stay in the center and observe) as well as the choice made or expected to be made by the partner.

Experiment 1: Pre-instruction about the type of action ameliorate joint performance

Background

The ability to coordinate actions among different individuals in order to achieve goals unattainable by single subjects if acting alone, has been observed across species. It might be regarded as an expression of collective behavior, maximally developed in humans and considered a key-element of successful evolution of our species (Boyd, 2018). Although several forms of coordination have been observed even for very simpler organisms such as insects, as well as viruses and bacteria, there is no doubt that our abilities to coordinate with others is much more sophisticated. One distinguishing element of this human abilities coordinate their actions reside in the exceptional ability to predict the behavior of others and to flexibly adjust own behavior to that of our co-agent (Boyd, 2018).

One form of collective behavior is expressed during motor interactions among different subjects, through their successful inter-individual motor coordination. In the literature, both the locutions “joint action” and “motor coordination” (or “coordinated action”) have been used to address different variations of such form of social behavior in humans and other species. Joint action and motor coordination, though, cannot be used as synonyms. Paraphrasing Sebanz et al. (2006) definition, the semantic set of the term “joint action” encompasses all those forms of motor coordination in space and time, between at least two individuals, aimed at producing a change in their surrounding environment. Therefore, while motor-coordination describes only the mere presence of a successful degree of synchronicity/complementarity between two or more individuals, joint action definition also requires the assumption of a shared goal (Butterfill, 2017).

The very first theoretical readout of motor control in the context of social interactions came from Wolpert et al. (2003)’s computational approach. In their work, socially connoted actions were suggested to rely on the same mechanisms that characterize individual actions: feedforward and feedback processes. Keller et al. (2016)’s work made a farther step, by revising Wolpert’s theory of social motor control to define joint action in musical ensembles.

The authors postulated the existence of joint internal model as a combination of self and other's internal models.

From a psychological perspective, Vesper et al. (2010) provided a model of the minimal, defining elements that characterize all types of joint action, which are: (i) the representation of a common goal; (ii) the activation of monitoring and prediction processes of own and other's action; (iii) the resort to coordination smoothers.

More recently, Pesquita et al. (2018) proposed a “predictive joint-action model” (PJAM), which states that joint action implies the existence of probabilistic internal models of the own and of the other's actions, integrated and maintained along the entire task. This process stands on three hierarchical computational levels: (i) goal representation, (ii) action planning and (iii) sensory routing. The novelty of this approach resides in describing joint action in terms of feedback and feedforward processes (computational approach), while taking into account the shared nature of high-level representations and the necessity of a contingent integration of self and other models, formed at the motor and sensory level (psychological approach).

During joint action planning, a debated issue is whether motor preparation consists of separate predictive representations for one's own and partner's performance or whether it is grounded on a predictive action representation of the dyadic behavior. In the latter case the operating unit is the dyad, whose respective action representation would be the core of the so-called “We-representation” (Knoblich et al., 2011; Vesper et al., 2010) or “we-mode” (Gallotti & Frith, 2013). Under this scenario, when individuals join their forces to achieve a common goal, there is a *a priori* sense of doing something together, and not “on my own” and independently from the others. Therefore, joint performances would be guided by the collective goals, which are specified through dedicated motor representation (della Gatta et al, 2017) rather than by each individual contribution.

In previous work conducted in our lab, a model of joint action on non-human primates has been developed, with the long-term goal of studying this phenomenon from a neurophysiological perspective. So far, we have demonstrated that monkeys are actually able to coordinate their action to achieve a common goal, by modulating their behavior on the basis of the new task demands imposed by the dyadic context (Visco-Comandini et al. 2015). We showed that inter-individual motor coordination comes with a cost, which affects performance, in non-human primates (Visco-Comandini et al. 2015) but also in humans whose joint-action abilities emerge during childhood (Satta et al. 2017). At the neural level, a first evidence of the representation of joint-action performance has been provided (Ferrari-Toniolo et al. 2019a), with the findings

of the population of ‘joint-action neurons’, a dedicated set of cells that changed their activity when the monkeys performed a given action in a dyadic context.

With the current work, we aimed at investigating whether and how pre-instruction cues providing anticipatory information about action context (individual vs dyadic) of future action can influence the dyadic behavior in non-human primates. This allowed us to test for the existence of a putative “We-representation” in monkeys that, similarly to that hypothesized in humans, may facilitate joint performance (Kourtis et al. 2019, Della Gatta et al 2017; Sacheli et al. 2018) by shaping action intentions at group level. Our hypothesis is that if the animals lack the sense of “we-ness” (Gallotti & Frith, 2013), a pre-cue provided about action context (SOLO vs TOGETHER) should not influence joint behavior, since an identical motor representation would be adopted by the animals, whether acting alone or together. On the contrary, if joint action plans rest on a predictive representation of the collective action, and therefore a “we-representation” is available, pre-cuing the type of representation (I vs we) of future action should benefit joint performance. To this purpose, we analysed the effect of pre-cuing on task performance, as well as the most relevant spatiotemporal aspects of task execution that we deemed to be implied in the success of inter-individual motor coordination.

To inquire these aspects, three couples of monkeys have been trained to perform an isometric task in two alternative conditions: individually (SOLO) or in coordination with the partner (TOGETHER). In both instances, a typical center-out task was adopted, consisting in guiding a visual object from the center of the screen towards an outer goal shown in one of the eight possible directions by applying a hand force on an isometric joystick. In this case, the directional array was adopted to increase the level of re-adaptation demand of the individual kinematic in both contexts, thus allowing the analysis of the behavior under a wider range of “motor scenarios”.

Two variations of the same task were adopted: the *no-Pre-Instructed task* (noPI), in which the social cue and the direction of the force to be applied were provided simultaneously (i); the *Pre-Instructed task* (PI), in which the social condition was instructed first and, after a certain delay period (instruction delay time, IDT), the information about the force direction was available. In the latter case, we imposed on the monkeys a sequential information coding, which we expected to allow them to prepare first the type of action required (individual or joint) and only subsequently to combine it with the appropriate, subtask-specific (i.e., direction-dependent), motor plan.

Methods

Animals

Five rhesus monkeys were used for this experiment (*Macaca mulatta*, all males): Monkey S, 6.5 Kg; Monkey K, 7.5 Kg; Monkey C, 9 kg; Monkey D, 8.5 Kg; Monkey D*, 11.5 Kg; Monkey P, 11 Kg. Monkey D* indicates data obtained from Monkey D tested around one year later. All efforts were made to optimize animal welfare. Animal care and housing procedures were in conformity with European (Directive 63-2010 EU) and Italian (DL. 116/92 and DL. 26/2014) laws on the use of non-human primates in scientific research.

Experimental apparatus

The five animals were paired to form three couples, as follows: Monkeys S and K (couple SK); Monkey C and D (couple CD); Monkey D* and P (couple DP).

The experimental set-up was conceived to minimize any potential interaction outside the task, to avoid potential source of interfering, uncontrolled variables.

During the experiment, each couple was placed in a darkened chamber. The two monkeys seated side-to-side on two primate chairs in front of a 40-inch monitor (100 Hz, 800-600 resolution, 32-bit color depth; monitor-eye distance: 150 cm; Fig. 1). A security distance of 60

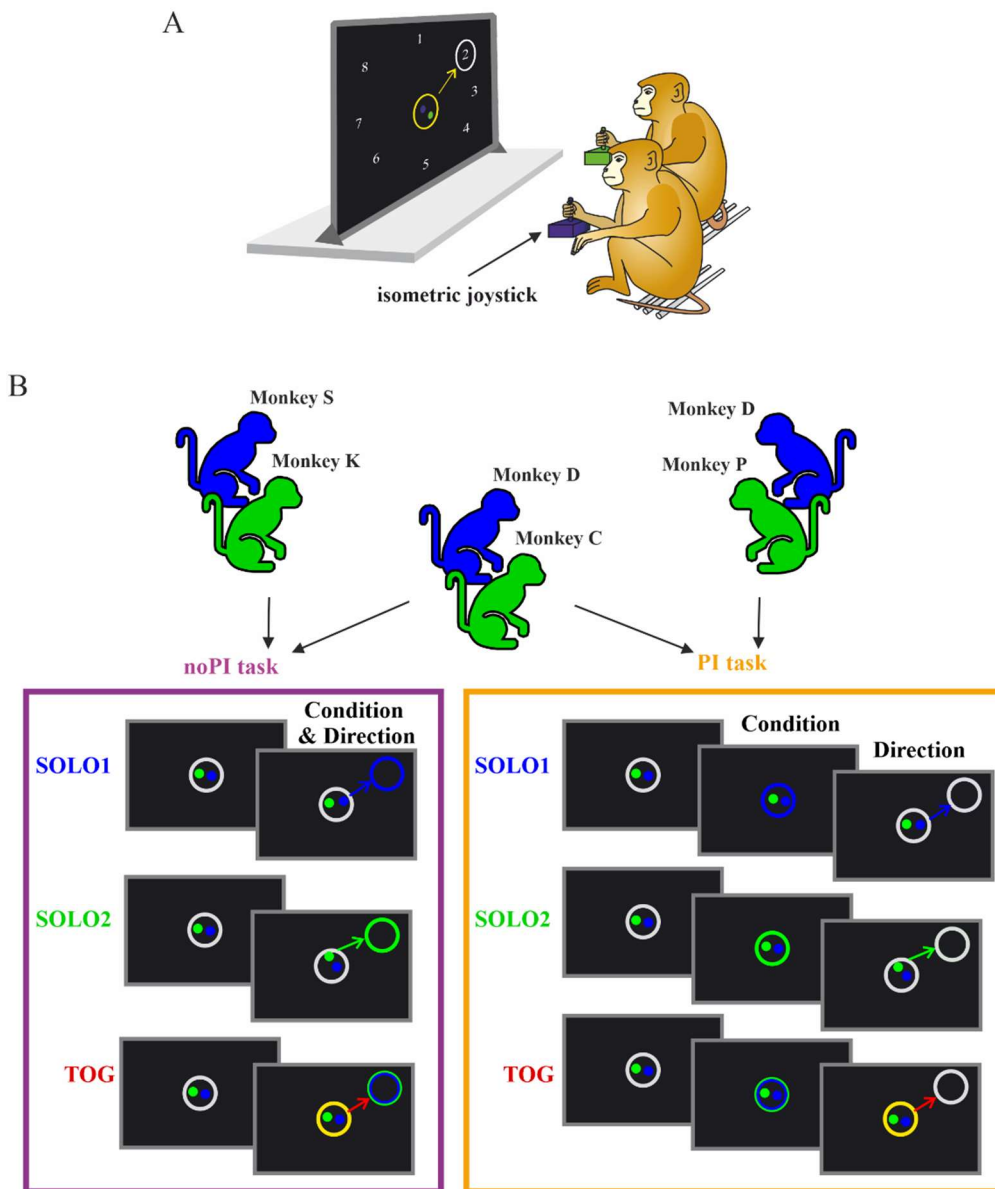


Figure 1. Experimental setup. (A) Two monkeys were placed in a darkened, sound-attenuated chamber and seated side-to-side on primate chairs in front of a common monitor. Both monkeys exerted a force on an isometric joystick to displace a colored visual cursor from a central control position toward a target located at one of eight possible locations on the screen, at 45° intervals on a circumference at 10 DVA radius. (B) The three couples were assigned to the different type of task as follows: SK couple performed the no-PI task (SKnoPI), DP performed the PI task (DPPI), while CD couple performed both the no-PI and the PI tasks. In the noPI task, the condition (SOLO1, SOLO2 or TOGETHER) and the direction of movement were instructed simultaneously. In the PI task, instead, trial type was pre-instructed by a delay time of 700-100ms, after which target location was shown. In the SOLO condition each monkey performed the task alone. In the TOGETHER condition, both monkeys had to cooperate in order to reach a common target, by adjusting in time both the intensity and direction of their force pulses on the respective joystick.

cm was always guaranteed, in order to prevent physical contact. The orientation and structure of the chair minimized also visual contact. During the experiment, monkeys were required to use always the same arm, while the other was gently restrained. Each animal was trained to

control a colored circular cursor (diameter: 0.6 degrees of visual angle; DVA) displaced on a black screen by applying a hand force on an isometric joystick (ATI Industrial Automation, Apex NC) in the two dimensions on the horizontal plane (sampling frequency: 1 kHz). The applied force was proportionally converted into a movement of the cursors on the x and y axis of the vertical plane of the monitor. The NIH-funded software package REX was used to control stimuli presentation and to collect behavioral events and force data.

Behavioral task

All monkeys performed an isometric directional center-out task in two intermingled conditions (SOLO and TOGETHER). Each recorded session could be of two types, depending on the variant of the same task that was adopted. In the first version, the information about condition and direction of each trial were provided all in once in a reaction-time paradigm (not Pre-Instructed task; no-PI). In the second version, the two information were instructed sequentially, with a delay period during which the action condition was pre-instructed. We defined the first task as not pre-instructed (no-PI) and the second one as pre-instructed (PI). Both tasks begun identically, with the presentation of an outlined light gray circle (2 DVA in diameter) on the center of the screen, and each animal had to bring its cursor inside the circle and hold it there for a variable control time (CHT, 500-1000ms).

After the CHT period, in the no-PI task, a peripheral target (outlined circle, 2 DVA in diameter) was presented in one of eight possible positions (at 45° angular intervals) at an eccentricity of 8 DVA. The target's color instructed the animals about the type of action (SOLO or TOGETHER condition) required to obtain a liquid reward. In this task's version, the action condition and future force direction were simultaneously instructed and following the appearance of this peripheral target (GO signal) the animals were required to bring their own cursors (together or in a solo fashion), on the new location to get the reward, within a given RT (100-800ms).

In the PI task, instead, the CHT was followed by an instruction delay time (IDT, 1000-1500ms), which started with the color change of the central target. This new color cued the monkeys on the future action condition (SOLO or TOGETHER) to be performed. During the IDT the animals were required to maintain their cursors within the central target, and when a light gray peripheral target (GO signal) appeared in one of the eight possible directions, they had to bring their own cursor toward the peripheral location, again within a given RT (100-800ms), together or individually, as instructed by the color of the central target during the IDT.

Cursors' and instructing targets' colors were always univocal for each monkey. In each dyad, monkey 1 was associated to blue and monkey 2 was associated to green. The SOLO condition for each monkey was thus instructed by one of these colors, while the TOGETHER condition was instructed by a bi-colored (blue and green) circumference.

In the SOLO1/SOLO2 condition, a blue/green circle was presented, and Monkey 1/2 was instructed to move its own cursor within the peripheral target, by applying a dynamic force on the joystick. It was then required to maintain the cursor on that final position for a variable target holding time (THT: 100-200ms) to gain a reward (0.5 ml of fruit juice). During SOLO1 and SOLO2 trials, instead each relative partner was required to keep holding its cursor inside the central target for the entire duration of the trial, to gain the 50% of the same liquid treat, irrespective of the partner's action success. In the TOGETHER condition, when the peripheral target was presented, both monkeys had to move their cursors towards it in a coordinated fashion, to both gain the same amount of reward provided for a successful SOLO action (0.5 ml), after holding the final position for a variable THT (100-200ms). For the entire duration of their cursors' movement, monkeys were constrained to stay within a maximum inter-cursor distance (ICD_{max}) of 5 DVA, which was remarked by a yellow circle encompassing the two cursors. The instantaneous position of the center of said visual object coincided with the mean value of the x and y coordinates of the two cursors. An $ICD > ICD_{max}$ resulted in the trial abortion and none of the two agents obtained the reward. This case was defined as inter-cursor distance error.

Trials corresponding to different action conditions (SOLO1, SOLO2, TOGETHER) and different directions were presented in an intermingled fashion and pseudo-randomized within a session of minimum 192 successful trials (3 conditions, 8 directions, 8 replications). The number of session collected was different for each pair. For SK and for DP pairs, 72 and 41 sessions were collected, respectively. For CD couple, instead, 12 sessions for the no-PI task, and 13 sessions for the PI task were acquired.

The couples were assigned to the different type of task as follows: SK couple performed the no-PI task (SK_{noPI}), DP performed the PI task (DP_{PI}), while CD couple performed both the no-PI and the PI tasks, in the sequence CD_{noPI} and then CD_{PI} .

Behavioral indexes

Successes and errors

For each pair as an index of performance we have computed the success rate both for SOLO and TOGETHER conditions, independently on the direction factor, to allow the overall comparison between conditions. In addition, for the TOGETHER condition, the inter-cursor distance error rate (ER_{ICD}) was also calculated and used as a more precise inverse index of performance goodness in this condition.

Reaction time and cursor peak velocity

The reaction time (RT) in each task was defined as the time elapsing from the presentation of peripheral target to the onset of the cursor's movement, which corresponded to the onset of the dynamic force application. Following this definition, RT was calculated as the time at which, for at least 90ms, the cursor's velocity exceeded by three standard deviations (SD) the average velocity signal from 50ms before to 50ms after the presentation of peripheral target. This measure was computed for each trial of each session.

The peak velocity (PV) was estimated for each trial of each session, as the maximum value of the cursor's tangential velocity.

Inter-individual differences

Inter-individual differences in reaction time (IID_{RT}) and in peak velocity (IID_{PV}) between the two subjects of each dyad were computed in both task's conditions. For SOLO condition, this index indicated the "starting" differences between the two subjects when working independently from one another. For TOGETHER condition, IID represented the degree of achieved inter-individual motor coordination. In particular, for each j -th session the indexes IID_{RT} and IID_{PV} were computed as the absolute value of the median difference between monkeys' RTs and PVs observed during all SOLO or TOGETHER trials, as follows:

$$IID_{RT,SOLO}(j) = \left| \frac{\sum_{i=1}^N (RT_{SOLO1,i}(j) - RT_{SOLO2,i}(j))}{N} \right|$$

$$IID_{PV,SOLO}(j) = \left| \frac{\sum_{i=1}^N (PV_{SOLO1,i}(j) - PV_{SOLO2,i}(j))}{N} \right|$$

$$IID_{RT,TOGETHER}(j) = \left| \frac{\sum_{i=1}^N (RT_{TOGETHER1,i}(j) - RT_{TOGETHER2,i}(j))}{N} \right|$$

$$IID_{PV,TOGETHER}(j) = \left| \frac{\sum_{i=1}^N (PV_{TOGETHER1,i}(j) - PV_{TOGETHER2,i}(j))}{N} \right|$$

Where i is the trial number, j is the session number and N is the total number of trials for the considered session.

Statistical analysis

We chose Shapiro-Wilk test to assess the normality of samples, since its power has been demonstrated to be the highest among equivalent tests (Razali & Wah, 2011). When samples were not normally distributed, non-parametric statistical test were applied.

Kruskal-Wallis test was adopted to compare success rates (SR) between SOLO1, SOLO2 and TOGETHER trials (factor: ‘trial type’, 3 levels), within each experiment. Dunn-Šidák test was used for multiple comparison between groups.

Wilcoxon rank sum test was applied to evaluate the performance in the no-PI and PI tasks (Factor: ‘Delay’, 2 levels), first by pooling pairs from the same task group, then by matching different couples that performed only one type of task (independent samples: SK_{noPI} vs DP_{PI}; SK_{noPI} vs DC_{PI}; SK_{noPI} vs DP_{PI}; DC_{noPI} vs DP_{PI}) and, finally, by using the data collected on the same couple (dependent samples: DC_{noPI} vs DC_{PI}) performing both the no-PI and PI task.

To evaluate whether the kinematic profile of each monkey could change depending on the movement condition, we performed a Wilcoxon rank sum test, in which SOLO and TOGETHER RTs and PVs were compared. This test was performed for each monkey within each dataset.

To inquire if there was a motor identity (i.e., a “individual motor signature”) that made it possible to distinguish one monkey’s behavior from another on the basis of its kinematic profile, RTs and PVs in SOLO condition were compared across monkeys, first within the no-PI group and then within the PI group (Kruskal-Wallis test, factor: monkey, 4 levels). Dunn-Šidák test was used to compare significant difference between all groups.

To identify whether the individual RTs and PVs varied with direction of force application in SOLO condition, a Kruskal-Wallis test (Factor: Direction, 8 levels) was also performed for each monkey.

To evaluate whether inter-individual differences in RTs and PVs correlate with TOGETHER performance goodness, we resorted to a repeated measure correlation method (‘rmcorr’ package, Bakdash & Marusich, 2018). IID_{RT}/IID_{PV} and ER_{IDC} were calculated for each kinematic context (i.e. direction) within each session. The number of sessions was considered as a repetition. Therefore, each correlation was ultimately performed on a pool of $8 \times n$ values, where n is the number of sessions for each dataset and kinematic parameter.

We then investigated the effect of the presence of a pre-instruction phase in the task (IP task) on monkey’s kinematics, in both SOLO and TOGETHER conditions. To this aim, we performed a Wilcoxon rank sum test, both by pooling all monkeys second to task group (no-IP

and IP) and by comparing the effect of pre-instruction on the kinematic of Monkey D and Monkey C from DC couple's datasets.

Finally, a Wilcoxon rank sum test was performed to enquire the effect of pre-instruction on IID_{RT} and IID_{PV} in TOGETHER condition, again both by pooling our datasets depending on the presence or absence of pre-instruction (no-IP and IP task groups), and by comparing the effect of pre-instruction on inter-individual differences couple DC's kinematics.

Excluding correlations, all statistics were performed with the aid of MATLAB software (R2019a).

Results

Performance across conditions and tasks

Our first goal was to identify a potential effect on the behavior of the context a given action is executed (SOLO vs TOGETHER) and the influence of the order in which instructions about the type of action and force directions, are provided (Figure 2). To this aim we compared (Fig. 2) the overall monkey success rates between action conditions and task versions (PI vs noPI).

First, success rates in SOLO1, SOLO2 and TOGETHER trials have been compared for each of the four datasets (Fig. 2A). A significant difference across these three trial types was found

dataset	Trial Types compared		SR
SK _{noPI}	SOLO 1	SOLO 2	0.8427
	SOLO 1	TOGETHER	0
	SOLO 2	TOGETHER	0
DC _{noPI}	SOLO 1	SOLO 2	$9.25 \cdot 10^{-04}$
	SOLO 1	TOGETHER	$6.77 \cdot 10^{-11}$
	SOLO 2	TOGETHER	0
DP _{PI}	SOLO 1	SOLO 2	0.1561
	SOLO 1	TOGETHER	0
	SOLO 2	TOGETHER	0
DC _{PI}	SOLO 1	SOLO 2	0
	SOLO 1	TOGETHER	0
	SOLO 2	TOGETHER	0.9763

Table 1. Multiple comparisons of performance for trial types. P values from post hoc analysis with Dunn-Šidák test. See figure 2A for medians representation.

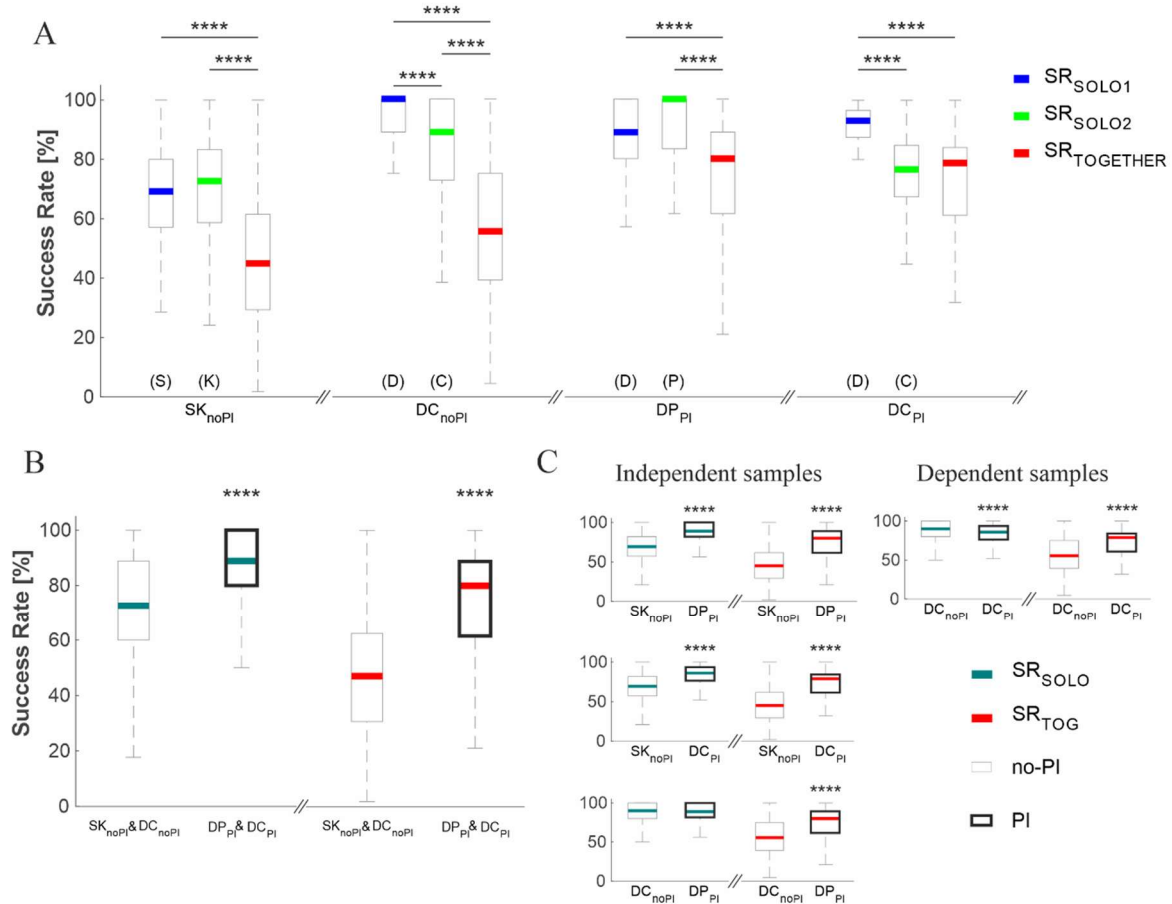


Figure 2. Performance. (A) Success rates (SR) comparison between SOLO1, SOLO2 and TOGETHER performed for all datasets, revealed lower SR for TOGETHER condition.

(B) Success rates (SR) comparison between no-PI and PI groups showed that the presence of a pre-instruction improves performance in SOLO and TOGETHER condition. (C) When comparing SR for no-PI and PI within different pairing of datasets, an improvement in performance related to the factor delay is confirmed only for TOGETHER condition.

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, **** = $p < 0.0001$

in all four cases (Kruskal-Wallis test; SK_{noPI}: $\chi^2(2) = 393.94$, $p = 2.86 \cdot 10^{-86}$; DC_{noPI}: $\chi^2(2) = 109.18$, $p = 1.96 \cdot 10^{-24}$; DP_{PI}: $\chi^2(2) = 149.58$, $p = 3.30 \cdot 10^{-33}$; DC_{PI}: $\chi^2(2) = 134.15$, $p = 7.41 \cdot 10^{-30}$).

Post hoc analysis (Table 1) revealed a significant reduction of the success rates for the TOGETHER condition with respect to the SOLO performances, in all instances with the exception of monkey C during the experiment with pre-instruction (C_{PI}), for which the high success rate shown in the TOGETHER condition in CD_{PI} sessions was not statistically different from its SOLO performance.

We then assessed if the performance of our groups was further influenced by the presence (PI) or absence of a pre-instruction phase (noPI) in the task (Fig. 2B). A significant improvement of performance was observed when the pre-instruction (PI) was provided, both in the SOLO

Data		Z	P
SK _{noD} vs DP _D	SR _{SOLO}	-22.87	9.96 · 10 ⁻¹¹⁶
	SR _{TOGETHER}	-16.51	2.92 · 10 ⁻⁶¹
SK _{noD} vs DC _D	SR _{SOLO}	-11.01	3.43 · 10 ⁻²⁸
	SR _{TOGETHER}	-11.11	1.08 · 10 ⁻²⁸
DC _{noD} vs DP _D	SR _{SOLO}	-0.32	0.7466
	SR _{TOGETHER}	-6.21	5.35 · 10 ⁻¹⁰
DC _{noD} vs DC _D	SR _{SOLO}	5.29	1.22 · 10 ⁻⁷
	SR _{TOGETHER}	-5.19	2.15 · 10 ⁻⁷

Table 2. Pre-instruction effect on performance. Wilcoxon rank sum test results. See figure 2C for medians representation.

and TOGETHER conditions (SR_{SOLO} Z = -20.32, p = 8.61 · 10⁻⁹²; SR_{TOGETHER} Z = -17.69, p = 5.00 · 10⁻⁷⁰). To check for a potential bias on the results due to a markedly lower performance for SK_{noPI} couple (Fig. 2A), we compared the success rates within three pairings of independent samples (SK_{noPI} vs DP_{PI}, SK_{noPI} vs DC_{PI} and DC_{noPI} vs DP_{PI}) and between the two dependent samples, obtained from testing the same couple on both versions of the task (DC_{noPI} vs DC_{PI}). As shown in Fig. 2C, in all cases a systematic amelioration emerged only in the joint action performance when a delay period pre-instructed the type of action to be performed to achieve the goal. The higher performance in the PI task associated to the SOLO condition, instead, was not observed in all instances. It was evident only when SK_{noPI} couple was included in the comparison, thus confirming the evidence of a general lower performance of these two monkeys, irrespective of the pre-instruction factor (Table 2).

In conclusion, a cue allowing the animal to prepare in advance the action jointly with another partner was beneficial to improve particularly dyadic performance. This result arises a question on why the pre-instruction has this facilitatory effect and whether it affects some particular aspects of motor behavior that might favour inter-individual coordination.

Effect of condition on monkeys' kinematics

To answer the question about which features of kinematics is affected by the presence of the pre-instruction signal, we focused on two parameters, as the reaction times (RTs) and peak of velocities (PVs), representative of the planning and execution phases of our isometric task, respectively. The modulation of these variables during joint performance respect to solo actions has already been documented in our previous study (Visco-Comandini et al. 2015).

In the present study we have re-evaluated the effect of type of action on kinematic profiles but analysing it separately for the noPI and PI sessions (Figure 3, Table 3).

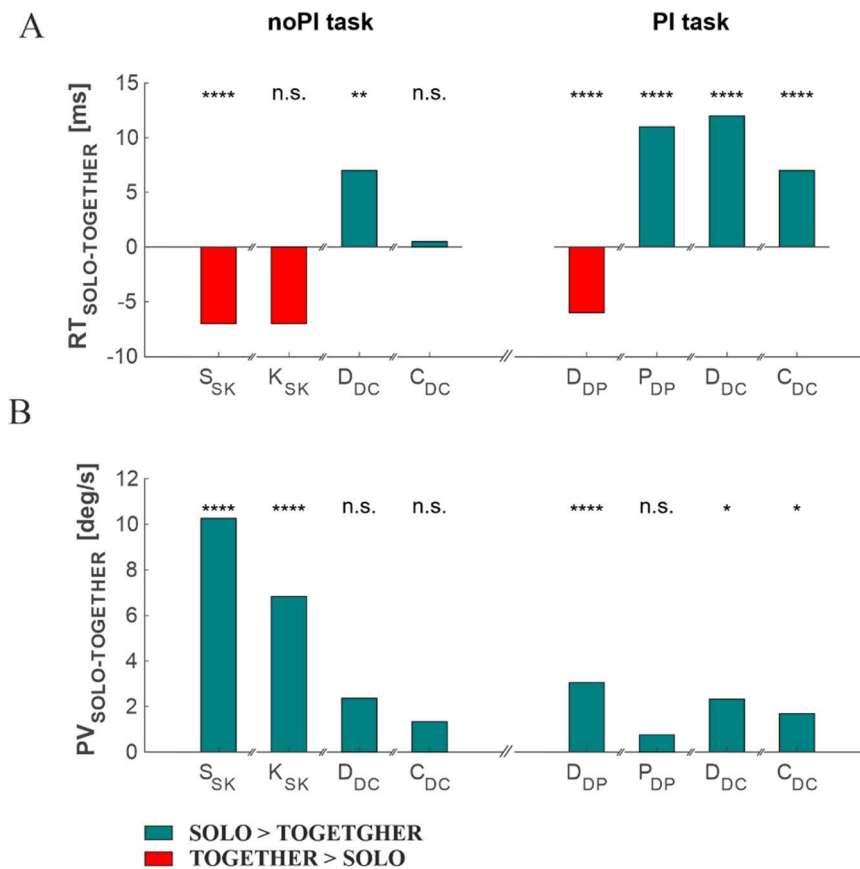


Figure 3. Effect of condition factor on kinematics. (A) Difference between the median RTs of SOLO and TOGETHER conditions. (B) Difference between the median PVs of SOLO and TOGETHER conditions.

A significant difference between SOLO and TOGETHER condition is indicated with the * symbol. The direction of such difference (SOLO > TOGETHER or TOGETHER > SOLO) is color coded (see legend).

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, **** = $p < 0.0001$

When pre-instructed about the future condition in which the action should have been executed (PI), three monkeys out of four showed a marked decrease of RTs in the TOGETHER condition with respect to the SOLO one (Fig. 3A). In absence of a pre-instruction of action type the results varied across animals. (Fig. 3A).

Looking at the execution phase of the task, we found that the peaks of velocity (PVs) were instead always reduced or at most remained unchanged when acting jointly respect to when the animal performed the task individually. This was true independently on the anticipatory instructions available to the animals.

These findings suggested that there are some behavioral invariances, such as the slowdown of cursor velocity during the TOGETHER condition and the tendency to reduce the RTs in the

		Data	Z	P	Fig.
RT	no-DELAY	S _{SK}	-9.10	$9.24 \cdot 10^{-20}$	3A
		K _{SK}	-0.18	0.8609	
		D _{DC}	2.86	0.0043	
		C _{DC}	1.22	0.2222	
	DELAY	D _{DP}	-7.81	$5.86 \cdot 10^{-15}$	
		P _{DP}	10.41	$2.17 \cdot 10^{-25}$	
		D _{DC}	11.99	$3.78 \cdot 10^{-33}$	
		C _{DC}	6.61	$3.90 \cdot 10^{-11}$	
PV	no-DELAY	S	24.84	$2.96 \cdot 10^{-136}$	3B
		K	17.53	$8.81 \cdot 10^{-69}$	
		D _{DC}	1.50	0.1326	
		C _{DC}	0.75	0.4531	
	DELAY	D _{DP}	10.40	$2.35 \cdot 10^{-25}$	
		P _{DP}	1.74	0.0818	
		D _{DC}	1.97	0.0487	
		C _{DC}	2.36	0.0183	

Table 3. Effect of condition on kinematics. Wilcoxon rank sum test.

joint performance particularly in presence of a PI delay period. However, we also observed a variety of inter-individual differences in the way each animal cope with the dyadic context. The next step was therefore to understand if and how these differences between the two interacting partners, can explain the emergence of different strategies and how those differences can be influential on the goodness of joint performance.

Individual and inter-individual differences during solitary action

We have shown that the animals did modulate their behavior during joint performance, respect to their individual action, although not in a univocal fashion. Hence, we wondered whether the way each monkey responded to the demands imposed by the joint contexts, could be explained by the degree of inter-individual differences between motor profiles of the two members of the dyads. To this aim, we first evaluated to which extent monkeys differed one another in their individual kinematic profiles, shown by the subjects when acting alone, i.e., during SOLO condition (Fig. 4).

We found a significant difference in RTs measured during SOLO condition across monkeys, both in no-PI and PI databases (noPI: $\chi^2(3) = 3121.48$, $p = 0$; PI: $\chi^2(3) = 6383.59$, $p = 0$; Fig.

4A). Similarly, also PVs differed across monkeys in both task types (noPI: $\chi^2(3) = 1777.90$, $p = 0$; PI: $\chi^2(3) = 5282.21$, $p = 0$; Fig. 4C). Post-hoc analysis confirmed that monkeys' behavior differed in at least one kinematic measure (Fig. 4B-D); p values in Table 4). We concluded, thus, that each monkey showed an individual kinematic profile, which made its cursor's motion

	Monkeys compared		RT	PV
no-DELAY	S - SK_{noD}	K - SK_{noD}	0	0
	S - SK_{noD}	D - DC_{noD}	0	0
	S - SK_{noD}	C - DC_{noD}	0	0
	K - SK_{noD}	D - DC_{noD}	0.9857	0
	K - SK_{noD}	C - DC_{noD}	0.0261	0
	D - DC_{noD}	C - DC_{noD}	0.4906	0.0211
DELAY	D - DP _D	P - DP _D	0	0
	D - DP _D	D - DC _D	0	0
	D - DP _D	C - DC _D	0	0
	P - DP _D	D - DC _D	0	0
	P - DP _D	C - DC _D	0	0
	D - DC _D	C - DC _D	0.0020	0.3025

Table 4. Multiple comparisons of kinematics between monkeys. P values from post hoc analysis with Dunn-Šidák test. See figure 4 (panels B and D) for an overall view.

distinguishable from the others'.

Data		Factor	df	χ^2	P	Fig.	
RT	SK_{noD}	S	Direction	7	176.33	$1.16 \cdot 10^{-34}$	4A
		K			143.71	$8.50e \cdot 10^{-28}$	
	DC_{noD}	D			145.21	$4.10 \cdot 10^{-28}$	
		C			107.07	$3.72 \cdot 10^{-20}$	
	DP _D	D			274.57	$1.61 \cdot 10^{-55}$	
		P			422.39	$3.76 \cdot 10^{-87}$	
	DC _D	D			910.42	$2.70 \cdot 10^{-192}$	
C		153.96			$5.98 \cdot 10^{-30}$		
PV	SK_{noD}	S			731.41	$1.16 \cdot 10^{-153}$	4B
		K			683.76	$2.19 \cdot 10^{-143}$	
	DC_{noD}	D			11.38	0.1228	
		C			35.56	$8.79 \cdot 10^{-6}$	
	DP _D	D			78.02	$3.49 \cdot 10^{-14}$	
		P			163.34	$6.35 \cdot 10^{-32}$	
	DC _D	D	75.63	$1.07 \cdot 10^{-13}$			
C		19.65	0.0064				

Table 5. Inter-individual differences in kinematics. Kruskal-Wallis test. See Figure 4 (panels A and B) for medians representation.

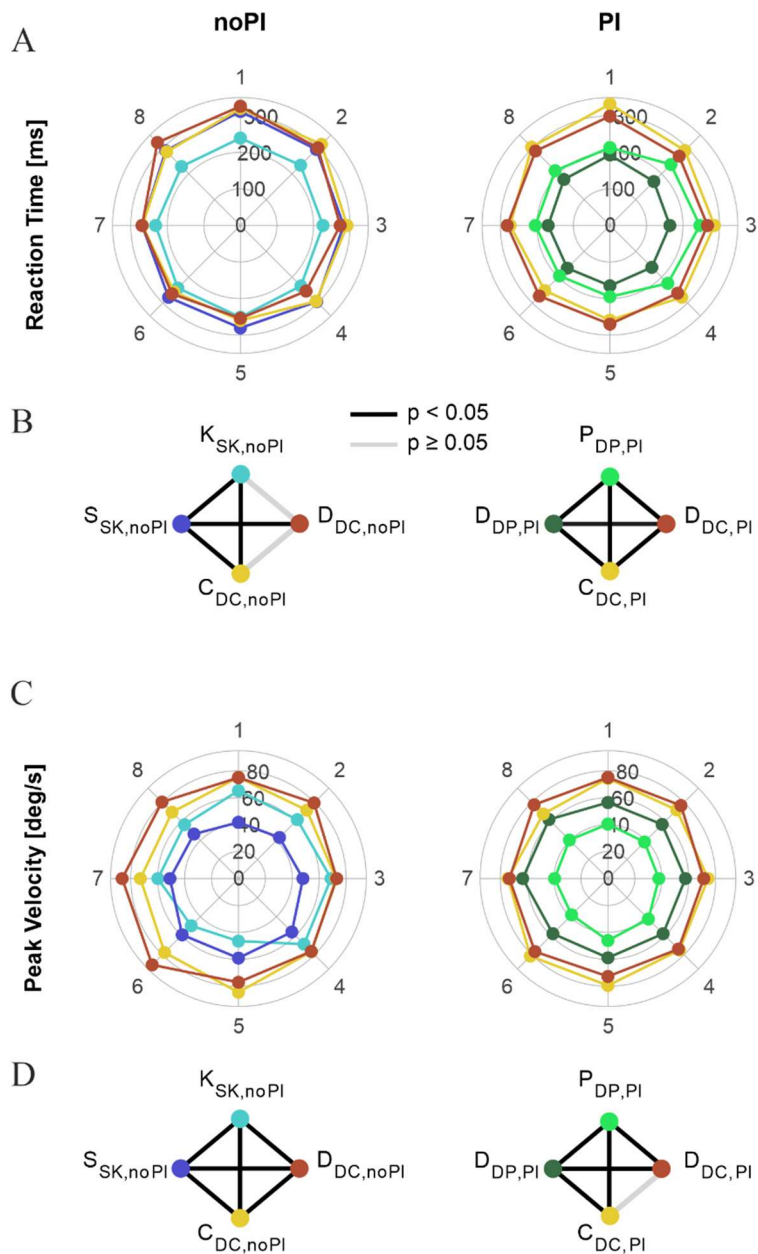


Figure 4. Inter-individual differences in kinematics during SOLO condition. (A) Median RTs for each monkey and direction measured during the SOLO condition for both no-PI and PI groups. (B) Overall representation of significant differences in RTs between pairs of monkeys. (C) Median PVs for each monkey and direction, measured during the SOLO condition for both noPI and PI groups. (D) Overall representation of significant differences in PVs between pairs of monkeys. In B,D black/gray segment indicates significant differences between RTs (B) and PVs (D) of the monkeys reported at the vertex of the diamond. For each monkey it is reported the database of reference.

Furthermore, we found that for each monkey both kinematics parameters significantly differed across directions, with the only exception of Monkey D's PVs within DC_{noPI} couple dataset (Fig. 4A-B; Table 5).

The question is whether the difference between the two “idiosyncratic” patterns shown by the individuals forming a dyad, as measured when they act independently from each other, predict their performance in TOGETHER condition.

Individual and inter-individual differences in TOGETHER performance

Once established a difference in individual kinematic profiles, we tested whether inter-individual differences evident in the kinematic profiles – which emerged in SOLO condition – correlated with performance in the TOGETHER condition (Fig.5).

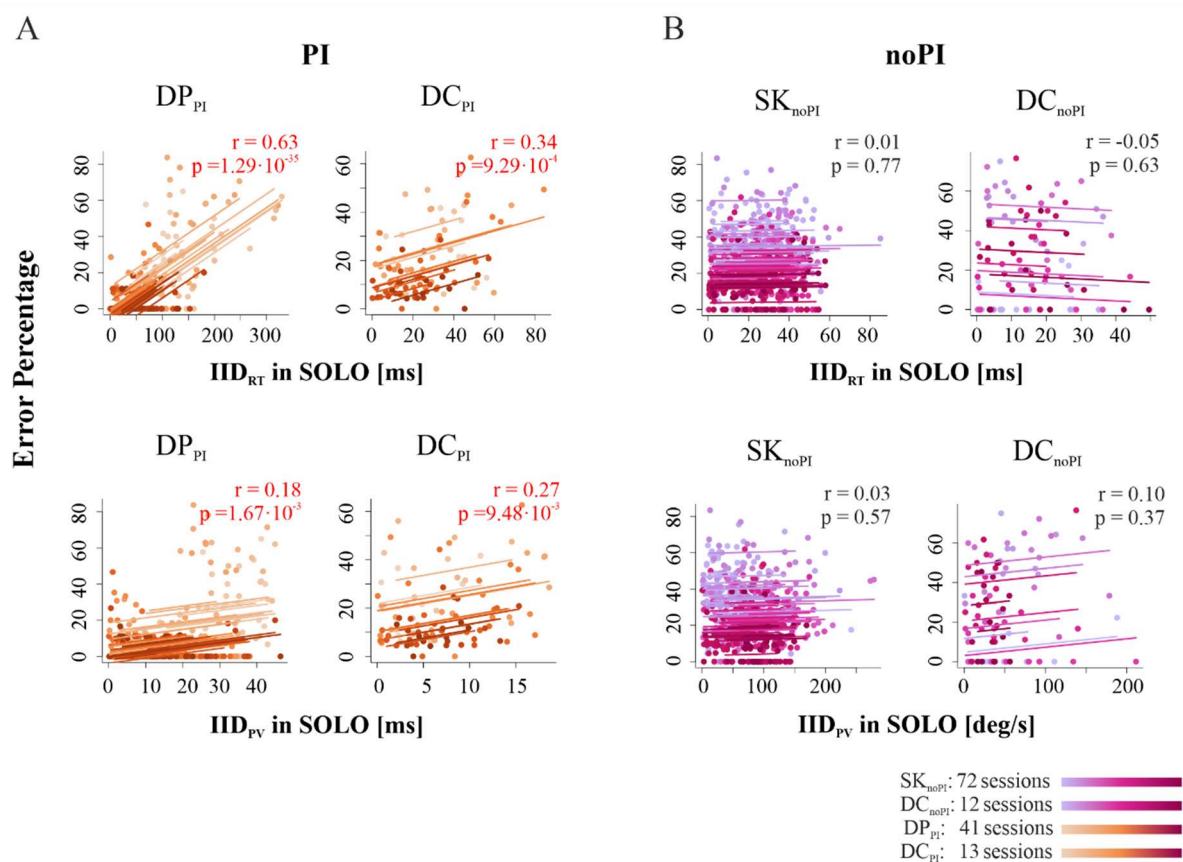


Figure 5. Inter-individual differences and TOGETHER performance. (A) Repeated measure correlation between mean IID_{RT} and ER_{IDT} and between mean IID_{PV} and ER_{IDT} for PI datasets. (B) Repeated measure correlation between mean IID_{RT} and ER_{IDT} and between mean IID_{PV} and ER_{IDT} for no-PI datasets.

Each point represents the combination of the two correlated variables for a n direction (1 to 8) in a n session (i.e. replication). Replications are color coded as in the legend.

In this case, we considered as a measure of the goodness of performance the inter-cursor distance error rate (ER_{ICD}), under the assumption that this index might reflect with more accuracy inter-individual motor coordination failure.

The extent of inter-individual differences in RTs and PVs was correlated with the probability to execute successfully the joint-action trials. Interestingly, we found that inter-individual

differences in RTs and PVs correlated significantly with errors in TOGETHER performance only when the type of action was pre-instructed in advance (PI task; Fig. 5A), while there was no evidence of such a correlation when the future action context was not pre-cued (Fig. 5B). Based on this observation, we further investigated how the pre-instruction of the movement condition (SOLO or TOGETHER) affected monkeys' behavior to result in the demonstrated facilitation of task execution in TOGETHER condition.

Effect of pre-instruction on monkeys' kinematics

In order to understand how the presence of a pre-instruction could improve TOGETHER performance, we first investigated how it influenced monkeys' behavior (Fig. 6). This analysis was first conducted by pooling all monkeys' kinematic parameters ('All' in Fig. 6 A-B) in two

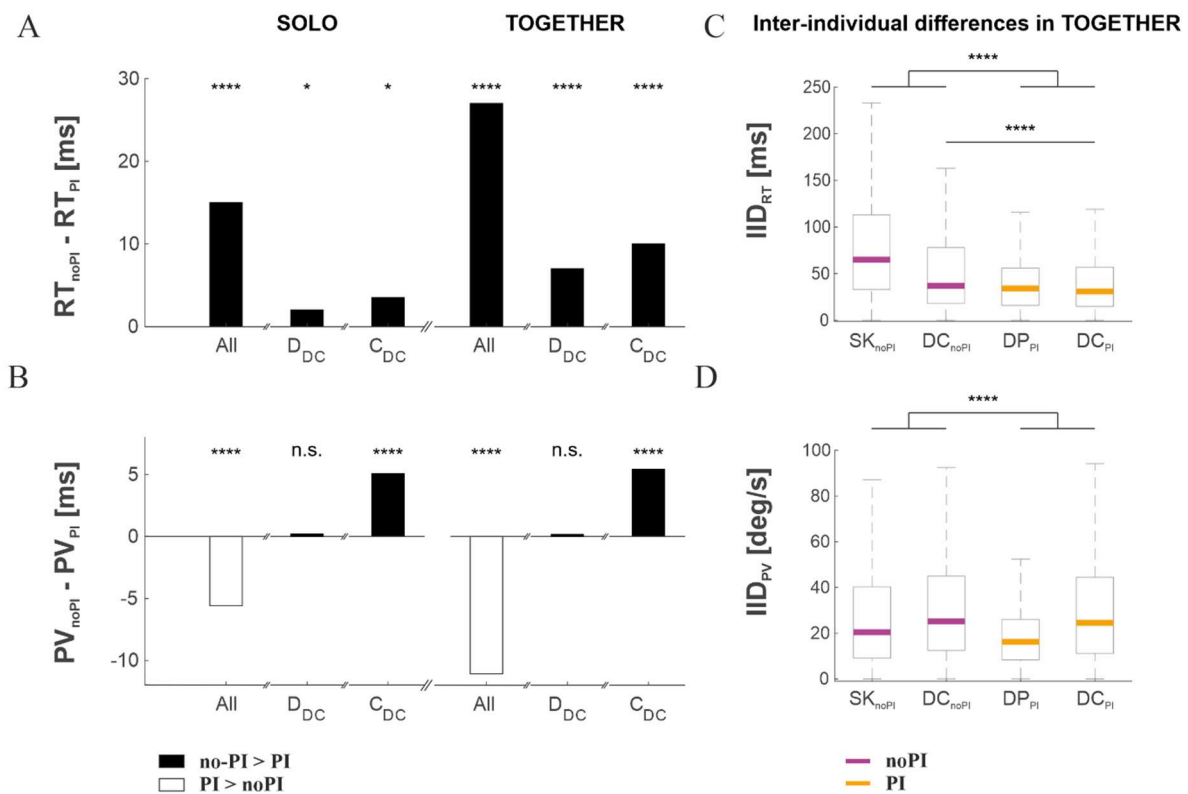


Figure 6. Influence of pre-instruction on movement condition on kinematics.

(A) Difference between the median RTs of noPI and PI task types, for all monkeys and for monkey D_{DC} and C_{DC}. (B) Difference between the median PVs of noPI and PI task types, for all monkeys and for monkey D_{DC} and C_{DC}. (C) Median inter-individual differences in RTs for each couple and task type in TOGETHER condition. (D) Median inter-individual differences in PVs for each couple and task type in TOGETHER condition.

The direction of such difference (noPI > PI or PI > noPI) is color coded (see legend).

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, **** = $p < 0.0001$

groups depending on the task version performed (i.e., no-PI and PI). As a confirmation of the obtained results, the same analysis was performed again for Monkey D and C (couple DC), which undertook both versions of the task.

	Data		Z	P	Fig.
RT	SOLO	All	26.48	$1.58 \cdot 10^{-154}$	4A
		D _{DC}	2.33	0.0196	
		C _{DC}	2.48	0.0130	
	TOGETHER	All	40.81	0	
		D _{DC}	4.42	$9.85 \cdot 10^{-6}$	
		C _{DC}	3.98	$6.86 \cdot 10^{-5}$	
PV	SOLO	All	-21.79	$2.95 \cdot 10^{-105}$	4B
		D _{DC}	0.50	0.6166	
		C _{DC}	4.56	$5.13 \cdot 10^{-6}$	
	TOGETHER	All	-40.85	0	
		D _{DC}	-0.38	0.7069	
		C _{DC}	4.61	$4.11 \cdot 10^{-6}$	
TOGETHER	IID _{RT}	All	36.12	$1.22 \cdot 10^{-285}$	4C
		DC	4.98	$6.27 \cdot 10^{-07}$	
	IID _{PV}	All	4.50	$6.75 \cdot 10^{-6}$	4D
		DC	0.50	0.6176	

Table 6. Inter-individual differences in kinematics. Wilcoxon rank sum test. See Figure 4 (panels A and B) for medians representation.

When pooling the data from all animals, we found that the pre-instruction about action condition reduced RTs both in SOLO and TOGETHER conditions (‘All’, Fig. 6A). This result was confirmed by comparing RTs in no-PI and PI tasks for monkey C and monkey D (Fig. 6A, Table 6). As for PVs, a significant increase of PVs for the pre-instructed trials was observed when pooling all datasets, both in SOLO and TOGETHER conditions (‘All’; Fig. 6B). However, this result could not be confirmed for monkey C and D, which either not changed or decreased their PVs (Fig. 6B, Table 6). We hypothesized hence that the result obtained by pooling all databases (‘All’ no-PI vs ‘All’ PI) could be biased by interindividual differences between subjects, in particular comparing SK_{noPI} and DP_{PI} behavior, that might not depend on the type of task *per se*.

In summary, we observed that the presence of pre-instruction anticipated cursor’s movement onset and occasionally decreased cursor’s speed in all task conditions. We concluded that pre-cuing action context might provide an optimal “kinematic setting” that ultimately could make inter-individual motor coordination easier. We therefore wonder if this facilitation effect could

be reflected in a reduction of inter-individual differences when the animals had to coordinate their action.

Pre-instruction optimizes inter-individual coordination in TOGETHER condition

We previously found that inter-individual differences in SOLO condition correlate with TOGETHER performance only for couples performing the PI task. We also showed that pre-instruction modifies monkey's kinematics, particularly by decreasing RTs and occasionally increasing PVs. We wonder then whether the presence of a pre-instruction was able to facilitate inter-individual coordination by reducing RTs and PVs inter-individual differences in TOGETHER condition.

We found that when provided of a pre-instruction signal monkeys were able to reduce more efficiently inter-individual differences in their RT (IID_{RT}) in TOGETHER condition (Fig. 6C, Table 6). This result was confirmed by both comparing all datasets and DC couple behavior when performing the two task versions. Inter-individual differences in PV (IID_{PV}), instead, seem to be reduced when no-PI and PI groups were compared by pooling all datasets, but no significant difference was found when comparing IID_{PV} between DC_{noPI} and DC_{PI} datasets (panel D, Table 6). This result could be explained again by biasing task-independent differences between SK_{noPI} and DP_{PI} when pooling all datasets together ('All' groups).

In conclusion, our findings indicate that the joint-performance facilitation observed when a pre-instruction was provided in advance, is associated indeed to a higher coordination between individuals, as suggested by an effective reduction of their behavioral differences.

Discussion

The current work inquired whether monkeys' joint performance can selectively benefit from a preparatory time given before acting together, with the aim to provide an experimental evidence of the animals' sense to act together, by disentangling the planning processes associated to joint action from those related to the actions per se.

An optimal 'kinematic setting' for acting together

We have previously demonstrated that macaque monkeys constitute a good model to study joint action behavior. They are in fact able to modulate their own action kinematics in order to reciprocally adapt their behavior (Visco-Comandini et al. 2015; Ferrari-Toniolo et al, 2019), when a joint action is requested to achieve a common goal. One of the main goals of this study is to investigate whether there are task contexts in which monkeys can improve their dyadic performance. In agreement with our previous results obtained both on humans and non-human primates (Visco-Comandini et al. 2015; Satta et al. 2017), the joint performance was found to be markedly lower when the animals had to share an action, respect to when acting alone. Interestingly, though, we found that when the type of action was cued in advance, throughout a dedicated delay period, joint action performance was significantly improved. Noticeably, the pre-instruction did not positively influence all trial types (namely individual and joint ones) but seemed to be specifically beneficial for dyadic behavior.

To understand how and why the pre-instruction improved joint action performance, we first studied how monkeys' kinematics changed in a dyadic context, respect to when the same action was performed individually. As previously demonstrated, monkeys were able to implement an active inter-individual motor coordination by anticipating the initiation of their movement (Visco-Comandini et al. 2015). It has been demonstrated that when we speed up action onset, RTs becomes less variable (Repp, 2005; Wagenmakers & Brown, 2007). In our previous study it has been shown that the overall RTs decrease was associated to a diminished RTs variability. Therefore, we hypothesize that RTs decrease might constitute a motor strategy adopted by the dyad to optimise their behavior. By increasing their behavioral predictability, the two interacting agents might facilitate their inter-individual coordination, as also shown in human studies (Vesper, et al., 2011; Masumoto & Inui, 2013; Sacheli et al., 2013).

The reduction of temporal variability within a joint action task context has been demonstrated, and it has been hypothesized that it might be a motor strategy adopted by the dyad aimed at increasing behavioral predictability to facilitate inter-individual coordination (Vesper et al., 2011). Given the effectiveness of such a strategy, it can be identified as a “coordination smoother” (Vesper et al. 2010), since by reducing behavioral variability of the interacting individuals increase their reciprocal predictability, thus favouring inter-individual motor coordination (Vesper et al. 2011).

In line with the cited work, we found that some monkeys tended to anticipate cursor's movement onset and/or decrease its speed when performing the task together. In some cases, though, they did not change cursor speed and even increased their reaction times. This idiosyncratic behavior during joint performance, can be explained by the differences in the kinematics shown by the two individuals when performing the same isometric task alone. It has been demonstrated, in fact, that changing one's own behavior to make it more predictable can be sometimes insufficient in a dyadic context, in particular when coping with marked inter-individual differences between the co-agents (Słowiński et al. 2016). The idea of strategic behavioral invariances is overcome by the necessity of taking into account the individual motor behaviors of the co-acting agents. Human studies have shown that individuals adjust in time their own behavior to that of the partner when performing a joint action task (Schmidt et al., 2011; Sebanz & Knoblich, 2009). In general, the implemented strategies are aimed at minimizing the behavioral differences between the two individuals engaged in the joint action. In particular, dyads performing a cooperative action showed a reduction in 'start synchronicity', measured as the absolute difference between reaction times of the two subjects (Sacheli et al., 2012). A significant reduction of inter-individual differences in reaction times and peak velocity, has been shown also in macaque monkeys trained to perform a joint-action (Visco-Comandini et al 2015; Ferrari-Toniolo et al. 2019a).

As showed by our results, each monkey exhibited different kinematics when performing the task alone (SOLO condition), which made the animals distinguishable in their idiosyncratic behavior from one another. Another aim of this study was to investigate indeed the effect of these inter-individual differences in influencing joint action performance. Our hypothesis was that a greater difference of the individual kinematic profiles of the co-agents, as shown during their 'solo' action, could hamper the motor coordination between the two members. Our findings indicate that the entity of the dyadic inter-individual differences of the motor behavior positively correlated with the chance of committing errors when performing the same action jointly. However, this correlation was found only when the couples performed the pre-instructed version of the task. This result could be interpreted by hypothesizing that monkeys could benefit of the pre-instruction to cope with the potential differences in the kinematics of their mates with respect to their own behavior. In the presence of anticipatory instruction, the smaller differences between the interacting agents both in the latency to start moving the cursor and in the speed to bring it from the center to the periphery, predicted a better dyadic

performance. In the absence of this pre-instruction about type of action, instead, monkeys' performance was independent of inter-individual differences.

We speculate that the reason of this correlation might reside in the optimal kinematics setting provided by the PI task, which favors interindividual synchronization in initiating the force application. We demonstrated in fact that an anticipatory preparation to the future action type systematically induces a reduction of RTs (both in SOLO and TOGETHER conditions) respect to the case in which no PI was provided. This is in line with the decrease in RTs already observed both in humans (Rosembaum 1980), and monkeys (Churchland et al. 2006; Snyder et al. 2006), with increasing duration of delays periods imposed between a pre-cueing of a movement and the actual go signal. Interestingly, the effect of delay on monkeys' RTs was shown only in the case of spatial uncertainty, that is when the direction of movement was provided at the end of the delay period (Snyder et al. 2006). This implies that the presentation of a PI promotes the typical change in kinematics that is well known to favour motor inter-individual coordination. Therefore, the tendency to anticipate the action initiation might foster the demonstrated ability of the dyad to decrease inter-individual differences while performing the task together. This aspect could be sufficient to favor inter-individual coordination during joint trials, increasing the probability to perform the task successfully, irrespective of other specifics of the action to be performed, such as its direction. It is important to notice, in fact, that what was primed in our PI version of the task, is not the goal of the action, but just the type of action (SOLO or TOGETHER).

In summary, pre-instruction seems to facilitate performance because it allows the monkeys to modulate their kinematic profiles by favoring inter-individual synchronization – particularly at movement onset. Under this perspective, reducing variability has not to be regarded as an active strategy to be more predictable (Vesper et al. 2011), but rather the opposite could be true: a reduction of motor variability can emerge in some facilitatory conditions, that naturally increase the probability of synchronous movements, with higher chance of a successful joint performance.

Evidence of “we-representation” in monkeys

There is a consolidated ethological knowledge that non-human primates are able to cooperate when coordinated actions are mandatory to achieve a common goal. In natural environments, chimpanzees (Boesch & Boesch, 1989) show different level of cooperation during hunting. In

particular, the third level of cooperation, that according to Boesch & Boesch's occurs when two individuals display similar actions on the same goal and try to synchronize their behavior, has been confirmed also when apes are tested in more controlled experimental settings. The ability and attitude to coordinate individual actions with those of co-specifics have been shown often by using the bar-pull apparatus introduced by Crawford (1937) on chimpanzees, and subsequently on orangutans (Chalmeau et al. 1997) and capuchin monkeys (Mendres & deWaals, 2000).

In a highly controlled experimental setting, our previous studies have shown that macaques are a good model to study the neural and cognitive bases of the motor coordination required by a joint-action context. Macaques are in fact able to modulate their own action kinematics, as to adapt their own behavior (Visco-Comandini et al. 2015; Ferrari-Toniolo et al, 2019a) to that of their co-acting partner. They are also able, when acting together, to apply behavioral strategies facilitating temporal synchronization and accuracy in spatial coordination.

The main goal of the present study was to explore the task contingencies favoring, therefore improving monkeys' performance in a joint action behavior. A way to approach this issue is to recourse to an "interactionism" perspective, holding that individuals, primed to interact, may count on an interpersonal awareness of their shared intention, rather than on continuous reciprocal mindreading by single agents (Gallotti & Frith, 2013). Theories of shared intentionality in humans claim that co-agents engaged in joint contexts represent their actions as pursued together based on a sense of 'we-ness', a fundamental pillar in psychology of collective behavior. Several human studies offer empirical support to the idea that joint action plan involve a motor representation of collective goals (Della Gatta et al. 2017; Kourtis et al. 2019; Sacheli et al. 2018), where an accurate Dyadic Motor Plan might subserve an efficient interaction. In this study we tested the existence of a 'we-representation' in monkeys, that, if present, might ameliorate the efficiency of inter-individual coordination. To this aim we have designed two versions of an isometric joint action task, which differed by the presence/absence of a pre-instructing cue about the type of action (Solo or Together) to be performed.

There is overwhelming evidence that movement pre-cueing about a future action influences motor planning (Rosenbaum, 1980). Pre-instructing about the effector to be used, movement direction, force, and movement extent (Deiber et al, 2005; Jentsch & Leuthold, 2002) lead to faster (i.e., shorter RTs) and more accurate responses, associated to an increased amount of advance information, which are likely to be processed at central level in motor programs. Our

hypothesis was that, if the monkeys were able to access a ‘we-mode’ representation of the interactive scene at motor level, once the instruction to act together with a partner is provided in advance, this anticipatory representation should be beneficial to the execution of joint behavior, making it faster and more accurate, as much as any preliminary hint about motor features of the task to be performed is beneficial to its execution. On the contrary, once the relative pre-instruction is provided, the lack of such motor “we-representation” should have no effects on the motor response or on the goodness of interactive performance. In agreement with our previous results obtained both in humans and non-human primates tested in similar isometric tasks (Visco-Comandini et al. 2015; Satta et al. 2017), we found that the joint performance deteriorates individual animals’ behavior as compared to solo action. Interestingly, we found that when the type of action was cued in advance throughout a dedicated delay period, joint behavior improved significantly, as documented by the success rates (Fig. 2). Noticeably, the pre-instruction did not positively influence undistinguishably the performance of all trial types (i.e., SOLO and TOGETHER) but seemed to be beneficial particularly for dyadic behavior (Fig. 2C). The effect of pre-cueing was reflected also on the RTs. First, the anticipatory preparation to the future action-type led to a significant reduction of the RTs in the TOGETHER conditions with respect to SOLO action (Fig. 3). Second, this reduction has to be considered in the context of an overall decrease of RTs (observed in both SOLO and TOGETHER trials) associated to the presence of the pre-cue (Fig. 6A), as discussed above.

These findings are in line not only with the effects that advance information exert on motor planning but also with similar results obtained in humans tested specifically during joint behavior (Kourtis et al. 2019). This study showed that pre-cueing information about joint-action context affects our planning processes and facilitates dyadic performance, probably thanks to a predictive cognitive and sensorimotor “We-representations”, emerging at the group-level.

As a further evidence of this representation and coherently with human studies, we found that in monkeys the pre-instruction about future action type exerts beneficial effects on inter-individual coordination. This is indicated by the significant decrease in the inter-individual differences between hand action onset times (reaction times) and force application speed (peak of velocity), typical of the TOGETHER trials (Fig. 6C-D). This suggests that pre-cueing might trigger a “we-mode” representation that leads to a significant amelioration of joint performance.

Intriguingly, a “we-representation” in primates can be inferred also from the ethological observations on the motivations driving the animals to pursue a joint behavior. A study on capuchins monkeys (Brosnan et al. 2006), using the bar-pull paradigm, showed that joint action was not affected by the equity of the rewards delivered to each of the two animals, but was rather positively influenced by the presence of high-value rewards offered to the dyad. Each animal was keen to pull the bar even when its partner in a given trial received a better offer. The joint success was therefore related to the reward value offered to the couple (“we” and not “I” from the monkeys’ perspective). Capuchins were instead sensitive to inequity, if systematically only one of the two partners regularly received the higher-value reward. This evokes the existence of a “we-mode” representation also in the processes which motivate the joint performance.

At neuronal level, we propose that this “we-representation” might have a correlate in the activity of premotor neurons recorded from the brains of macaques engaged in a joint action experiment identical to that of the present study (Ferrari-Toniolo et al 2019a). These neurons, defined as “joint-action cells”, changed their firing when a given action was performed jointly with a partner, as compared to when the identical action was executed in a solo fashion. The same study has shown that their functional role during dyadic performance was more grounded in a predictive coding (see Friston, 2005) of own and other actions, rather than on mirror-like mechanisms. This is in line with the predictive nature of the “we-representation” that facilitates the performance of dyadic behavior.

Neural markers related to representation of joint behavior have been shown in the EEG study by Kourtis et al (2019), which demonstrated that pre-specifying joint configuration modulate the amplitude of several EEG indices of cognitive (P600) and sensorimotor representations (alpha/mu rhythm and late CNV) related to action planning.

In conclusion, our results offer empirical evidence of a sensorimotor representation of collective behavior macaques. Pre-cueing favors the emergence of a We-mode which exerts an overall beneficial effect on the inter-individual coordination.

Experiment 2: Acting alone or together? Behavioral underpinnings of action type selection in non-human primates

Background

Imagine you are a student preparing for a final exam. You are given two options: either working on a group project to pass the exam (option A) or studying alone for it (option B). Sure, the group project (option A) requires a lot of energies and can have less predictable outcomes, since it requires to coordinate different people, settle inevitable disagreements, avoid distractions and so forth. On the other hand, studying alone (option B) could be an easier solution, particularly if you have developed a successful learning method. But what would you choose if the group project exam would be worth the double number of credits? Deciding whether to act alone or jointly with others to achieve a common goal, requires a fine ability to carefully evaluate the costs and gains entailed. Moreover, the propensity to act with others can drastically change depending on other circumstances. If the group-study exam were to be the only option available, in fact, very few students would decide to not give it a try, despite the potentials difficulties a student can encounter when interacting with others.

From a strictly motor control perspective, when we perform an action, motor commands and their consequences are highly dependent on the physic of our body and its surroundings (Wolpert & Ghahramani 2000). To act in synergy with another individual we need thus to integrate within our internal model of the world also those changes that are not directly produced by our own actions. As soon as another actor enters the scene, hence, our environment becomes more unpredictable. This issue was recognized since motor planning and action in social context became object of study (Wolpert et al. 2003). Including another agent in our model of the world, here conceived as the field of our potential actions (Bufacchi and Iannetti 2018) brings in a higher degree of uncertainty, due to the low control that we have both on his/her actions and intentions. When coordinating with others, in fact, we have to deal with the lack of control that we have not only on others' motor output, but also on their decisions. The need to cope with this high degree of unpredictability is what makes inter-individual motor coordination such a costly task. This cost can be defined on two main dimensions: the social

gamble and the coordination cost. Herein, we define the social gamble as the risk related to the lack of control on partner's choice, and the coordination cost as the cognitive effort related to the higher degree of motor control required while coordinating with a partner.

The ability to integrate in real time internal models of self and others' actions, as well as to recur to coordination smoothers to facilitate the task, have been pointed out as key features that enable us to successfully engage in joint action (Pesquita et al. 2018). Among the strategies used to ease inter-individual coordination, we have previously demonstrated that the reduction of individual variability and inter-individual differences in spatial and temporal aspects of motor behavior emerge during inter-individual motor coordination both in humans (Vesper et al. 2011, Satta et al. 2017) and non-human primates (Visco-Comandini et al. 2015, *Experiment 1*). Resorting to these strategies has been demonstrated to imply a cost, evident from a decrease of performance when acting together (Satta et al. 2017, Visco-Comandini et al. 2015, *Experiment 1*).

Why to cooperate, then, if it can be so demanding and/or risky? Because this can bring us some advantages. For example, it can make a task easier (e.g., moving a table; Whan et al. 2018) or allowing the achievement of a goal with higher value (e.g., producing a complex symphony; Keller et al. 2014).

In a recent study the concept of 'coefficiency' – namely the optimization of aggregate, rather than individual cost – has been introduced and applied to unveil how people distribute the cost when performing a joint action. It was demonstrated that overall humans show a cooperative behavior in which the individuals are willing to pay more to optimize the joint performance (Török et al. 2019). How do non-human primates deal with joint action costs though is not clear yet.

Monkeys' propensity to engage in risky tasks with uncertain outcomes have been demonstrated to be flexibly modulated by the type of task in conventional chair seated, computer-controlled settings (Farashashi et al. 2018). On the other hand, against the general finding that these primates are prone to gamble, a risk aversion attitude has been recently demonstrated in a more ecological experimental setting (Eisenreich et al. 2019).

Moreover, it has been shown that monkeys are able to consider partner's behavior to make economic decision in a dyadic context. In fact, previous history of dyad's choices has been shown to influence the propensity to cooperate (Haroush and Williams, 2015), while partner's action visibility seems to determine the type of social strategy adopted in choosing together (Unakafov et al. 2019).

Do monkeys take into consideration the cost of inter-individual motor coordination as well, when deciding whether to engage in a joint action task? To answer this question, we designed a sequential choice task in which two monkeys can choose between acting alone or together, based on different associated payoffs.

Materials and Methods

Animals

Two male rhesus monkeys were used for the experiment (*Macaca mulatta*): Monkey M, 9 Kg; Monkey T, 10 Kg. In the present work, Monkey M will be addressed as Mk1, while Monkey T will be addressed as Mk2. Animal care and housing procedures were in conformity with European (EU Directive 63-2010) and Italian (DL. 26/2014) laws on the use of nonhuman primates in scientific research.

Experimental setup

The experimental setup is illustrated in Fig. 1A. Both monkeys were trained to control a cursor of 0.6 degrees of visual angle (DVA) diameter, displaced on a black screen by applying a dynamic force on an isometric joystick (ATI Industrial Automation, Apex NC) in the two dimensions of the horizontal plane (sampling frequency: 1 kHz). The amount of force was proportionally converted into a movement of the cursors on the x and y axis on the vertical plane of the monitor, so that a force of 1 N corresponded to the display of the cursor from the central position to an eccentricity of 1.25 DVA). The NIH-funded software package REX was used for task control and behavioral data collection. Monkeys were required to always use the same arm to perform the task, while the other arm was gently restrained. In both cases the joystick was controlled with the left hand, since both monkeys showed a preference in using their left limb at the early stages of their training.

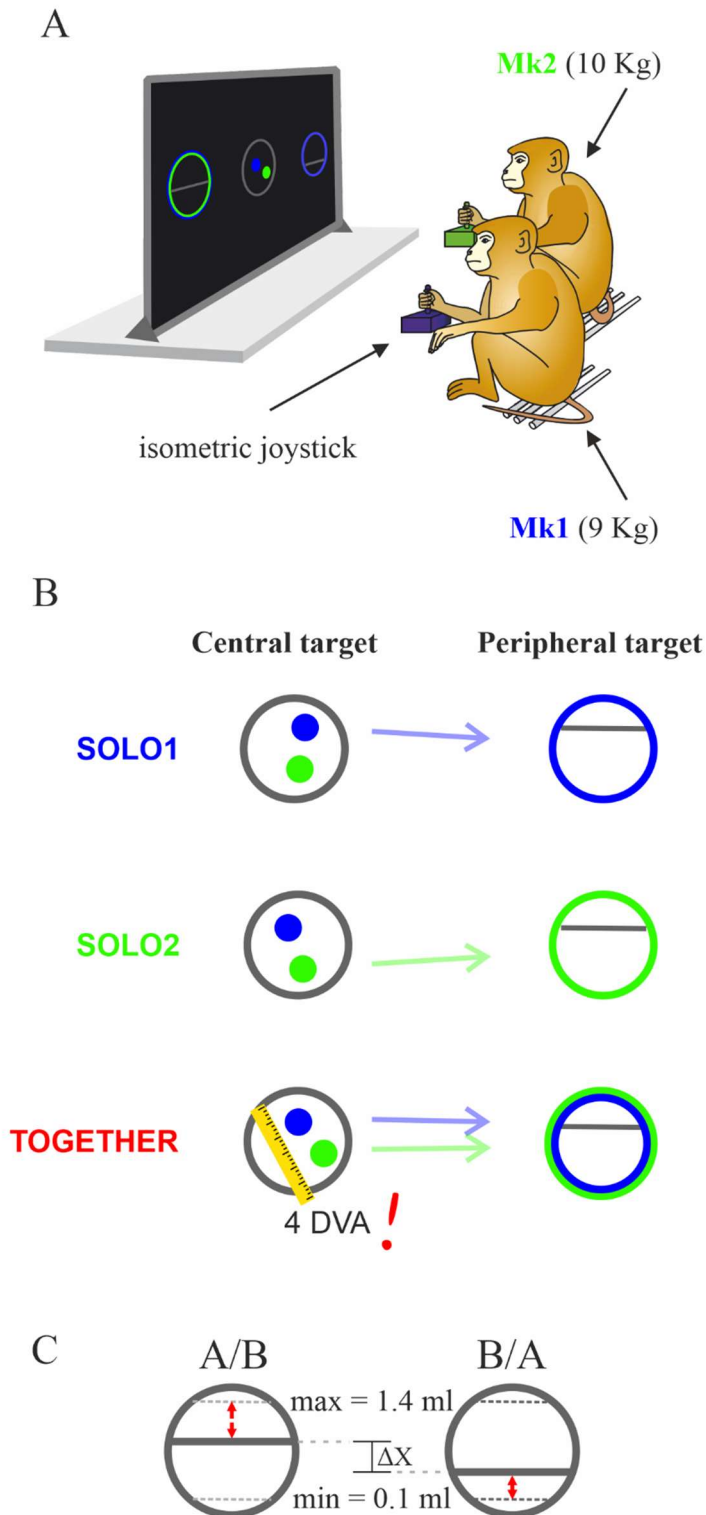


Figure 1. Experimental setup and task conditions.

(A) Two monkeys were placed in a darkened, sound-attenuated chamber and seated side-to-side on primate chairs in front of a common monitor. Both monkeys exerted a force on an isometric joystick to displace a colored visual cursor from a central control position toward a target located at one of eight possible locations on the screen, at 45° intervals on a circumference at 8 DVA radius.

(B) The action type condition was defined by two levels: in SOLO condition, one of the two monkeys (either MK1 or MK2) could gain a reward by moving its cursor alone to reach a target. In the TOGETHER condition, the two monkeys obtained both a reward by reciprocally coordinating their forces to bring jointly their cursors into a target, without exceeding an inter-cursor distance threshold of 4 DVA. (C) the reward condition was defined by five classes of relative difference ($\Delta 0, \dots \Delta 4$). The payoff absolute value was randomly assigned to each option on a trial-by-trial basis, with two constrains: (i) keeping fixed the delta between the two offers, (ii) and not exceeding pre-defined minimum and maximum amounts (0.1ml-1.4ml).

The two monkeys were placed in a soundproof chamber, seated side-to-side on two primate chairs in front of a 40-inch monitor (100 Hz, 800-600 resolution, 32-bit color depth; monitor-eye distance: 150 cm). A security distance of at least 60 cm was always guaranteed, to prevent physical contact. The orientation and structure of the chair minimized also direct visual contact. During data collection eye movements of both animals were monitored and sampled

at 1 kHz through an infrared oculometer (Arrington Research) and stored together with joystick force signals and key behavioral events.

Behavioral task

Three tasks were used in the present work. A first ‘SOLO/TOGETHER’ training task (i) was adopted to replicate previous results about joint action behavioral features in non-human primates (Visco-Comandini et al. 2015). A first version (Test 1) of the ‘SOLO vs TOGETHER’ choice task (ii), which was used in the latest learning phase, required the animals to choose between acting alone or together based on the associated payoff. The main aim of this task was to test for monkey’s ability to discriminate between reward offers of different sizes and to establish the optimal relative and absolute reward levels necessary to assess the cost of acting together. A second version (Test 2) of the ‘SOLO vs TOGETHER’ choice task (iii), consisting in an optimized version of the previous version, was used to finely quantify the perceived cost of acting together. The number of trials collected for each type of task was: 6372 trials (10 sessions) for the training task; 9314 trials (28 sessions) for the Test 1 task; 4983 trials (9 sessions) for the Test 2 task.

Training task

The monkeys were trained to perform an isometric center-out task requiring the application of force on an isometric joystick, to control their own cursor (Blue, Mk 1 and green Mk2) in eight different directions, either individually (SOLO condition) or jointly with their partner (TOGETHER condition). The action type condition was defined by two ways of performing the task (Fig. 1B). In the first one, a designed monkey (either Mk1 or Mk2) had to perform a simple center-out cursor movement, irrespective of the partner’s behavior (SOLO condition). In the second one, the two animals had to coordinate their forces to bring their cursors toward the peripheral target together (TOGETHER condition). In this latter case, a specific spatial constraint was imposed, to ensure inter-individual motor coordination: while moving together, both monkeys had to keep the distance between their cursors under a defined threshold of 4 DVA, for the entire duration of the center-out cursor trajectory. These two types of action were hence differentiated both by motor and social compounds. The two conditions thus defined, were instructed using the monkey-specific color code mentioned above: a blue circle instructed an individual action for Mk1 (SOLO1); a green circle instructed an individual action for MK2 (SOLO2). A bicolor (blue/green) circumference was used to indicate a TOGETHER condition.

In this latter case, the color of the outer and inner circle was assigned randomly, so that either the outer circle was blue and the inner green or, vice versa, the outer was green and the inner blue. All task's objects and targets were simple outlined circles of 0.2 DVA of thickness and 4 DVA of diameter. A univocal cursor of 0.6 DVA of diameter was assigned to each monkey, using the following color code: blue for MK1, green for MK2.

Test 1 task

To test monkeys' preference between action types, they were called to perform a center-out task in order to choose between two options (A and B), defined by five main features: (i) presentation order during the instruction phase, (ii) brightness (trial-contingent identity of the object), (iii) action type (moving the cursor alone or in coordination with the other monkey), (iv) reward difference (equal, higher in A or higher in B by a fixed interval, variable in its absolute level), and (v) target location during the choice phase (left or right). These features were well balanced throughout a pseudo-randomized design, to control any potential biasing effect on behavior. The choice was made by moving the cursor from a central target to the peripheral target associated to the chosen option.

Each choice option was associated to a certain amount of reward, on a trial-by-trial basis. The reward consisted of water drops. Two aspects were taken into account: the absolute and relative amount of reward. With the term 'absolute reward', we refer to the actual amount of reward associated to each option. We talk about 'relative reward', instead, to indicate the difference between the reward assigned to option A and option B. Five classes of increasing 'relative reward' (Δ) were used in the present task. The absolute reward for each option offered in each trial was randomly defined, with two constraints: (i) keeping fixed the relative reward between the two options; not exceeding the maximum and minimum reward amounts of 0.10 ml and 1.40ml respectively. The reward deltas were fixed as follows: $\Delta_0 = 0$ ml; $\Delta_1 = 0.15$ ml; $\Delta_2 = 0.30$ ml; $\Delta_3 = 0.45$ ml; $\Delta_4 = 0.60$ ml. The payoff value was thus assigned to the two options through the following equation:

$$Rew = r \pm \frac{u}{2} \times \Delta$$

Where r is the randomly assigned reward amount, u is the unit of reward difference (0.15ml in this case), and Δ is the delta size.

The task was programmed so that the higher reward was associated either to option A and or to option B, in a balanced way. The amount of reward was represented by the height of a grey bar displayed inside the outlined circle representing each offered option (Fig. 1C).

The task temporal structure is represented in Figure 2. Each trial was characterized by two main phases: the instruction phase (IP) and the choice phase (CP). During the IP, the animals were informed of the two options offered for that specific trial, displayed in sequence in a central (i.e., spatially neutral) position of the screen. Each option (A and B) was presented for 600-650ms, followed by a delay of 300-350ms. After this, the two cursors and a grey central target appeared, and each monkey was trained to place the cursor inside that target and hold it in there for a center holding time (CHT) of 1000-1400 seconds. Only then, the two same options appeared again, one displaced on the left and the other on the right (in a randomized way), at 8 DVA from the center. After a predictable instruction delay time (IDT) of 700-800ms, the two options disappeared, leaving in their place only two neutral grey circles, and the monkeys were allowed to move their cursors from the central target towards one or the peripheral targets (dynamic force time, DFT), accordingly to the choice made, or to defect the trial, if the options were deemed to be not worth the effort. The movement had to be performed within a time-window of 2000ms, otherwise the trial was aborted. Once one target was reached and the cursor/s kept inside it for a short target holding time (THT, 100-160ms), one or both monkeys – depending on the action type of the selected target – received the chosen amount of reward, (REW).

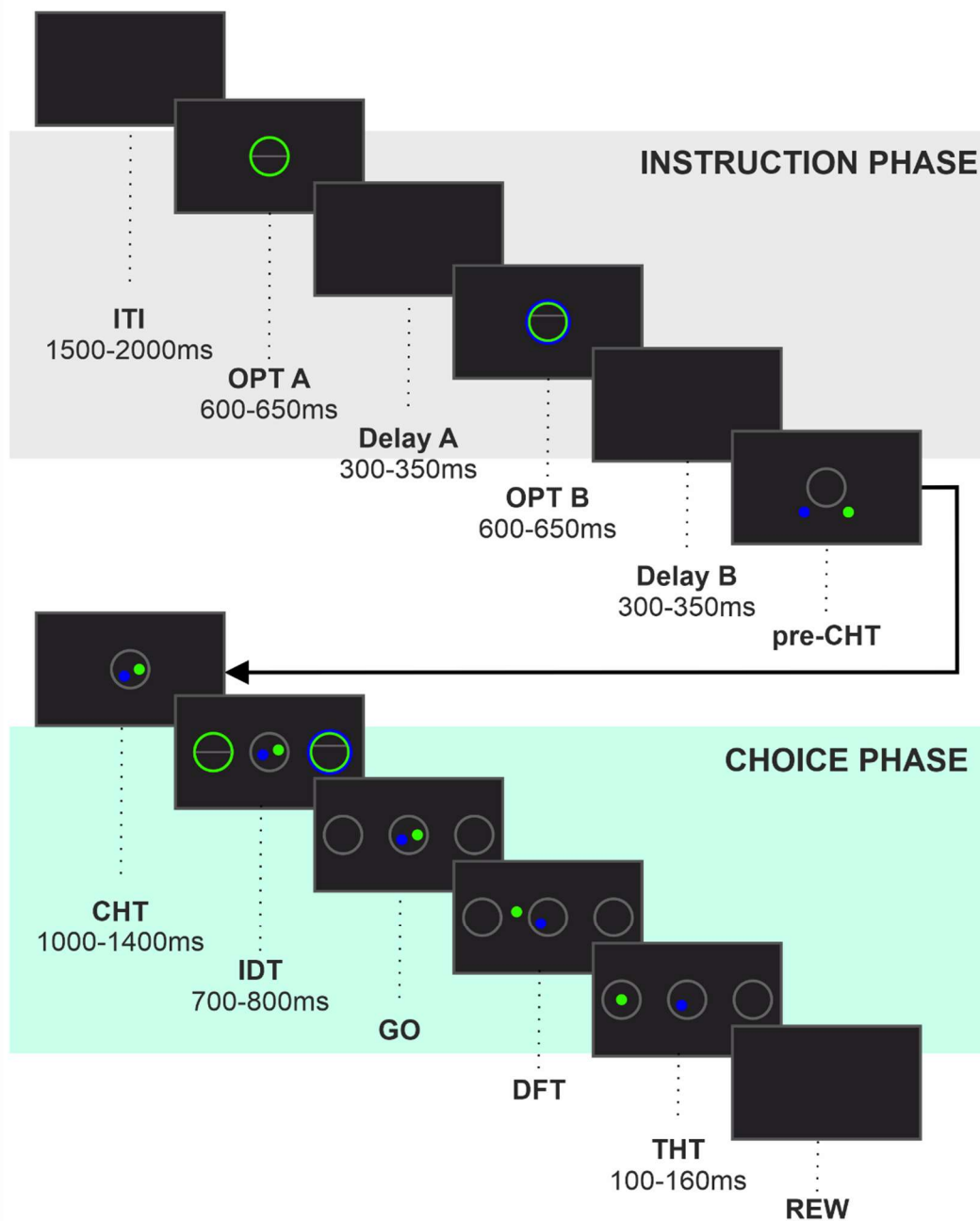


Figure 2. Task time course. Each trial was characterized by two main phases: the instruction phase (IP) and the choice phase (CP). During the IP, the animals were informed of the two options offered for that specific trial, displayed in sequence in a central (i.e., spatially neutral) position of the screen. Each option (A and B) was presented for 600-650ms, followed by a delay of 300-350ms. After this, the two cursors and a grey central target appeared, and each monkey was trained to place the cursor inside that target and hold it in there for a center holding time (CHT) of 1000-1400ms. Only then, the two options appeared again, one displaced on the left and the other on the right (in a randomized way), at 8 DVA from the center. After a predictable instruction delay time (IDT) of 700-800ms, the two options disappeared, leaving in their place only two neutral grey circles, and the monkeys were allowed to move their cursors from the central target towards one or the peripheral targets (dynamic force time, DFT), accordingly to the choice made, or to defect the trial, if the options were deemed to be not worth the effort. The movement had to be performed within a time-window of 2000ms, otherwise the trial was aborted. Once one target was reached and the cursor/s kept inside it for a short target holding time (THT, 100-160ms), one or both monkeys – depending on the action type of the selected target – received the chosen amount of reward, (REW).

Five possible types of choice contexts (CC), in fact, were defined by the combination of the

two options' action types. In one case, MK1 had to choose between two SOLO1 options, while MK2 could keep the cursor in the central target, in order to get what MK1 would choose and get, by performing a successful center-out cursor movement (SOLO1 vs SOLO1 choice context). Symmetrically, MK2 could choose between two SOLO2 options, while MK1 could keep the cursor in the central target, in order to get what MK2 would choose and get by performing a successful center-out cursor movement (SOLO2 vs SOLO2 choice context). When the two monkeys were offered of two TOGETHER options, they had to choose together (joint decision) one option and coordinate their cursors' movement toward the same target to gain a reward (TOGETHER vs TOGETHER choice context). In this case, they could not get any reward by keeping their cursor in the center, going alone, or choosing opposite targets. SOLO1 vs SOLO1 (S_1 vs S_1), SOLO2 vs SOLO2 (S_2 vs S_2) and TOGETHER vs TOGETHER (T vs T) choice contexts were considered as controls, since in those three cases no actual choice between action types was possible. In the latter two choice contexts, one monkey – the “ruler” – was called to choose between going alone or together. The choice of the ruler monkey determined – hence the name – the “rules of the game” in that specific trial, so that if he chose to go alone, the other one could gain the same reward by keeping its cursor inside the central target, but if he chose the TOGETHER target, then the only option for both to win their treat became to coordinate their action and reach together the same target. In this context, the other monkey could simply follow a passive strategy and try to predict and adapt to the ruler choice or adopt a more proactive strategy and try to influence the ruler. For example, he could always keep the cursor in the central target, hoping for the ruler to choose the SOLO, or anticipate the choice by starting earlier to move towards the TOGETHER target. When MK1 was designed as the ruler, the choice context was indicated as SOLO1 vs TOGETHER (S_1 vs T). Similarly, then MK2 was designed as the ruler, the choice context was indicated as SOLO2 vs TOGETHER (S_2 vs T). The description of the five choice contexts is summarized in Table 1. In order to allow the monkeys to keep track of the identity of objects of the same color (example, two blue circles, corresponding to two SOLO1 options), two different brightness were applied (for example, SOLO1 for option A was dark blue, while SOLO1 for option B was light blue). The brightness factor was assigned randomly in each trial to the two offered options,

Choice context	Ruler	Partner
SOLO1 vs SOLO1	MK1 can choose between two reward options or abstain from choosing.	MK2 can hold its cursor in the centre to obtain the same reward gained by MK1 .
SOLO2 vs SOLO2	MK2 can choose between two reward options or abstain from choosing.	MK1 can hold its cursor in the centre to obtain the same reward gained by MK2 .
TOGETHER vs TOGETHER	MK1 and MK2 can chose together (joint decision), between two reward options. Reaching the same target together, while maintaining a defined inter-cursor distance (joint action), is the only way to succeed.	
SOLO1 vs TOGETHER	MK1 can choose between two social conditions , to which two reward options are associated, or abstain from choosing. By choosing, he will define the rules of the game, that will be either SOLO1 's or TOGETHER 's.	MK2 can try to predict MK1 's choice and either adapt to it or try to influence it in a more assertive way.
SOLO2 vs TOGETHER	MK2 can choose between two social conditions , to which two reward options are associated, or abstain from choosing. By choosing, he will define the rules of the game, that will be either SOLO2 's or TOGETHER 's.	MK1 can try to predict MK2 's choice and either adapt to it or try to influence it in a more assertive way.

Table 1. Choice context rules. Each choice context was characterized by a certain set of rules, which monkeys had to follow in order to gain their reward.

to avoid a potential related bias. The possible outcomes of choice in these different contexts are schematized in Table 2. The combination of presentation order during the instruction phase, action type, and reward within each choice context are summarized in Figure 3A.

Test 2 task

The test task differed from the training task in three features: (i) the absolute reward was not randomized but rather fixed; (ii) the unit of reward difference was doubled, from $u = 0.15$ ml to $u = 0.30$ ml; (iii) the color's brightness of the offered object was homologated, since demonstrated to bring unnecessary information.

Reward deltas were computed by the new equation:

$$Rew = r_{min} + u \times \Delta$$

Where r_{min} is the minimum absolute reward amount necessary to maximize the chances that monkeys will choose the trial, u is the unit of reward difference and d is the delta size. The value of r_{min} was estimated in three steps. First, we collected the reward amount for each chosen trial in $\Delta 0$ trials and we ordered those values in ascending order. Then, we computed the mean of the first 20% of values, separately for each condition. This method was preferred to using the sharp minimum, since we deemed it to be more robust against outliers. Finally, we selected the minimum reward r_{min} by choosing the higher value amongst the means computed for each condition within each choice context.

	MK1's behaviour	MK2's behaviour	MK1'S reward	MK2's reward
SOLO1	T	O/T	+	-
	T	C	+	+
	O/C	O/C/T	-	-
SOLO2	O/T	T	-	+
	C	T	+	+
	O/C/T	O/C	-	-
TOGETHER	T	O/C	-	-
	T	T	+	+
	O/C	O/C	-	-
	O/C	T	-	-
	DT	DT	-	-

Table 2. Possible choice outcomes. In SOLO condition, the monkey called to action had the chance to gain a reward by reaching a target, irrespective of his partner's behavior, while the partner could gain the same reward by keeping its cursor in the central target only if the other monkey performed the center-out movement correctly. In TOGETHER condition, instead, the only chance for both animals to gain a reward was to coordinate their action successfully to reach a common target.

Legend: T = same target chosen; DT = different target chosen; O = cursor out from the central target; C = cursor within the central target; + = rewarded; - = not rewarded. The darker colored rows correspond to the optimal successful trial for both animals for each condition type.

Trials classification

Trial classification is schematized in Figure 3B. A trial was considered 'engaged' if the IDT epoch was reached in the trial's timecourse (Fig. 2). In that case, in fact, we could be guaranteed

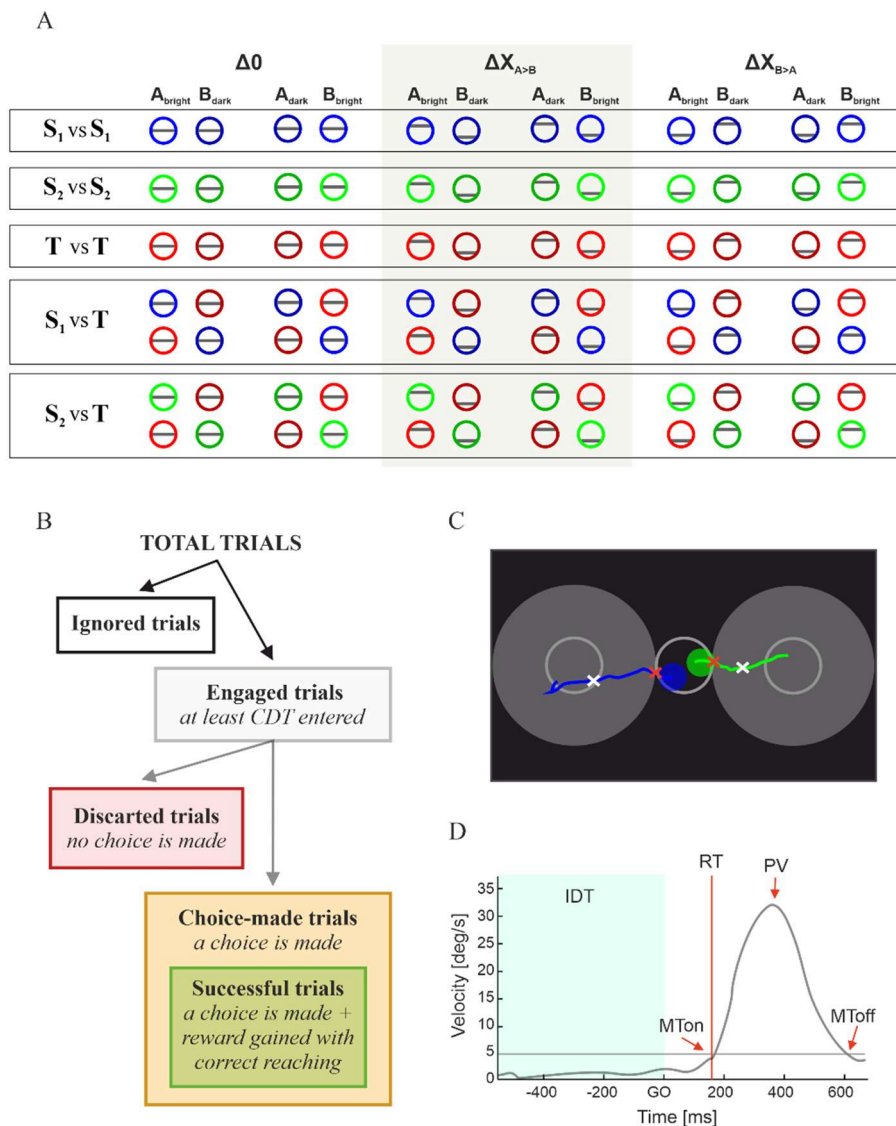


Figure 3. Choice contexts, trial classification and kinematics computing. (A) The combination of presentation order during the instruction phase, brightness, action types, and reward difference is schematized. Target location during the choice phase is not represented for simplicity. Five choice contexts were defined depending on which action types were assigned to the two options: three control choice contexts, in which the same action type was assigned to the two alternatives (i.e., SOLO1, SOLO2 or TOGETHER); two SOLO vs TOGETHER choice contexts, in which a choice between the two action types was possible. (B) A trial was considered engaged if the IDT epoch was reached, otherwise it was classified as ignored. After the IDT phase started, and the trials were hence not ignored, the animals had two options: either to abstain and discard the trial or to make a choice. If after making a choice (choice-made trials) the center-out movement was performed correctly, that trial was classified as successful. (C) The chosen option for each trial was detected by our algorithm, as soon as the cursor exit the central target and entered a surrounding area (6 DVA of radius; dark gray circles on the figure) of one of the peripheral targets, during the DFT. An additional algorithm was applied offline, in order to corroborate and refine choice assignment. A choice was confirmed or added if cursor's mean position on the horizontal plane during the movement time (white x) was exceeding its mean position during the IDT of 3 standard deviations (blue and green shaded circles). (D) Movement onset was extracted from cursor's signal as the time in which cursor velocity exceeds of 3 standard deviations and for at least 80ms a velocity threshold defined as the mean velocity during the last 200ms of the CHT. Similarly, Movement offset was assigned when cursor velocity was below the above-mentioned threshold for at least 80ms. The time elapsing between the GO signal and MTon was considered as the Reaction Time (RT), while the peak velocity (PV) was calculated as the maximum cursor's tangential velocity, within a time-window included between MTon and MTOff.

of the general motivation of the monkeys to engage the task. After the IDT phase started, and

the trials were hence not ignored, the animals had two options: either to abstain and discard the trial or to make a choice. In this way, it was possible to divide the total number of trials in a session in three groups: ignored, discarded and choice-made trials. Within the choice-made trials, a subset of them, the successful trials, was identified as all trials in which a choice was made and the cursor's movement to reach the target associated to the chosen object was performed correctly and the respective reward gained. As for the T vs T choice context, choice-made and discarded trials could be in turn divided in subgroups considering that this was the only case in which the choice was equally shared between the two agents. In this case, we considered as choice-made trials only those ones that were approached by both monkeys, while discarded ones were all those in which one monkey at least decided to defect the trial.

The chosen option for each trial was detected by our algorithm, as soon as the cursor exit the central target and entered the surroundings of one of the peripheral targets, during the DFT. The surrounding of each peripheral target was defined as a circular area with 6 DVA of radius, centered on the target. An additional algorithm was applied offline on the collected data, in order to corroborate and refine choice assignment. A choice was confirmed or added if cursor's mean position on the horizontal plane during the movement time was exceeding its mean position during the IDT of 3 standard deviations. This two-step detection is represented in Figure 3C. For the analysis of choice behavior we focused on all 'choice-made' trials, while only successful trials were used for the analysis of motor behavior and performance.

Chosen options were classified considering two criteria: the condition associated to that option (i.e., SOLO or TOGETHER action type) and the choice context, in which the condition was either actually chosen (SOLO vs TOGETHER choice context) or imposed (control choice contexts). Therefore, chosen options were labeled as the choice context within they were made for same-condition control context (S₁ vs S₁, S₂ vs S₂ or T vs T), while the chosen option was specified in SOLO vs TOGETHER choice contexts as follow: S₁ chosen (S₁ vsT), T chosen (S₁ vsT), S₂ chosen (S₂ vsT), T chosen (S₂ vsT).

Behavioral indexes

Percentage of engaged trials

The median percentage of engaged trials (engagement rate, ER) was computed for each choice context and *i* session as follows:

$$ER_{CC,i} = \frac{n \text{ engaged trials}}{\text{total trials CC}} \times 100$$

Where:

- ER indicate the engaged trials rate for a given choice context CC, in the i -th session
- n stands for ‘the number of’

The median percentage of engaged trials was additionally computed for each reward delta within each choice context and for each session:

$$ER_{\Delta X,i} = \frac{n \text{ engaged trials}}{\text{total trials } \Delta X} \times 100$$

Where $0 \leq \Delta X \leq 4$

Similarly, the same index was computed within each choice context for the three classes of absolute reward:

$$ER_{LX,i} = \frac{n \text{ engaged trials}}{\text{total trials } L} \times 100$$

Choice and no-choice rates

No-Choice Rates (no-CRs) have been calculated for each choice context, negative, null, and positive reward delta, and i session, as follows:

$$\text{no-CR}_{CC,\Delta X,i} = \frac{N \text{ discarded trials}}{N \text{ engaged trials}} \times 100$$

Where $-4 < \Delta X < 4$ and n stands for ‘the number of’

Discarded trials in TOGETHER choice context has been divided into three sub-groups, depending on which monkey defects the trial (both, Mk1 or mk2), so that:

$$\text{no-CR}_{\text{TOG}} = \text{no-CR}_{\text{TOG,MK1 defects}} + \text{No-CR}_{\text{TOG,MK2 defects}} + \text{No-CR}_{\text{TOG,BOTH defect}}$$

Choice Rates (CRs) have been calculated for each choice context, negative, null, and positive reward delta, and i session, as follows:

$$CR_{CC,\Delta X,i} = \frac{n \text{ chosen option}}{n \text{ choice-made trials}} \times 100$$

Where $-4 \leq \Delta X \leq 4$ and n stands for ‘the number of’

For SOLO and TOGETHER choice contexts, in which a choice was possible only between two identical conditions (e.g., two SOLO targets), the two options given were considered as two different objects, and for each of them the following question was asked:

How often has an object been chosen (CR) when its reward is lower ($-\Delta 4, -\Delta 3, -\Delta 2, -\Delta 1$), equal ($\Delta 0$), or higher ($+\Delta 1, +\Delta 2, +\Delta 3, +\Delta 4$) then the reward associated to the other option? In this case, hence:

$$CR_{-\Delta X} + CR_{\Delta 0} + CR_{+\Delta X} = 100\%$$

The rates at which both monkeys chose different targets in TOGETHER choice context have been excluded since extremely rare (median = 0 for both monkeys for all deltas).

For SOLO vs TOGETHER choice contexts, the two options were considered as different objects (i.e., SOLO and TOGETHER), so that for each of them the following question was

asked: How often has this action type been chosen (CR) when its reward is lower ($-\Delta 4, -\Delta 3, -\Delta 2, -\Delta 1$), equal ($\Delta 0$), or higher ($+\Delta 1, +\Delta 2, +\Delta 3, +\Delta 4$) then the reward associated to the other one? In this case, hence:

$$CR_{\text{SOLO},-\Delta X} + CR_{\text{TOGETHER},+\Delta X} = 100\%$$

$$CR_{\text{SOLO},+\Delta X} + CR_{\text{TOGETHER},-\Delta X} = 100\%$$

Indifference point and reward discrimination

Choice rates (median values) across reward deltas were fitted by the following logistic curve:

$$y_{\text{fit}} = y_{\text{min}} + \frac{y_{\text{max}} - y_{\text{min}}}{1 + 10^{(\rho - x) \times \eta}}$$

Where:

- y_{fit} is the fitted curve
- y_{min} is the minimum choice rate
- y_{max} is the maximum choice rate
- $x = -\Delta 4, -\Delta 3, -\Delta 2, -\Delta 1, \Delta 0, +\Delta 1, +\Delta 2, +\Delta 3, +\Delta 4$
- ρ is the delta at which the choice rate is 50%
- η is the sigmoid steepness

Logistic curve's parameters were estimated by a machine learning algorithm using the `sigm_fit` function for Matlab (version 1.5.0.0). Sigmoid's ρ value represented the 'indifference point' between the two offers, while the steepness η was considered as an index of monkey's ability to discriminate between offered payoffs.

Absolute reward choice rate

Absolute reward has been classified offline in three classes of absolute reward level: *Low* (0.10-0.54 ml); *Medium* (0.55-0.97 ml); *High* (0.98-1.40 ml). We computed the absolute reward Choice Rates (AbsCR) to represent the rate at which a on object with an absolute reward level L was chosen when offered. This index was computed for each reward level, within each reward delta group, and i session as follows:

$$\text{AbsCR}_{\text{CC},L,\Delta X,i} = \frac{n_{\text{chosen } L}}{n_L} \times 100$$

Where:

- L is the absolute reward level (Low, Medium or High)
- n_L is the number of times in which that L level appears in one of the two options, in all trials (when the two options are associated to the same level, that occurrence is counted just once)
- $n_{\text{chosen } L}$ is the number of times in which, when this level appears, it is chosen.

For SOLO vs TOGETHER contrasts, this Choice Rate is computed twice:

- When the chosen reward is associated to a SOLO condition (i.e. SOLO chosen)
- When the chosen reward is associated to a TOGETHER condition (i.e. TOGETHER chosen)

Reward gain optimization indexes

The percentage of trials in which the highest reward was chosen (HRCR) was computed for each i session and within each choice context, as follows:

$$\text{HRCR}_{CC,i} = \frac{n \text{ high reward chosen trials}}{n \text{ total trials } CC} \times 100$$

The percentage of reward effectively gained (EGR) by each monkey out of the total maximum amount of reward offered was computed for each i session and within each choice context as follows:

$$\text{EGR}_{CC,i} = \frac{\text{total reward gained in } CC}{\text{total maximum reward offer in } CC} \times 100$$

A theoretical EGR was also computed as the maximum reward that monkeys could gain by choosing systematically only one action type. This ideal value was adjusted by weighing it for the actual reward that the monkeys were able to get in the choice control contexts as follows:

$$\text{Threshold}_{\text{SOLO1,Mk}} = \frac{\text{ASO}_{S1 \text{ vs } S1}}{100} \times \text{max}$$

$$\text{Threshold}_{\text{SOLO2,Mk}} = \frac{\text{ASO}_{S2 \text{ vs } S2}}{100} \times \text{max}$$

$$\text{Threshold}_{\text{TOGETHER}} = \frac{\text{ASO}_{T \text{ vs } T}}{100} \times \text{max}$$

Where max is the maximum amount of reward obtainable theoretically by always choosing the same action type (either SOLO or TOGETHER).

$\text{Threshold}_{\text{SOLO}}$ was used to indicate the effort minimization threshold, namely the weighed maximum reward that monkeys could gain by choosing systematically only SOLO action type.

$\text{Threshold}_{\text{TOGETHER}}$ was used to indicate the effort maximization threshold, namely the weighed maximum reward that monkeys could gain by choosing systematically only TOGETHER action type.

As a more general index of monkeys' predisposition to choose TOGETHER's option we also computed the sharp choice rate of TOGETHER condition within SOLO vs TOGETHER choice contexts, for each i session:

$$CR_{CC,i} = \frac{n_{TOGETHER\ chosen}}{n\ choice-made\ trials} \times 100$$

Successes rates

For each condition c – whether imposed or chosen – and i session we have computed the success rate as follows:

$$SR_{c,i} = \frac{n\ successful\ trials}{n\ chosen\ option} \times 100$$

Where n stands for ‘the number of’

Similarly, SR were computed within each reward delta or reward absolute level as follows:

$$SR_{c,\Delta X,i} = \frac{n\ successful\ trials}{n\ chosen\ option} \times 100$$

$$SR_{c,L,i} = \frac{n\ successful\ trials}{n\ chosen\ option} \times 100$$

Relative reward effect on choice

A linear model was fit to rates, as distributed across reward deltas, using the following model:

$$y_{fit} = m \times x + i;$$

Where:

- y_{fit} is the fitted curve
- $x = \Delta 0, \Delta 1, \Delta 2, \Delta 3, \Delta 4$
- m is the steepness
- i is the intercept (i.e., the value y_{fit} takes for $x = 0$)

The steepness m of the fitted lines was used to estimate a potential linear effect of delta sizes on choice behavior. This parameter was always associated with a statistic that compared the significant difference between delta groups.

Reaction Time

Movement onset (MTon) following the GO signal (i.e., IDT epoch end) was extracted from cursor’s signal as the time in which cursor velocity exceeds of 3 standard deviations and for at least 80ms a velocity threshold defined as the mean velocity during the last 200ms of the CHT. Similarly, Movement (MToff) offset was assigned when cursor velocity was below the above-mentioned threshold for at least 80ms.

The time elapsing between the GO signal and MTon was considered as the Reaction Time (RT) and computed for each t trial of each i session as the movement onset following the GO signal, which was signaled by the end of the IDT epoch. An example of this computation is provided in Fig. 3D.

Peak velocity.

The peak velocity (PV) was calculated for each t trial of each i session, as the maximum cursor's tangential velocity, within a time-window included between movement onset and offset.

Statistical analysis

To assess the normality of samples Shapiro-Wilk test was used. When samples were not normally distributed, non-parametric statistical test were applied.

Wilcoxon rank sum test was used to compare reaction times and peak velocities between conditions (2 groups: SOLO and TOGETHER) and between monkeys (2 groups: MK1 and MK2), in the control task. Kruskal-Wallis test was applied to compare success rates between SOLO1, SOLO2 and TOGETHER trials.

Kruskal-Wallis test was used to compare the percentage of engaged trials across choice contexts, to assess monkey's general motivation to approach the task and its variation across choice contexts. To investigate whether relative and absolute reward could influence the monkey's propensity to ignore or engage a trial, we compared the percentage of engaged trials across reward deltas (5 groups: $\Delta 0$, $\Delta 1$, $\Delta 2$, $\Delta 3$, $\Delta 4$) and reward levels (3 groups: Low, Medium, High) within each choice context, by mean of a Kruskal-Wallis test.

Kruskal-Wallis test was performed to compare Absolute Reward Choice Rates between absolute reward groups (3 groups: Low, Medium, High) and between relative reward groups ($\Delta 0$, $\Delta 1$, $\Delta 2$, $\Delta 3$, $\Delta 4$), within each condition, imposed or chosen.

Kruskall-wallis was performed to compare the rate at which monkeys chose the highest reward within a trial (HRCR) between choice contexts (5 groups: S_1 vs S_1 , S_2 vs S_2 , T vs T, S_1 vs T, S_2 vs T). In addition, the reward gained by both monkeys within the SOLO vs TOGETHER choice contexts was compared to the computed maximum reward that they could have gained by choosing systematically only the individual action type (i.e., the effort minimization threshold) by mean of a Wilcoxon rank test, performed four times, namely for each monkey as taking part as a ruler in his own SOLO vs TOGETHER choice contexts, or as taking part as a partner when the other monkeys was playing the ruler's role. In order to spot the inter-independence of monkeys' propensity to choose to act together across sessions, the Choice Rates of TOGETHER action type in SOLO vs TOGETHER choice contexts, as computed for the two monkeys, were correlated across sessions by mean of the Spearman's rank correlation.

Kruskal-Wallis test was performed to compare Success rates across imposed and chosen conditions (7 groups: S_1 vs S_1 , S_2 vs S_2 , T vs T, S_1 chosen in S_1 vs T, T chosen in S_1 vs T, S_2

chosen in S₂ vs T, T chosen in S₂ vs T) and between absolute reward groups (3 groups: Low, Medium, High) and between relative reward groups ($\Delta 0$, $\Delta 1$, $\Delta 2$, $\Delta 3$, $\Delta 4$), within each group of imposed and chosen conditions.

Given that the monkeys could chose freely whether to approach one offer or discard a trial, the number of successful trials for each compared group had highly variable sample sizes. For this reason, the minimum sample size n was calculated, and random samples of $n = 152$ elements were selected from each group, to compare reaction times and peak velocities across imposed and chosen conditions. To this aim, a Kruskal-Wallis test was performed to compare the following 10 groups: S₁ (S₁ vs S₁), S₂ (S₂ vs S₂), T₁ (T vs T), T₂ (T vs T), S₁ chosen (S₁ vs T), T₁ chosen (S₁ vs T), S₂ chosen (S₂ vs T), T₂ chosen (S₂ vs T), T₁ chosen (S₂ vs T), T₂ chosen (S₁ vs T). In this case, the subscript of T (either 1 or 2) indicates which monkey executes the action of the two engaged in a joint action. This analysis was performed 100 times, each time on different randomly defined groups of n size.

Dunn test for post hoc (with Šidák correction for multiple comparison) was applied when appropriate to perform multiple comparison between groups.

Results

Learning joint action

Monkeys were initially trained to perform a center-out task in eight directions, either alone or together, as previously done in our lab (Visco-Comandini et al. 2015). Success rates were significantly different across trial types (SOLO1, SOLO2 and TOGETHER; Kruskal-Wallis test; $\chi^2(2) = 159.81$, $p = 1.98 \cdot 10^{-35}$). Performance in TOGETHER condition was lower than that observed for SOLO trials (SOLO1 against TOGETHER: $p = 0$; SOLO2 against TOGETHER: $p = 4.33 \cdot 10^{-15}$). The analysis of monkey's velocity profiles revealed, on one side a significant reduction of RT when the animals performed jointly respect to when they moved their cursor individually (Wilcoxon test; $Z = 19.70$, $p = 1.86 \cdot 10^{-86}$). On the other side, we found that the PVs were overall significantly lower in TOGETHER condition (Wilcoxon test; $Z = 27.39$, $p = 3.49 \cdot 10^{-165}$) in both monkeys. In addition, MK2 showed markedly lower PV in SOLO condition, compared to MK1 (Wilcoxon test; $Z = 11.80$, $p = 3.76 \cdot 10^{-32}$). These results met our previous findings, which demonstrated that coordinating action is costly – as affects

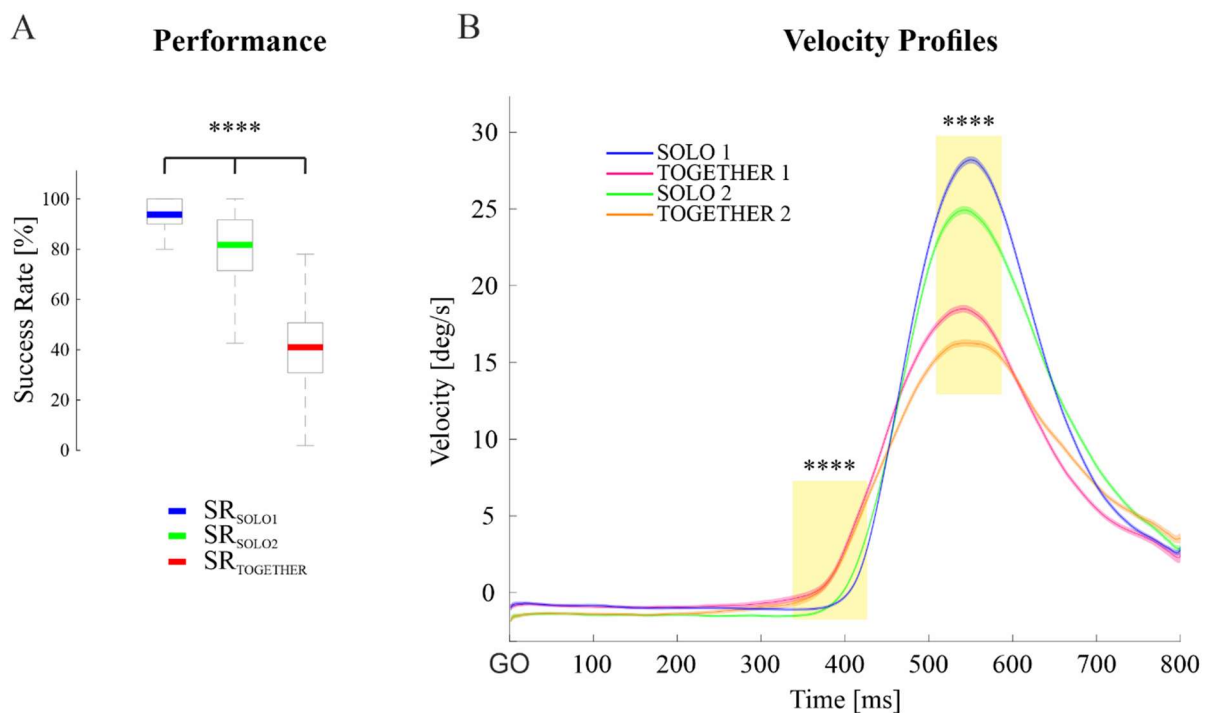


Figure 4. Joint action adaptations and performance (A) Median success rates for SOLO1, SOLO2 and TOGETHER trials in the training task. Monkey’s performance in TOGETHER condition was markedly lower (Kruskal-Wallis test, $p < 0.05$), when compared to SOLO conditions. Moreover, Mk2’s performance was lower than Mk1’s when acting alone. **(B)** Velocity profiles calculated for both monkeys performing SOLO and TOGETHER conditions in the control task. Movement onset and cursor speed were significantly reduced (Wilcoxon test; $p < 0.05$) when acting jointly (TOGETHER condition), compared to when acting alone (SOLO condition). Reaction time lag and peak reduction are highlighted in yellow
* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$

task performance – and requires a modulation of motor behavior. Such adaptation consists of two features: cursor’s movement start anticipation, which is deemed to boost inter-individual synchronization, and cursor’s speed reduction, as a tradeoff for accuracy.

Engaged trials and choice context inference

As a preliminary step, we first compared the percentage of ‘engaged’ trials (Fig. 5A), namely those trials in which the monkey reached in the temporal sequence of the task the phase when the two options (A and B) were simultaneously presented (IDT; Fig. 2). A significant difference across choice context was found (Kruskal-Wallis test; $\chi^2(4) = 312.21$, $p = 2.51 \cdot 10^{-66}$). Post hoc analysis (see Tab. 3) revealed that TOGETHER vs TOGETHER choice context trials were engaged with the lowest median rate (73%), while SOLO vs SOLO and SOLO vs TOGETHER choice contexts trials were engaged more often. It is worth noting that preliminary information about the upcoming choice contexts (SOLO vs SOLO, TOGETHER vs TOGETHER, or SOLO

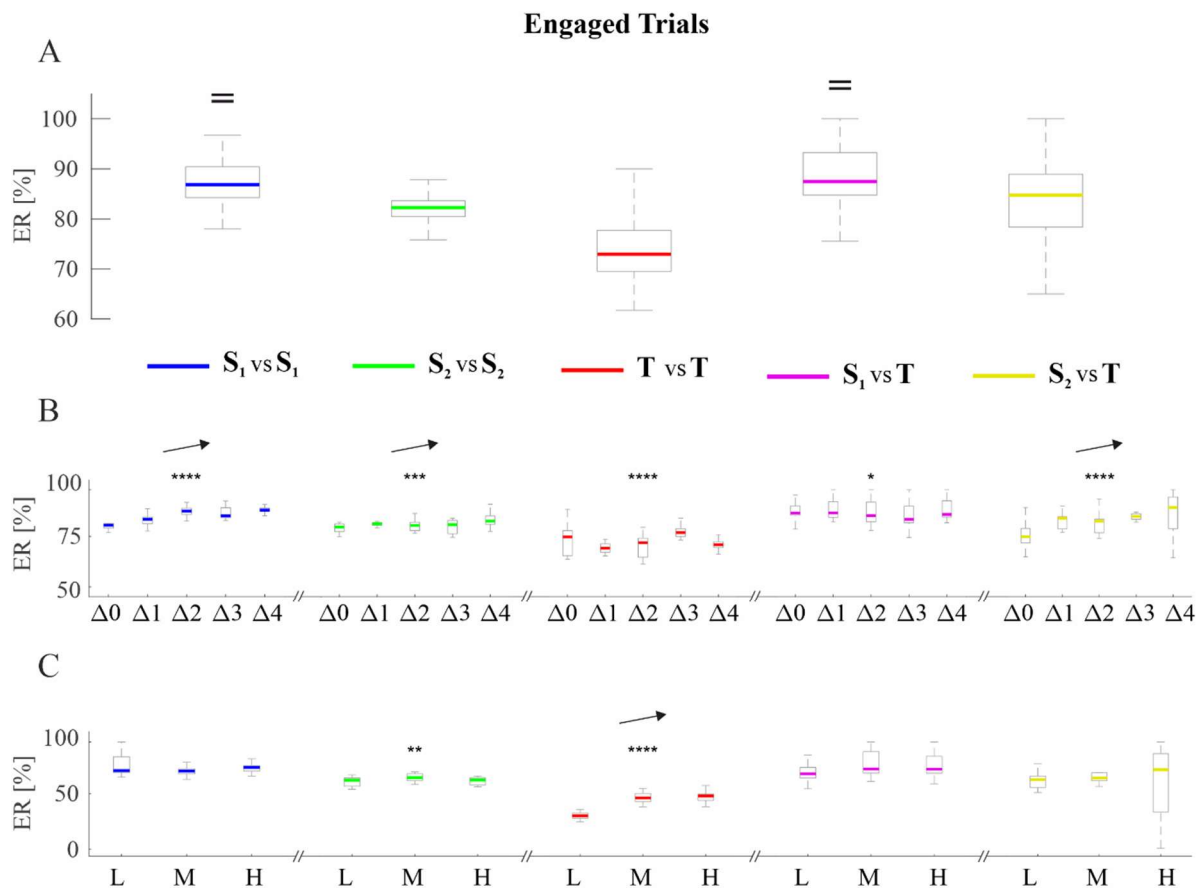


Figure 5. Engaged trials and choice contexts. (A) Median rates of trial engagement (ER) across choice contexts. A significant difference in the percentage of fulfilled trials emerged across all choice contexts (Kruskal-Wallis test, $p < 0.05$), with the T vs T choice context being engaged at the lowest rate, and with the only exception of S_1 vs S_1 and S_1 vs T choice contexts, which showed the same ER (as indicated by the symbol =). (B) Median ER computed for each delta group within each choice contexts. The difference between the two options' payoff influenced all choice contexts (Kruskal-Wallis test, $p < 0.05$), but only in S_1 vs S_1 , S_2 vs S_2 and S_2 vs T choice contexts trials were increasingly fulfilled for increasing deltas (as indicated by the arrows). (C) Median ER computed for each absolute reward level group within each choice contexts. A significant effect of absolute reward level was found only in S_2 vs S_2 and T vs T, but an increasing ER for higher reward levels was found only within T vs T choice context (as marked by the arrow).

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$

vs TOGETHER) was available to the animals by the serial sequence of Opt A and Opt B, prior to the choice phase. Mk1 showed the higher rate of 'engaged' trials (87%), with no difference between the S_1 vs S_1 and the S_1 vs T choice contexts, while Mk2 showed a higher rate in S_2 vs T trials (85%) compared to the S_2 vs S_2 trials (82%). These results demonstrate that: (i) monkeys' motivation to approach the task was generally high, spanning from 73% to 87%. Second, (ii) the animals were able to infer the type of trial already in the instruction phase, when the offered options were disclosed in sequence, as evident from the influence of the factor 'choice context' on their rate of 'engaged' trials.

Choice contexts compared		P value	
		ER	no-CR
SOLO 1 vs SOLO 1	SOLO 2 vs SOLO 2	1.01·10⁻⁸	0.9997
TOGETHER vs TOGETHER	SOLO 1 vs SOLO 1	9.92·10⁻⁹	9.92·10⁻⁹
	SOLO 2 vs SOLO 2	9.92·10⁻⁹	9.92·10⁻⁹
	SOLO 1 vs TOGETHER	9.92·10⁻⁹	9.92·10⁻⁹
	SOLO 2 vs TOGETHER	9.92·10⁻⁹	9.92·10⁻⁹
SOLO 1 vs TOGETHER	SOLO 1 vs SOLO 1	0.8224	0.2052
	SOLO 2 vs SOLO 2	9.92·10⁻⁹	0.2958
	SOLO 2 vs TOGETHER	4.57·10⁻⁶	0.2783
SOLO 2 vs TOGETHER	SOLO 1 vs SOLO 1	8.00·10⁻⁴	3.81·10⁻⁴
	SOLO 2 vs SOLO 2	0.0434	8.54·10⁻⁴

Table 3. Dunn-Šidák test for multiple comparison of choice contexts' engagement rates and no-choice rates.

Choice context		Factor	df	χ^2	P	Figure panel
ER	SOLO 1 vs SOLO 1	Delta	4	44.12	6.09·10⁻⁹	5B
	SOLO 2 vs SOLO 2			19.29	6.89·10⁻⁴	
	TOGETHER vs TOGETHER			42.47	1.33·10⁻⁸	
	SOLO 1 vs TOGETHER			10.26	0.0363	
	SOLO 2 vs TOGETHER			29.35	6.63·10⁻⁶	
	SOLO 1 vs SOLO 1	Levels	2	4.47	0.1072	5C
	SOLO 2 vs SOLO 2			9.58	0.0083	
	TOGETHER vs TOGETHER			47.77	4.23·10⁻¹¹	
	SOLO 1 vs TOGETHER			5.29	0.0712	
	SOLO 2 vs TOGETHER			2.70	0.2586	
No-CR	SOLO 1 vs SOLO 1	Delta	4	1.08	0.8970	6C
	SOLO 2 vs SOLO 2			1.56	0.8164	
	TOGETHER vs TOGETHER			11.42	0.0223	
	SOLO 1 vs TOGETHER			1.94	0.7474	
	SOLO 2 vs TOGETHER			8.31	0.0808	

Table 4. Kruskal-Wallis test ($p < 0.05$) for reward deltas and levels comparison within choice contexts' engagement rates. Kruskal-Wallis test for reward deltas comparison within choice contexts' no-choice rates.

We further investigated whether the amount of reward had an influence on the motivation to reach the choice phase. To this purpose we analyzed the potential influence of the 'relative' and 'absolute' reward on the monkey's propensity to ignore or engage a trial. When comparing the percentage of engaged trials across reward deltas (Fig. 5B), we found a significant difference between deltas in all choice context (Tab. 4). Nevertheless, as evident from post hoc analysis (Tab. 5), only in S_1 vs S_1 , S_2 vs S_2 and S_2 vs T choice contexts a tendency to increase the percentage of 'engaged' trials for increasing delta sizes was evident. In the other cases, the

Choice contexts	Deltas compared			Levels compared		
	$\Delta 0$ vs $\Delta 2$	$\Delta 2$ vs $\Delta 4$	$\Delta 0$ vs $\Delta 4$	L vs M	M vs H	L vs H
SOLO 1 vs SOLO 1	$9.27 \cdot 10^{-6}$	0.9665	$2.85 \cdot 10^{-7}$	-	-	-
SOLO 2 vs SOLO 2	0.7166	0.0247	$2.26 \cdot 10^{-4}$	0.0125	0.0347	0.9325
TOGETHER vs TOGETHER	0.4806	0.9998	0.3683	$1.42 \cdot 10^{-8}$	0.9712	$4.17 \cdot 10^{-9}$
SOLO 1 vs TOGETHER	0.5076	0.6900	0.9986	-	-	-
SOLO 2 vs TOGETHER	0.2311	0.1797	$1.86 \cdot 10^{-4}$	-	-	-

Table 5. Dunn-Šidák test for multiple comparison of reward deltas and levels' engagement rates. Only those differences between deltas that are sufficient to spot an increasing of rates for increasing reward difference are reported.

significant difference across deltas was of difficult interpretation. When considering the percentage of 'engaged' trials divided second to the absolute reward level of the higher of the two offers (Fig. 5C), we found a significant difference only in two choice contexts (Tab. 4). Post hoc comparison revealed higher rates of 'engaged' trials for Medium and High reward offers only in T vs T choice context (Tab. 5). While relative reward seemed to impact the rate of 'engaged' trials, absolute reward had a clear effect only in T vs T group. In general, Mk2 seem to be more sensitive to options' value modulation. Reward seemed hence to influence in a mild fashion the motivation of monkeys to engage a trial.

Discarded trials and no-Choice rates

If a trial was not ignored, it meant that monkeys were at least willing to take the chance to see to which target (left or right) each offered option (A or B) was associated. We computed the median time spent in the central target once the IDT epoch was entered. We found that monkeys waited around 735 ± 36 ms (i.e., between 87% and 96% of the maximum duration of the epoch), irrespective of whether a choice was made. Once this phase was reached, hence, monkeys waited almost until the end of the CDT before deciding whether to make a choice or discard the trial. Such behavior emerged spontaneously since it was not imposed by the task.

First, we compared no-Choice Rates (no-CR) across choice contexts (Fig. 6A). A significant effect of choice context factor emerged (Kruskal-Wallis test; $\chi^2(4) = 375.98$, $p = 4.29 \cdot 10^{-80}$). Post hoc tests (Tab. 3). revealed that in T vs T choice context the median no-CR was markedly higher than the others. Moreover, S_2 vs T context showed a higher no-CR in compared to S_1 vs S_1 and S_2 vs S_2 choice contexts. We then analyzed how no-Choice Rates (no-CR) varied across reward deltas. First, we fitted a line to the median no-CR computed for each delta group (Fig.

6B). Only T vs T choice context showed a clear descending slope signifying an increasing tendency to engage a trial for higher deltas. When comparing median no-CR across deltas, in fact, a significant difference across groups emerged only in the T vs T choice context (Fig. 6C, Tab. 4). We further investigated if this effect could be affected also by the absolute level of

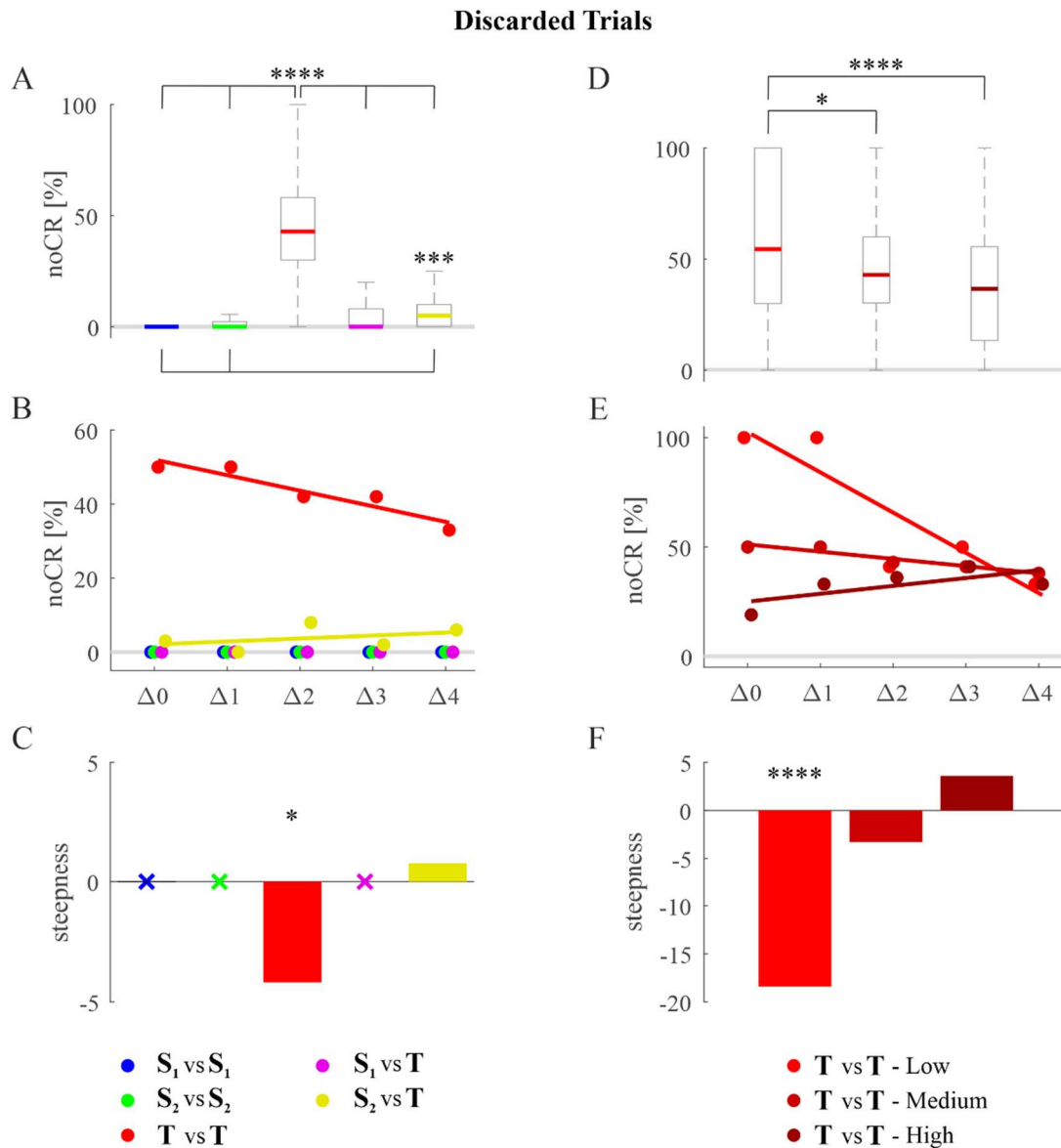


Figure 6. Title. (A) Median no-choice rates (no-CR) were compared across choice contexts (Kruskal-Wallis test, $p < 0.05$), showing higher median rates for T vs T choice contexts, compare to all the others. S_2 vs T choice context was also significantly higher than SOLO's. (B) To analyzed how no-CR changed across reward deltas, we fitted a line to the median no-CR computed for each delta group. (C) Only T vs T choice context showed a clear descending slope signifying an increasing tendency to engage a trial for higher deltas. This observation was confirmed by comparing no-CR across deltas within T vs T choice context (Kruskal-Wallis test, $p < 0.05$). (D) A significant difference between median reward level groups of no-CR within T vs T choice context was found. Specifically, trials with a low reward level as the maximum reward offered were discarded significantly more often. (E) The linear fit of median noCR across deltas performed for each reward level group revealed a marked decrease of no-CR for increasing delta only for the Low group. (F) Only the Low group, in fact, the linear fit revealed a marked and significant, negative steepness. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$

reward. We therefore divided all trials within T vs T choice context second to the absolute reward level of the higher of the two offers (Fig. 6D). A significant effect of this factor was found (Kruskal-Wallis test; $\chi^2(2) = 22.50$, $p = 1.30 \cdot 10^{-5}$). Specifically, T vs T trials with Low reward were discarded with a significant higher rate, when compared to the ones associated to Medium and Lower reward (Dunn-Šidák test; Low vs Medium: $p = 0.0186$; Low vs High: $p = 6.88 \cdot 10^{-6}$). By performing a linear fit on the distribution of no-CRs across deltas within each absolute reward level group (Fig. 6E), we found that the relative reward significantly affected the no-CR only when the reward of the higher offer was Low (Kruskal-Wallis test; Low: $\chi^2(4) = 31.94$, $p = 1.97 \cdot 10^{-6}$; Medium: $\chi^2(4) = 4.85$, $p = 0.3027$; High: $\chi^2(4) = 2.72$, $p = 0.6053$). Only the Low group, in fact, the linear fit revealed a marked and significant, negative steepness (Fig. 6F). This result was mainly explained by the fact that when the reward offered was low and the relative reward difference null or minimal ($\Delta 1$), no choice was made in almost the 100% of cases.

In summary, when choosing between two TOGETHER targets monkeys defected trials more often and their rate of defected trials was influenced both by the relative and absolute reward at stake.

Choice-made trials and choice rates

When a trial was engaged, a choice was made. In order to understand monkeys' ability to discriminate between rewards when performing the action alone or together, a sigmoid curve was fitted to the median rates for which a target Both monkeys, when choosing between two SOLO (Fig. 7A-B) or two TOGETHER (Fig. 7C) targets, were able to discriminate between different rewards offered and clearly aim for the most convenient option, as evident from the similar steepness estimated from fitting a logistic curve to data. In fact, logistic curve's steepness was the same in all conditions, although more variable for TOGETHER vs TOGETHER choice context, as evident from the wider confidence of interval for the estimated parameter (Fig. 7C). Once established that both monkeys could finely discriminate between different offers both when acting alone or together, we wanted to see if they could take into account action cost when choosing between two different action types. When the chance to choose between a SOLO and a TOGETHER target was given, both monkeys show a utter preference for the SOLO condition, regardless of the offer (Fig. 7D). This preference decreased for a reward difference in favor of the TOGETHER option higher than 0.15ml ($\Delta 1$), thus increasing TOGETHER choice rate from 0 to 30% in Mk1, and to 50% in Mk2. Our

interpretation was that the reward difference between the two conditions was not wide enough to compensate the cost of coordinating with the partner.

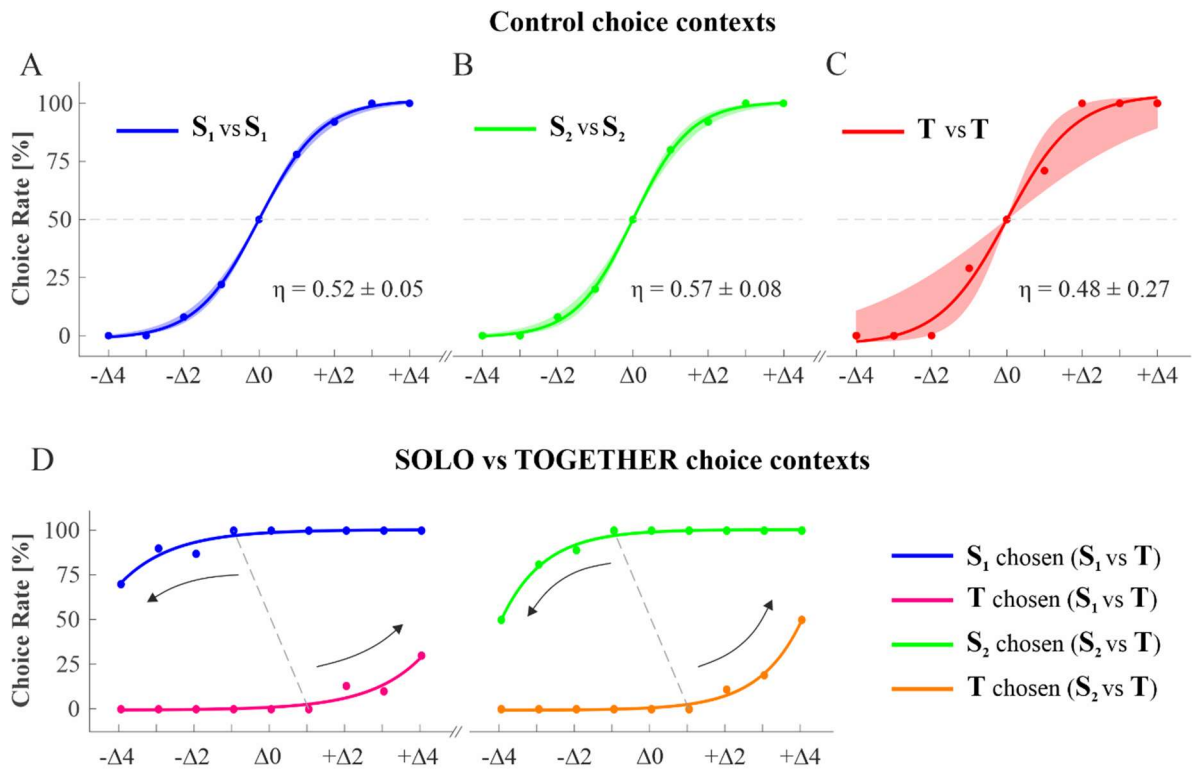


Figure 7. Choice rates in all choice contexts. A sigmoid function was fitted to the median choice rates (CRs) computed for each signed delta, indicating how often an object was chosen when its reward was lower (+ $\Delta 1$, + $\Delta 2$, + $\Delta 3$, + $\Delta 4$), equal ($\Delta 0$), or higher (+ $\Delta 1$, + $\Delta 2$, + $\Delta 3$, + $\Delta 4$) then the reward associated to the other option. Both monkeys, when choosing between two SOLO (A-B) or two TOGETHER targets (C), were able to discriminate between different rewards offered and clearly aim for the most convenient option. The steepness of the fitted curves was more variable in T vs T choice contexts, as evident from its confidence interval. (D) When the chance to choose between a SOLO and a TOGETHER target was given, both monkeys show a utter preference for the SOLO condition, regardless of the offer. This preference decreased for a reward difference in favor of the TOGETHER option higher than 0.15ml ($\Delta 1$), thus increasing TOGETHER choice rate from 0 to 30% in MK1, and to 50% in MK2, as indicated by the curve, symmetrical arrows

To further understand this result, we evaluate how absolute and relative reward combines to influence monkeys' choice. Absolute Reward Choice Rates (AbsCRs; i.e., the rate at which a target with an absolute reward level (Low, Medium or High) was chosen when offered, was computed for each reward delta within each group obtained by the combination of action type chosen and choice contexts.

The probability of the choice in favor of a certain amount of 'absolute' reward was plotted against the Deltas indicating the differences between the two options, in a gray-scale matrix (Fig. 8A). Different matrices were plotted for each type of choice context (SOLO vs SOLO, TOGETHER vs TOGETHER, and SOLO vs TOGETHER) and also for the action type chosen

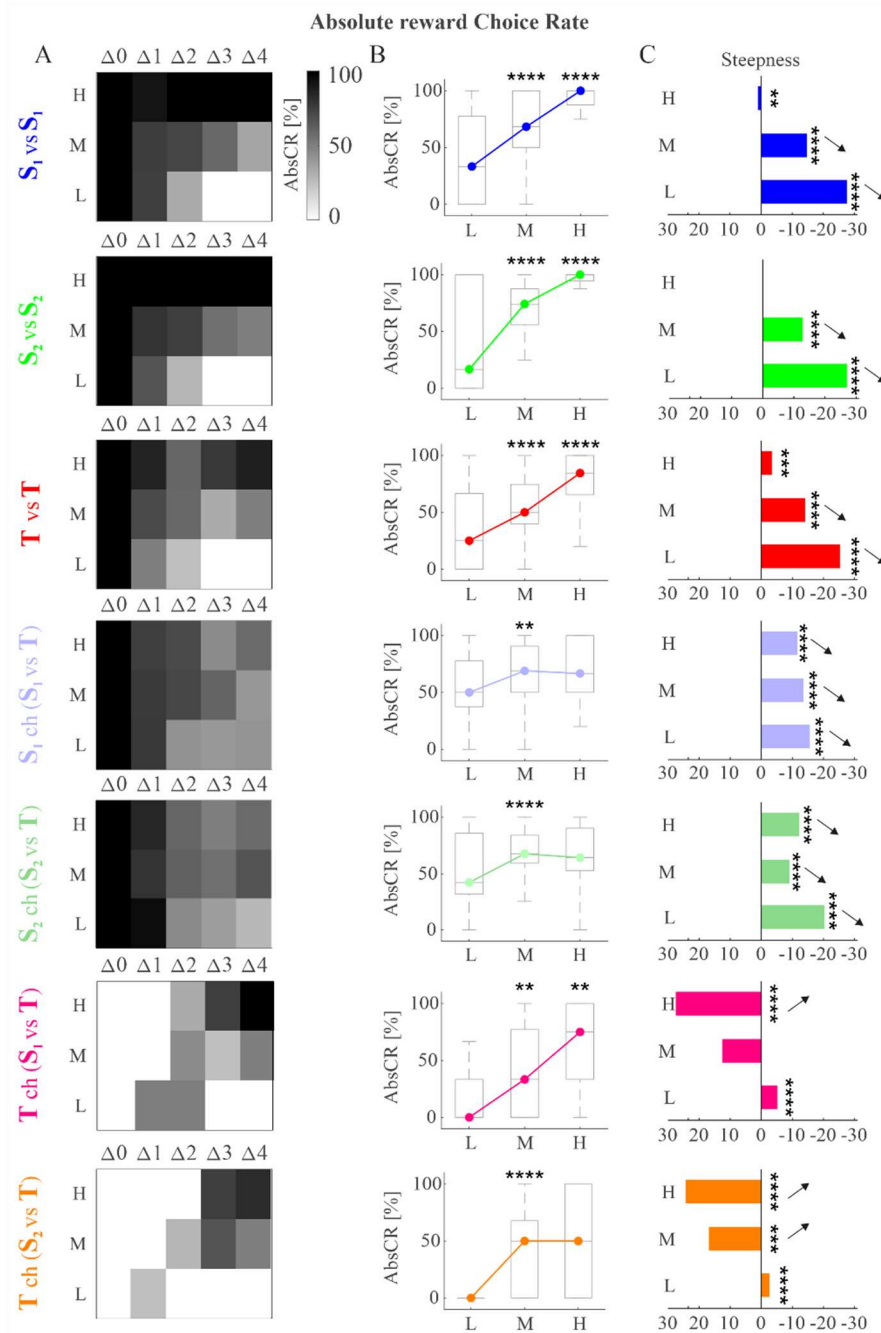


Figure 8. Absolute reward influence on choice across deltas and conditions. (A) Absolute rewards choice rates (AbsCR), as computed for each absolute reward level (Low, Medium, High) and across reward deltas for each group of imposed (i.e., from control choice contexts) and chosen (i.e., from SOLO vs TOGETHER) conditions, are represented in grayscale matrixes. Three patterns of choice emerged: a reward-based choice pattern, evident in control conditions, and two action type-dependent complementary pattern (SOLO vs TOGETHER). (B) Median AbsCR computed for each delta group within each choice contexts. AbsCRs differed across level groups, showing increasing AbsCR for higher levels, but with different profiles that remarked the three patterns evident in panel A. (C) Slopes of the linear fit performed across delta groups for each reward level (Low, Medium, High) within each condition, imposed and chosen. AbsCRs are influenced by reward difference between the two offers, again confirming three characteristic pattern what distinguish SOLO chosen and TOGETHER chosen trials from SOLO and TOGETHER ones (as from control choice contexts). The upward arrow indicated a significant increase of AbsCRs for increasing deltas, while the downward arrow indicated a significant decrease of AbsCRs for decreasing deltas.

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$

(e.g., “TOGETHER chosen”), when the animals had to select the type of action to obtain their

reward.

At a preliminary qualitative assessment, three main patterns of relative-absolute reward combination emerged. The first one, was characterized by a clear reduction of choice rates for low and medium rewards, at increasing the relative reward between the two option. This pattern was observed in the three control choice contexts, i.e., S_1 vs S_1 , S_2 vs S_2 and T vs T ones. The second pattern was defined by a reduction of the choice rate that mainly followed the relative reward increase, and it appeared to be less sensitive to the absolute reward level. This scheme was associated to SOLO chosen trials. Finally, a third, patchier pattern characterized the two TOGETHER chosen conditions. In this latter case, low rewards and in the context of low deltas were almost never chosen, with a drastic increase of choice rates on the top-right corner (Medium-High x $\Delta 3$ - $\Delta 4$). To quantify these observations, AbsCRs were compared within each group of imposed and chosen targets by mean of a Kruskal-Wallis test (Fig. 8B) and a significant effect of absolute reward level factor was found in all cases, thus confirming the general tendency of a target to be chosen more often when its absolute reward was increased (Tab. 6). Post hoc analysis (Dunn-Šidák test) confirmed the differences between the three main patterns described above: in control choice contexts the AbsCR increased in a uniform way; when choosing a SOLO target, the median AbsCR for Low reward targets was higher than the one observed in control choice contexts but tended to increase less for Medium and High groups, compared to the Low group; in a complementary fashion, median AbsCR for Low group in TOGETHER chosen were null, but the increase from Low to Medium AbsCR was more marked.

To assess if the propensity to choose a certain reward level when presented could change between reward deltas, we evaluated the steepness of a linear fit performed across deltas for each reward level group (Low, Medium, High), within each imposed and chosen condition group (Fig. 8C). Additionally, a Kruskal-Wallis test was performed to compare Absolute Reward Choice Rates between relative reward groups ($\Delta 0$, $\Delta 1$, $\Delta 2$, $\Delta 3$, $\Delta 4$), along with a Dunn-Šidák test to confirm the monotonicity of values for increasing deltas – and hence the actual significance of the estimated steepness. Again, three patterns emerged. In control choice contexts, High reward targets were chosen almost irrespective of the reward difference between the two offers, while Medium and Low reward targets were chosen less often for increasing reward deltas, as should be expected for a reward-driven decision style. In SOLO chosen trials, Low, High, and Medium reward were chosen less often for increasing deltas. In TOGETHER chosen trials, instead, High reward targets were chosen more often for increasing deltas,

Medium reward targets AbsCRs were either not modulated by the relative reward, or again increased for increasing deltas, while Low reward was not modulated in any clear direction.

Action type & choice		Factor	df	χ^2	P	Figure panel	
AbsCR	SOLO 1 (S ₁ vs S ₁)	Levels	2	132.47	1.72·10⁻²⁹	8B	
	SOLO 2 (S ₂ vs S ₂)			141.41	1.97·10⁻³¹		
	TOGETHER (T vs T)			83.14	8.84·10⁻¹⁹		
	SOLO 1 chosen (S ₁ vs T)			23.51	7.85·10⁻⁶		
	TOGETHER 1 chosen (S ₁ vs T)			39.12	3.17·10⁻⁹		
	SOLO 2 chosen (S ₂ vs T)			27.54	1.05·10⁻⁶		
	TOGETHER 2 chosen (S ₂ vs T)			37.51	7.15·10⁻⁹		
	SOLO 1	Deltas	4	Low	112.47	2.16·10⁻²³	8C
				Medium	76.22	1.10·10⁻¹⁵	
				High	17.54	0.0015	
	SOLO 2			Low	102.49	2.91·10⁻²¹	
				Medium	78.44	3.73·10⁻¹⁶	
				High	2.43	0.6575	
	TOGETHER			Low	62.07	1.06·10⁻¹²	
				Medium	53.8	5.79·10⁻¹¹	
				High	18.87	0.0008	
	SOLO 1 chosen			Low	73.46	4.22·10⁻¹⁵	
				Medium	81.65	7.79·10⁻¹⁷	
				High	60.98	1.81·10⁻¹²	
	TOGETHER 1 chosen	Low	40.50	3.41·10⁻⁸			
Medium		1.98	0.7401				
High		10.09	0.0389				
SOLO 2 chosen	Low	80.05	1.70·10⁻¹⁶				
	Medium	57.14	1.16·10⁻¹¹				
	High	79.89	1.83·10⁻¹⁶				
TOGETHER 2 chosen	Low	28.19	1.13·10⁻⁵				
	Medium	20.93	0.0003				
	High	29.89	5.15·10⁻⁶				

Table 6. Kruskal-Wallis test for absolute reward choice rate (AbsCR) between absolute reward and between relative reward groups within each condition, imposed (i.e., control choice contexts) or chosen (i.e., SOLO vs TOGETHER choice contexts)

In summary, while in the control contexts (S₁ vs S₁, S₂ vs S₂ and T vs T) both absolute and relative reward guided choice behavior in a balanced way, in SOLO vs TOGETHER contexts, in which a clear action type preference emerged, the absolute and relative reward associated to the two action types were characterized by two complementary styles of choice: the SOLO chosen one, in which reward influence on choice was reduced, and the TOGETHER chosen one, in which choice behavior was strongly influenced by the absolute and relative reward convenient combination. As in control choice contexts the decision style

Action type & choice	Levels compared			Deltas compared			
	L vs M	M vs H	L vs H	Level	$\Delta 0$ vs $\Delta 2$	$\Delta 2$ vs $\Delta 4$	$\Delta 0$ vs $\Delta 4$
SOLO 1 (S ₁ vs S ₁)	2.40·10 ⁻⁵	1.06·10 ⁻¹¹	0	L	6.90·10 ⁻⁶	0.0089	1.11·10 ⁻¹⁵
				M	5.25·10 ⁻⁴	4.72·10 ⁻⁴	8.88·10 ⁻¹⁵
				H	0.4336	0.9998	0.8505
SOLO 2 (S ₂ vs S ₂)	4.24·10 ⁻⁵	4.51·10 ⁻¹³	0	L	1.00·10 ⁻⁶	0.0243	1.11·10 ⁻¹⁵
				M	1.05·10 ⁻⁴	0.0217	2.00·10 ⁻¹²
				H	-	-	-
TOGETHER (T vs T)	2.78·10 ⁻⁴	7.92·10 ⁻⁷	0	L	0.0473	0.0054	1.59·10 ⁻⁹
				M	0.3723	0.1148	1.17·10 ⁻⁴
				H	5.68·10 ⁻⁴	0.0774	0.8056
SOLO 1 chosen (S ₁ vs T)	2.55·10 ⁻⁴	0.9344	2.61·10 ⁻⁵	L	1.85·10 ⁻⁶	0.8865	4.92·10 ⁻¹⁰
				M	8.93·10 ⁻⁵	0.0010	1.11·10 ⁻¹⁵
				H	4.48·10 ⁻⁴	0.7509	2.37·10 ⁻⁷
TOGETHER 1 chosen (S ₁ vs T)	0.0055	0.0060	1.27·10 ⁻⁹	L	0.5555	4.97·10 ⁻⁶	0.7254
				M	-	-	-
				H	0.9752	0.3146	1.0000
SOLO 2 chosen (S ₂ vs T)	3.20·10 ⁻⁶	0.8541	1.02·10 ⁻⁴	L	0.0019	0.0051	2.81·10 ⁻¹¹
				M	4.92·10 ⁻⁶	1.0000	2.38·10 ⁻⁵
				H	3.44·10 ⁻⁷	1.0000	1.85·10 ⁻⁸
TOGETHER 2 chosen (S ₂ vs T)	1.83·10 ⁻⁵	0.3500	2.15·10 ⁻⁸	L	0.9891	5.18e·10 ⁻⁴	0.5290
				M	0.3995	0.3308	0.0049
				H	0.9939	1.69·10 ⁻⁴	0.0080

Table 7. Dunn-Šidák test for multiple comparison of absolute reward choice rate (AbsCR) between absolute reward and between relative reward groups within each absolute reward level group was performed, for each imposed (i.e., control choice contexts) or chosen (i.e., SOLO vs TOGETHER choice contexts). Only those differences between deltas that are sufficient to spot an increasing of rates for increasing reward difference are reported.

was a reward-based, in SOLO vs TOGETHER choice contexts it was action type-dependent. These results confirm that the economic choice was, in this latter case, markedly subdued to the motor and social aspects that distinguish the two conditions.

The cost of inter-individual coordination

Driven by our hypothesis that the delta size was not sufficient to compensate the cost of coordinating with the partner, we tested the same monkeys in the same task, but augmenting the differences in the amount of reward offered within each choice. In particular we doubled the delta size and fixed the reward levels, to finely quantify their perceived cost of acting

together. By doubling the unit of reward difference between the two options to $u = 1.20\text{ml}$, the action type preference drastically changed for both monkeys

(Fig. 9A-B). The SOLO action was not always preferred, and 100% of choice rate in favor of the TOGETHER action was observed for a difference in the two options' values above 0.90 ml. The indifference point between the TOGETHER and SOLO offers was found at around $\Delta = 0.30\text{ ml}$, indicating the *perceived cost of acting together*. If the choice between SOLO and TOGETHER were mainly based on the reward value, with no cost difference between the two actions, the indifferent point would have lied at $\Delta 0$. Our findings show instead that when monkeys chose between acting alone or together, their preference was not mainly dictated by the offer nor by their action preference, but rather based on a tradeoff between cost and utility of acting together.

To establish whether the two monkeys' choice strategy was aimed at increasing the chances of gaining the higher reward possible from each trial, we computed how often monkeys aimed at the maximum offer of the trial in control and SOLO vs TOGETHER choice contexts (Fig. 10A). The comparison between high reward choice rates (HRCR), showed a significant difference across choice contexts (Kruskal-Wallis test; $\chi^2(4) = 19.19$, $p = 7.212 \cdot 10^{-4}$). Post hoc analysis (Dunn-Šidák test) showed that in the SOLO vs TOGETHER choice contexts the animals effectively aimed at the higher offer similarly to when they were choosing alone between two individual actions. In the T vs T choice context, instead, this tendency was found significantly lower when compared to the other two control choice contexts (comparison with S_1 vs S_1 : $p = 2.78 \cdot 10^{-04}$; comparison with S_2 vs S_2 : $p = 0.0473$). We wonder then if such strategy could be effective to optimize the reward that monkeys could gain during a session from SOLO vs TOGETHER trials. To clarify this point, we compared the actual percentage of reward gained out of the total amount offered within a session (EGR index) in SOLO vs TOGETHER trials, with the effort minimization threshold (i.e., the maximum reward that monkeys could gain by choosing systematically only the SOLO action type; Fig. 10B). The maximum reward gainable by choosing only one action type was theoretically around 70%. The actual maximum gain that monkeys could have get by choosing always TOGETHER targets over SOLO ones, was found to be very low (median: 15%), while the actual maximum gain that they could have get by choosing always to act alone was between 51% and 61%, depending on each monkey's individual ability to perform the center out task (when choosing between two SOLO targets) and to hold the target in the center (when the partner was choosing between two SOLO targets). By comparing the actual percentage of the reward gained out of the total amount offered within

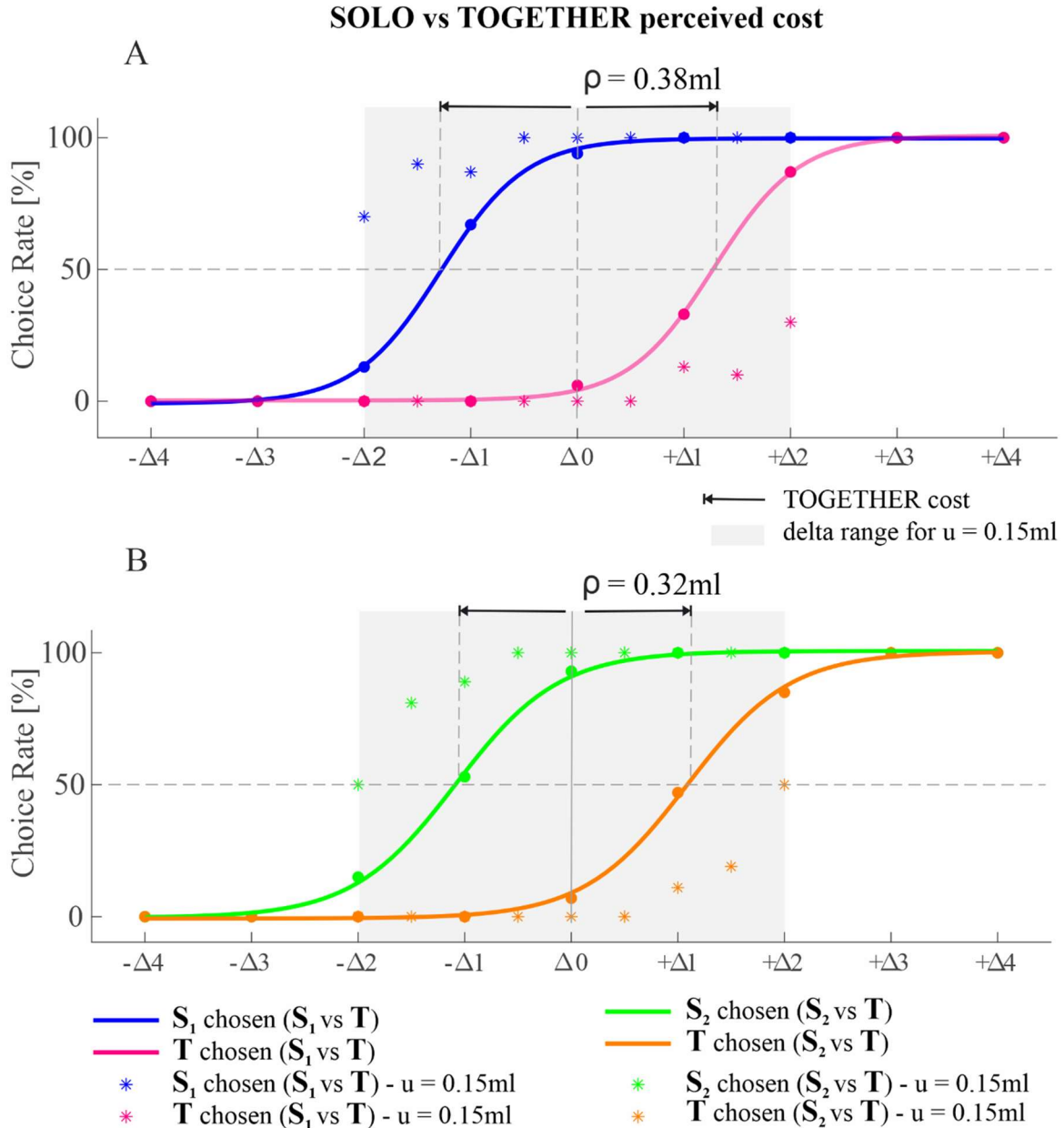


Figure 9. Subjective cost of actin together. (A-B) Sigmoid functions fitted to monkey's choice rates for SOLO and TOGETHER conditions within SOLO vs TOGETHER choice contexts for the test task, represented in superposition to the choice rates computed for SOLO vs TOGETHER choice contexts for the training task. By doubling the unit of reward difference between the two options from $u = 0.60\text{ml}$ (training task) to $u = 1.20\text{ml}$ (test task), the action type preference drastically changed and the perceived cost of acting together emerged as a shift of the indifference point between the two action types offered, which was of $\rho = 0.38\text{ml}$ for Mk1 and $\rho = 0.32\text{ml}$ for Mk2.

a session (EGR) in SOLO vs TOGETHER with these thresholds, only in S_1 vs T choice context monkeys' gain was significantly exceeding the amount that they could have gain by ignoring completely all TOGETHER's targets (Wilcoxon test: S_1 vs T Mk1: $Z = 2.38$, $p = 0.0171$; S_1 vs T Mk2: $Z = 2,30$, $p = 0.0217$). When Mk1 was playing as a ruler, hence, both monkeys managed to gain around 5-8% more than what they could have get by choosing systematically the SOLO option. When Mk2 was designed as the ruler, instead, there was no evident convenience of the

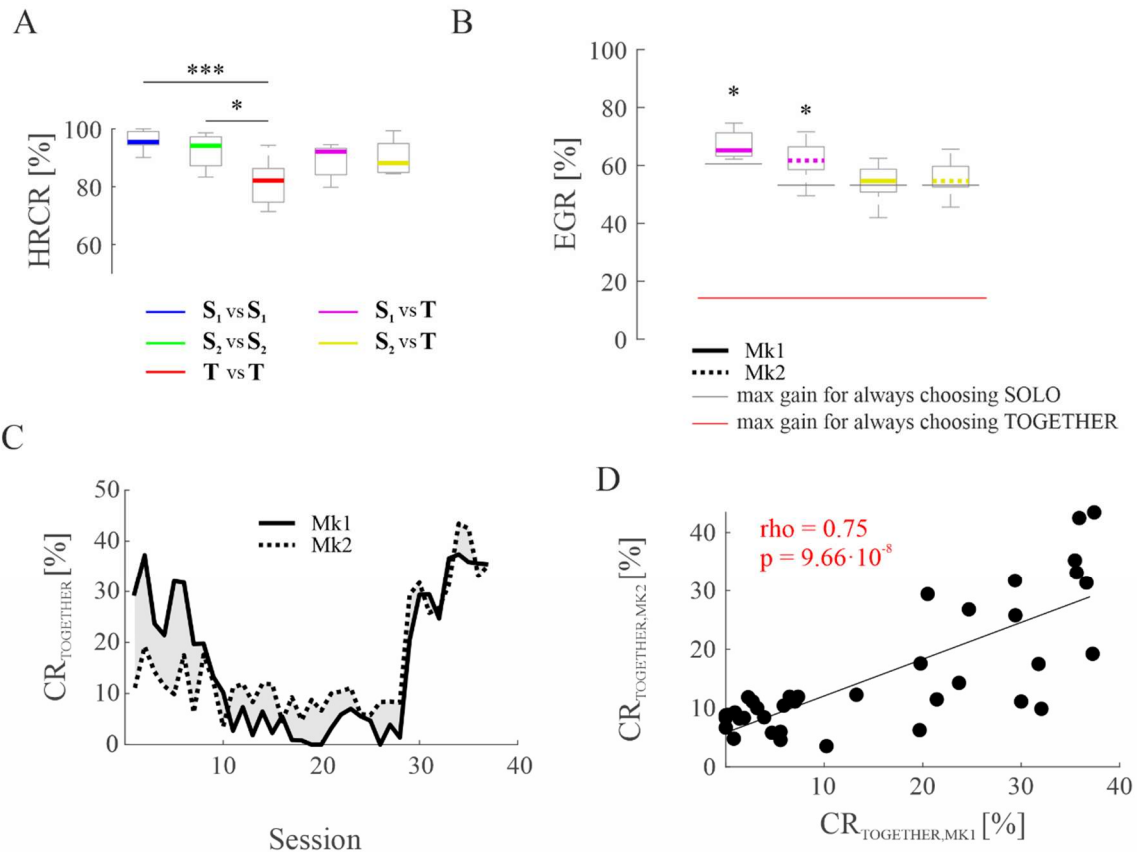


Figure 10. Reward gain optimization strategy. (A) Median high reward choice rate (HRCR) were compared across choice contexts (Kruskal-Wallis test, $p < 0.05$), showing a lower tendency to aim for the higher reward in T vs T choice contexts, compare to the two other control choice contexts. (B) The median effective gain rate (EGR) indexes, indicating the reward gained by both monkeys within the SOLO vs TOGETHER choice contexts, were compared to the effort minimization threshold, defined as the weighed maximum reward that they could have gain by choosing systematically only the SOLO action type (Wilcoxon rank test, $p < 0.05$). A higher EGR was evident only in the S_1 vs T choice context, for both the ruler (Mk1) and the partner (Mk2) (C) The rate at which TOGETHER condition was chosen over SOLO's by each monkey in each session ($CR_{TOGETHER}$) within SOLO vs TOGETHER choice contexts. is represented (D) A correlation between Mk1 and Mk2 TOGETHER choice rates in SOLO vs TOGETHER choice contexts emerged.

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$

“aim at the higher” choice strategy showed by the monkeys, compared to the “always choose the safest and easier option” strategy.

Since we demonstrated that monkeys estimated similarly the cost of acting together and adopted similar choice strategies, we wonder if there could be an interdependence between monkeys' predisposition of acting together. Monkeys' $CR_{TOGETHER}$ in SOLO vs TOGETHER choice contexts seemed to vary congruently across sessions (Fig. 10C). In fact, a significant correlation between Mk1 and Mk2's $CR_{TOGETHER}$ was found (Spearman correlation: $\rho = 0.75$, $p = 9.66 \cdot 10^{-8}$; Fig.10D). The propensity to choose to reach a target together when playing as a ruler, thus, was reciprocally influenced by the attitude of the partner to choose this condition when it was his turn to play the same role.

Action type effect on performance

We previously shown in this study (*Experiment 1* and training task of *Experiment 2*), as well as in previous experiments (Visco-Comandini et al, 2015), that when the animals, had no choice between action types, but just asked to achieve their goals either alone or together, in the TOGETHER condition the success rate was significantly lower, respect to the SOLO one. Similar results were found when monkeys got to choose between two options. A significant difference in Success Rates (SRs) emerged when comparing all groups obtained by the combination of choice context and the action type performed (Kruskal-Wallis test; $\chi^2(6) = 806.18$, $p = 7.12 \cdot 10^{-171}$; Fig. 11A). SRs in TOGETHER condition were always significantly lower than SOLO's, as revealed by post hoc analysis (Dunn-Šidák test). Moreover, SRs did not differ within each action type (SOLO and TOGETHER), thus confirming an overall coherence of task difficulty when monkeys were performing the same type of action (individual or joint), irrespective of the choice contexts in which it was performed (control or SOLO vs TOGETHER choice context).

Action type & choice		Factor	df	χ^2	P	Figure panel
SR	SOLO 1 (S ₁ vs S ₁)	Deltas	4	4.62	0.3286	11B
	SOLO 2 (S ₂ vs S ₂)			2.94	0.5671	
	TOGETHER (T vs T)			15.41	0.0039	
	SOLO 1 chosen (S ₁ vs T)			3.80	0.4344	
	TOGETHER 1 chosen (S ₁ vs T)			8.17	0.0854	
	SOLO 2 chosen (S ₂ vs T)			0.90	0.9242	
	TOGETHER 2 chosen (S ₂ vs T)			15.67	0.0035	
	SOLO 1 (S ₁ vs S ₁)			2.38	0.3037	
	SOLO 2 (S ₂ vs S ₂)	10.17	0.0062	11C		
	TOGETHER (T vs T)	31.97	1.14·10⁻⁷			
	SOLO 1 chosen (S ₁ vs T)	2.39	0.3021			
	TOGETHER 1 chosen (S ₁ vs T)	20.19	4.13·10⁻⁵			
	SOLO 2 chosen (S ₂ vs T)	1.21	0.5473			
	TOGETHER 2 chosen (S ₂ vs T)	9.25	0.0098			

Table 8. Kruskal-Wallis test ($p < 0.05$) for Success Rates (SRs) comparison between absolute reward and between relative reward groups within each condition, imposed (i.e., control choice contexts) or chosen (i.e., SOLO vs TOGETHER choice contexts).

We investigated hence whether relative and absolute reward could influence performance. SRs across delta groups were computed and compared (Kruskal-Wallis test) within each group of action type –both control and chosen ones (Fig. 11B). No significant difference was found

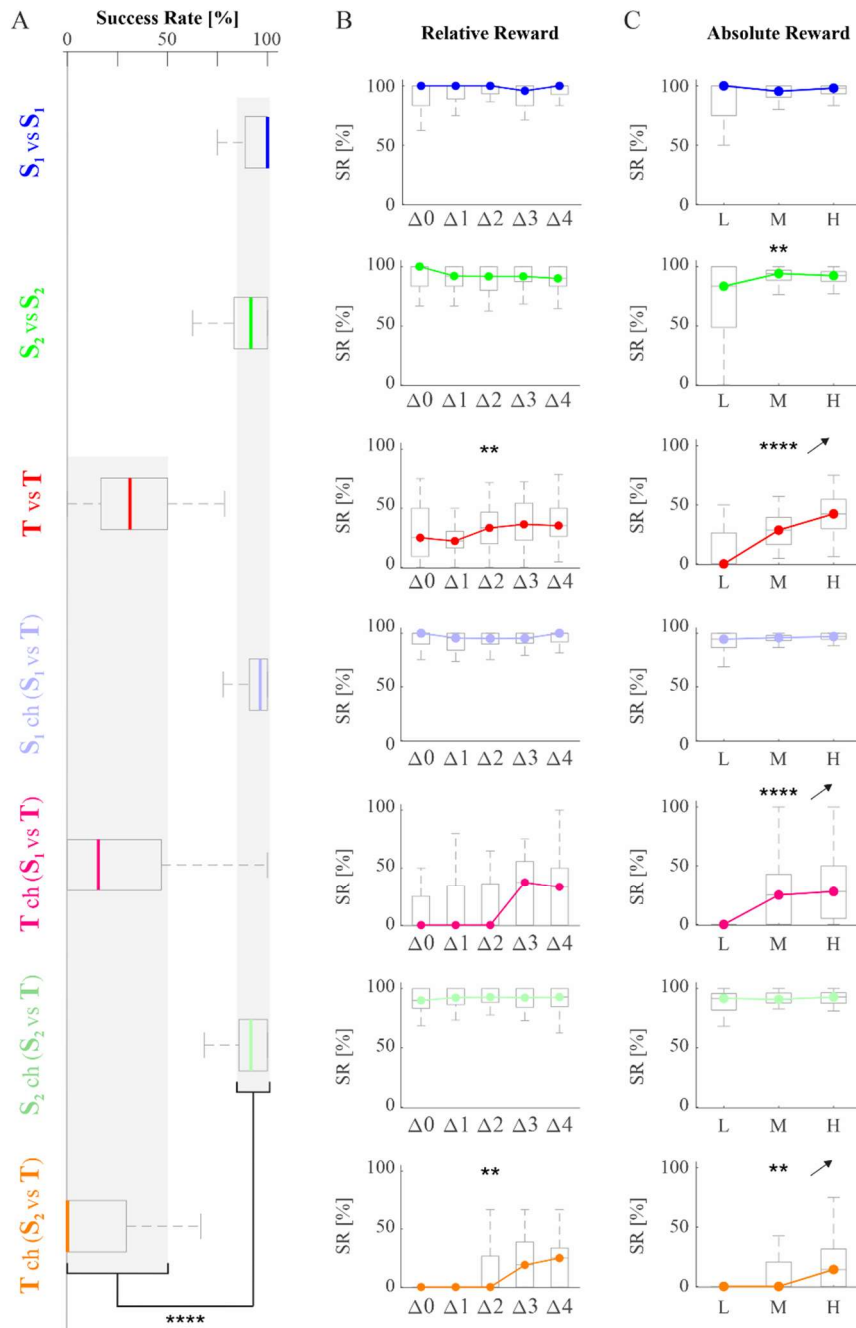


Figure 11. Success rates for chosen targets. (A). Median success rates (SRs) were compared across imposed and chosen conditions (Kruskal Wallis test). SRs in all TOGETHER groups were significantly higher when SRs in SOLO conditions (B) Median SRs computed for each delta group within each imposed and chosen condition. An overall effect of relative reward on SRs was evident only in T vs T and T chosen (S_2 vs T) groups, but a tendency to increase SR for higher deltas was not confirmed by post hoc analysis (Dunn-Šidák test). (C) Median SRs computed for each absolute reward level group within each imposed and chosen condition. A significant tendency to increase SR in TOGETHER groups for higher absolute reward levels was found, as confirmed by post hoc analysis (upward arrows). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$

across deltas for all SOLO groups (S_1 vs S_1 , S_1 chosen in S_1 vs T, S_2 vs S_2 , S_2 in S_2 vs T), while an overall effect of relative reward was evident in T vs T and T chosen (S_2 vs T) groups (Tab. 8). Post hoc analysis though, did not confirm a tendency to increase SR for higher deltas in

these two cases (Tab. 9). By comparing SRs across absolute reward levels within each group of action type – again as combined with control or SOLO vs TOGETHER contexts – a significant difference emerged for all TOGETHER groups (i.e., T vs T, T chosen in S_1 vs T, T chosen in S_2 vs T), and for S_2 vs S_2 group (Fig. 11C, Tab. 8). Post hoc analysis confirm a tendency to increase SRs when at increasing the reward absolute amount associated to each option only for TOGETHER groups (Tab. 9).

In summary, the cost of inter-individual motor coordination was confirmed by an evident decrease of performance also in those tasks in which monkeys had to choose between two offers. Monkeys were able to improve their performance when acting together when presented with higher reward offers.

Action type & choice	Deltas compared			Levels compared		
	$\Delta 0$ vs $\Delta 2$	$\Delta 2$ vs $\Delta 4$	$\Delta 0$ vs $\Delta 4$	L vs M	M vs H	L vs H
SOLO 1 (S_1 vs S_1)	-	-	-	-	-	-
SOLO 2 (S_2 vs S_2)	-	-	-	0.0162	1.0000	0.0181
TOGETHER (T vs T)	0.9209	0.9774	0.2350	0.0030	0.0565	$5.47 \cdot 10^{-8}$
SOLO 1 chosen (S_1 vs T)	-	-	-	-	-	-
TOGETHER 1 chosen (S_1 vs T)	-	-	-	0.0052	0.6308	$3.36 \cdot 10^{-8}$
SOLO 2 chosen (S_2 vs T)	-	-	-	-	-	-
TOGETHER 2 chosen (S_2 vs T)	0.5583	0.7977	0.0765	0.1279	0.5647	0.0071

Table 9. Dunn-Šidák test for multiple comparison of success rates (SRs) between absolute reward and between relative reward groups within each absolute reward level group was performed, for each imposed (i.e., control choice contexts) or chosen (i.e., SOLO vs TOGETHER choice contexts). Only those differences between deltas that are sufficient to spot an increasing of rates for increasing reward difference are reported.

Motor preparation and speed-accuracy trade off

We previously demonstrated that Mk1 and Mk2 changed their cursors' kinematics when acting together, relative to when they acted alone (training task). To replicate this result and investigate the potential effects of choice on cursor's movement kinematics, we analyzed monkeys' velocity profiles as expressed in the two tasks (training and test tasks) in which they were called to choose between two offers. A Kruskal-Wallis test was performed for 100 times on n size random samples (were $n = 152$) for each compared group. In Figure 12 one representative sample is shown. Both in control choice contexts and in SOLO vs TOGETHER choice contexts, a clear difference between SOLO's and TOGETHER's velocity profile was evident (Fig. 12A). Reaction times were compared across all groups (Fig. 12B), showing an overall significant difference for all 100 replications. Post hoc analysis (Dunn-Šidák test)

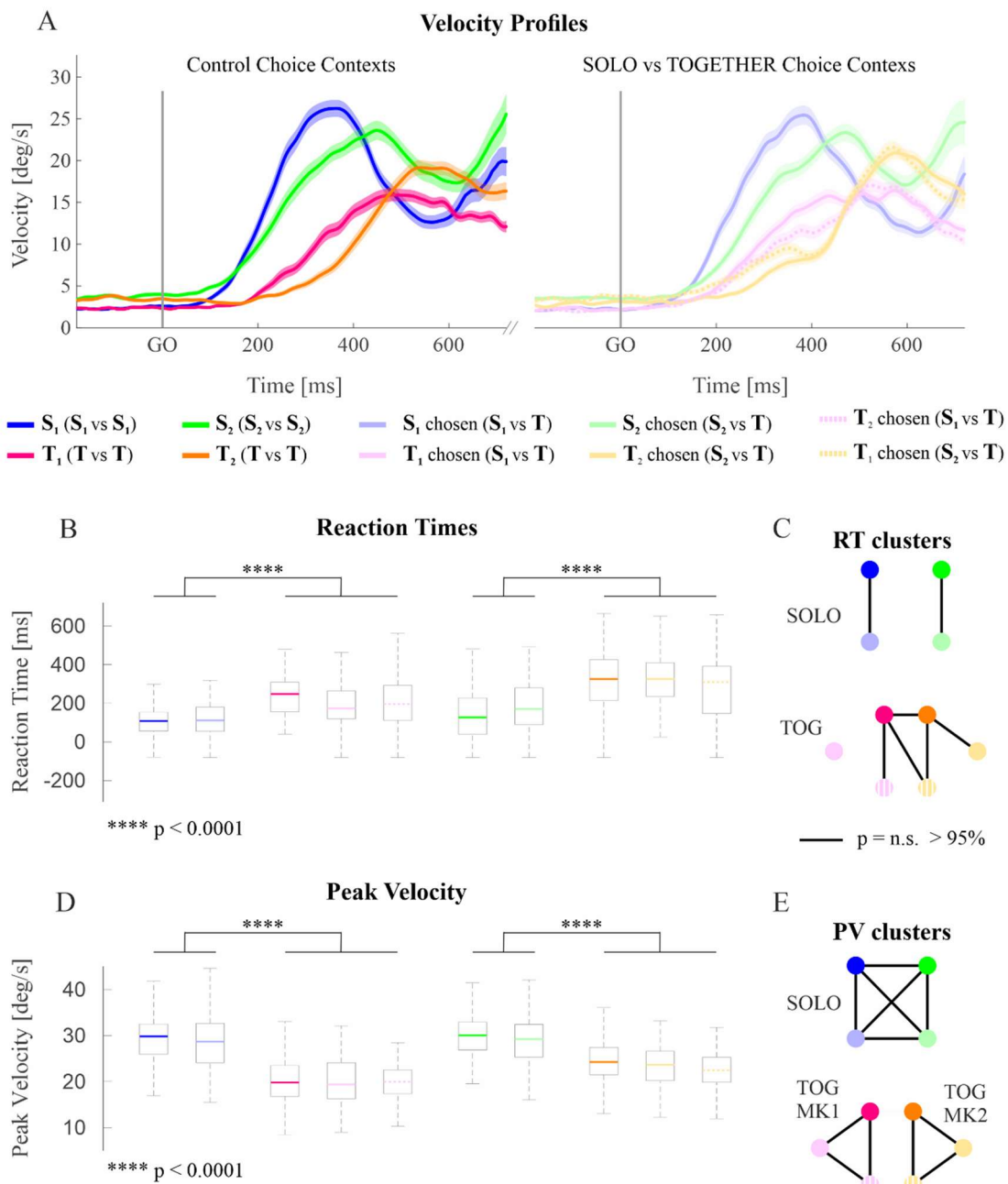


Figure 12. Velocity profiles analysis. A bootstrap analysis was conducted for 100 replications on n size random samples, where $n = 152$ for each compared group, by mean of Kruskal-Wallis test ($p < 0.05$) and Dunn-Šidák test for multiple comparison. A representative random sample is represented. **(A)** Velocity profiles of the representative case reported for control and SOLO vs TOGETHER choice contexts. **(B)** TOGETHER's reaction time (RT) were longer than SOLO's, as shown in the example, and **(C)** tendentially clustered in two different groups, as evident by the percentage of non-significant p values obtained by performing multiple comparison between all groups (Dunn-Šidák). **(D)** TOGETHER's peak velocity (PV) was lower than SOLO's, as shown in the example. **(E)** Three clear clusters emerged, as evident by the percentage of non-significant p values obtained by performing multiple comparison between all groups (Dunn-Šidák): PV in SOLO groups, Mk1's PV in TOGETHER condition, and Mk2's PV in TOGETHER condition

revealed that both monkeys prolonged their reaction times when moving their cursors towards a TOGETHER target, both in TOGETHER vs TOGETHER and SOLO vs TOGETHER choice contexts. The percentage of times in which the comparison between two groups was not

significant was used as an index of RT similarity and represented in Fig. 12C. As evident from the graph, RTs were more similar within SOLO conditions, and within TOGETHER conditions, thus forming two main clusters. These findings suggest that each monkey, when free to choose between two targets postpone its movement initiation, as to wait the choice between the two options of the other animal.

Peak velocities were compared across all groups as well (Fig. 12D, with a significant difference emerging for all 100 replications. Post hoc analysis (Dunn-Šidák test) revealed that both monkeys reduced their cursors' speed when reaching a TOGETHER target, both in TOGETHER and SOLO vs TOGETHER choice contexts. The percentage of times in which the comparison between two groups was not significant was used as an index of PV similarity and represented in Fig. 12E. As evident from the graph, PVs were markedly clustered in three groups of similar velocity: SOLO, TOGETHER as performed by MK1, and TOGETHER as performed by MK2. Therefore, in line with our previous studies, monkeys markedly changed their velocity profiles when coordinating their forces to bring the cursors to the shared final target, thus paying a cost to acting together.

Discussion

In the present study we investigated the monkey's ability to assess the cost of acting together when deciding between acting alone or together with a partner. Two rhesus monkeys were trained to perform a sequential choice task in which they could choose between acting alone or together based on the offered payoff. We found that monkeys were able to recognize this cost and use it to make decisions about acting jointly with their partner. The cost of acting together was defined on two main dimensions that we deemed to influence the monkeys' decision to coordinate their action: the social gamble and the coordination cost. To cope with these two complex and interdependent features of joint action cost, monkeys managed to adapt both, their choice style, and their motor behavior – as we will discuss in the following paragraphs.

Value subjectivity and context-dependency

Monkeys were motivated to perform the task and were able to distinguish between choice contexts already during the instruction phase, when the offered options were disclosed in sequence. Reward absolute and relative values had instead a mild effect on monkeys' motivation to fulfill a trial. The difference between the payoff associated to the two options seems to improve the already very high propensity of both monkeys to not ignore trials, when a solitary action was possible. Moreover, their tendency to ignore trials when two joint action options were offered, was strongly diminished by increasing the absolute reward level of the maximum offer. Therefore, long before monkeys could make any choice, some signs of context-dependency on monkey's motivation to take part in a trial emerged. This effect became even clearer during the choice phase, in which monkeys could decide whether to approach one of the two offered options, or to discard both and pass to the following trial. In this case, a stronger effect of reward on behavior emerged. Particularly, when the two monkeys got to choose between two targets both associated to the joint action condition, they tend to discard more trials, with at least one of them abstaining from choosing. Whenever the chance to act alone was given in at least one of the two options, monkeys rarely discarded any trial and a choice was made almost in all cases, providing thus already an indirect measure of the higher cost of acting together, as perceived by both monkeys. Once monkeys made a choice, though – as evident from the analysis of the choice rates – their ability to discriminate between different reward amounts and to aim at the higher offer was consistent in all those choice contexts in which the same action type was associated to the two options. This fact confirms that the monkeys understood the meaning of the reward cues and that they were able to discriminate even the smaller reward interval with sufficient precision. Yet, the context in which they were called to make a choice influenced the monkeys' behavior, seemingly modulating the value attributed to the alternative actions to be potentially performed. These results are not surprising, since it is well known that the outcomes of our decisions depend on the context in which we take them. As a matter of fact, a context-dependency of monkeys' evaluation behavior has been widely demonstrated (e.g., Hayden & Platt 2007, Louie et al. 2011; Abitbol et al. 2015; Ferrucci et al. 2019; Ferrari-Toniolo et al. 2019b). The high degree of variability shown by individuals in different contexts and across time has been imputed to some physiological properties that our brain displays when engaged in decision making (Padoa-Schioppa 2013; Webb et al. 2014; Abitbol et al. 2015). Moreover, valuation processes are believed to be intrinsically subjective since their outcome widely varies not only within, but also across individuals. “Subjective

value” is an established notion used in the neuroeconomic field to indicate a value assigned by the individual to a particular action-outcome contingency by weighing up the costs and benefits associated to it (Conteras-Huerta et al. 2020). This definition is in line with the “common currency” theory, first introduced by Samuelson (1948), which states that our brain can integrate different types of relevant features (such as reward and effort) of available offers on a common scale, to allow us to decide which one to prefer. In the latest years, the rationality of this valuation process has been questioned and its idiosyncrasy and heuristic nature has been more and more underlined (Gigerenzer & Gaissmaier 2011; Levy & Glimcher, 2012). Its premise, though, remains unchanged: deciding requires valuating, which consists of making two options commensurable by translating their relevant features into a common currency.

Choice strategy: establishing a fair trade

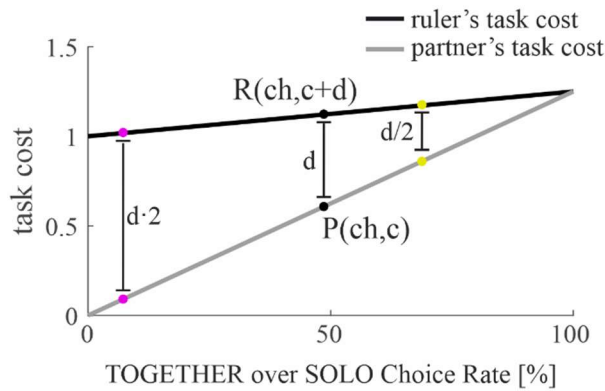
After a general assessment of the influence of reward on monkeys’ behavior, which was possible with a first, explorative version of our sequential choice task (*test 1* task), we tested the monkey’s preference on a new version of the same task, with a fixed minimum reward offer and doubled deltas’ size (*test 2* task). In this case, monkeys’ choice behavior was not merely subdued to their action type preference, but rather based on a finer tradeoff between the cost and utility of acting together. Interestingly, we observed that both monkeys aimed at optimizing their trial-contingent utility, namely, to get the higher reward possible from each trial. This strategy was consistently preferred despite it did not ensure to maximize the overall reward gained during their daily reward session. By flexibly adjusting their choice behavior in the attempt to maximize their trial-contingent gain, in fact, they could obtain either none or a small advantage in comparison to the reward that they could have gained by simply choosing the solitary action, even when maximally inconvenient, minimizing their individual effort. Our monkeys showed hence an overall risk seeking behavior, particularly when the payoff difference between the two options was sufficiently high, in coherence with what observed by Hayden et al. (2008). Moreover, as evident from the fluctuation in choice rates of TOGETHER condition across sessions, the two animals were able to flexibly adjust their risk propensity in agreement with what has been demonstrated by Farashashi et al. (2018).

Our task was conceived so that the ideal strategy to get the highest gain possible would imply to always choose the higher rewarded offer. On the other hand, adopting the latter choice style would have not been advantageous in practice, since acting jointly was more costly, and the

actual chances of gaining a reward together were markedly lower, as evident from the analysis of success rates. Our monkeys were able to integrate ideal goals and realistic outcomes in a weighed decision style, by establishing a similar payoff threshold above which they were willing to pay the cost of inter-individual motor coordination to try to gain a higher reward than the one offered for the solitary action. It is important to notice that each monkey, when assigned as the ruler in SOLO vs TOGETHER trials, was free to adopt whichever choice strategy he deemed convenient. Yet, both monkeys followed the same choice style (i.e., to prefer joint over solitary action only above a certain threshold of payoff difference). Establishing a cost threshold to act together allowed to reduce the social gamble (i.e., partner's choice unpredictability) implied by acting together.

Moreover, and most surprisingly, we showed that the propensity of the two monkeys to choose joint action over individual action correlated across sessions. Not only, hence, monkeys agreed on a similar cost of sharing action, but how often they decided to choose to act jointly instead than alone dependent on how often their partner made a similar choice. This result is in line with the modulation of cooperative behavior already observed in rhesus macaques by mean of an iterated prisoner dilemma paradigm (Haroush and Williams 2015). It seems that our monkeys' propensity to pay the cost of inter-individual motor coordination was based on a fair trade with their partner that was adjusted dynamically across sessions. This reciprocal behavior allowed to evenly distribute effort between the two members of the dyad. In fact, if one monkey would choose to work always alone when playing as the ruler, he would make all the effort to gain a reward for both the elements of the dyad in his SOLO vs TOGETHER trials. A fair trade would require the other monkey to behave similarly, sparing all the effort as well to the generous partner, when it was its turn to be a ruler. On the other hand, if one ruler would decide more often to try to coordinate action to achieve a higher reward, his partner would expect a roughly equal degree of collaboration when playing the ruler role (Fig. 13). In this sense, our monkeys were able to aim for efficiency, namely the minimization of aggregate, rather than individual costs of an action for a fixed benefit (Török et al. 2019). The unilateral minimization of individual cost, despite being possible, would have established an unfair distribution of effort that neither of the two members of the dyad considered acceptable, as inferable from our results.

It needs to be noticed that rhesus monkeys have been demonstrated to be poorly prone to cooperative and pro-social behaviors, and to preferably aim at individual utility (Haroush and Williams 2015, Ong et al. 2020). In line with the literature, the observed behavior cannot be



	Mk1	Mk2
SOLO1 vs TOGETHER	$c_1 + d_1$	c_1
SOLO2 vs TOGETHER	c_2	$c_2 + d_2$

$$\text{Mk1's total cost: } C_1 = c_1 + d_1 + c_2$$

$$\text{Mk2's total cost: } C_2 = c_2 + d_2 + c_1$$

$$d_1 = d_2 \rightarrow \text{fair distribution of costs}$$

$$d_1 > d_2 \vee d_1 < d_2 \rightarrow \text{unfair distribution of costs}$$

Figure 13. An ideal model of cost distribution between monkeys. On the left, we represent an arbitrary model of cost distribution in the dyad: the ruler's and partner cost difference, indicated as d , spans from a maximum, when the ruler chooses always to act alone, and the partner has to simply keep the cursor inside the central target, to 0, which describes the condition in which the ruler decides always to coordinate with the partner. On the right, the global cost for each monkey of SOLO vs TOGETHER choice contexts is formalized mathematically, to demonstrate that if they chose the joint action type with difference rates, an unfair distribution of cost would be established. An example is provided on the cost scheme (left), where we indicate with the purple dots Mk1's choice rate and with the yellow dots Mk2's choice rates, as projected on the cost functions. In this case, Mk1 would be paying an unfair higher cost of $\frac{3}{2}d$.

interpreted as prosocial, since no individual cost at the mere benefit of the other was paid. Our monkeys' choice strategy can be rather interpreted in terms of a dynamic balance between individual utilities, in which the social repercussions of the own behavior on the partner's one were taken into consideration. Rhesus monkeys have been in fact demonstrated to be able to display a sense of fairness, once reached the adult age (Hopper et al. 2013). This ability to compromise and establishing fare trades for sharing actions shown by our dyad, definable as an aptitude to fairness, has been suggested to constitute, along with pro-sociality, an evolutionary prerequisite of human capability of cooperating with others (Yamamoto & Takimoto 2012).

As a last remark, it must be underlined that, given the feeding nature of reward, a satiation effect within and across sessions must had influence the monkey's choice behavior – at least to some extent. Nevertheless, this factor alone is insufficient to explain the observed monkey's fluctuations in choice behavior, and a systematic analysis of this issue goes beyond the scope of the current work.

Measuring the cost of acting together

When no choice was given between action types, monkeys' preference was merely reward-based. When given the chance to choose between acting alone or together, monkey's choice was instead influenced by the cost of inter-individual motor coordination. We have

conceptualized this cost as characterized by social and motor components. In the paragraph above, we have discussed how the two monkeys coped with the social aspect of our task. A discussion on how the actual coordination cost, clearly recognized by our dyad, can be defined and assessed becomes pivotal at this point.

The term “joint action” has been used to indicate a variety of behavioral contexts in which two or more individuals act together. Inspired by the definition originally proposed by Sebanz and collaborators (Sebanz et al. 2006), we refer here to “joint action” any to any form of motor interaction whereby two or more individuals, sharing an intention, coordinate their actions in space and time to achieve a common goal. Even though in the literature on joint object control it has been argued that coordinating action is able to increase the dyad success rate (Whan et al. 2018), making a task easier cannot be considered as a defining feature of joint action. In some cases, in fact, even if more effortful and/or risky, coordinating with others is preferred, since it can make achievable goals otherwise precluded to the single individual (e.g., Keller et al. 2014). In a similar way as reciprocity and fairness do not always imply pro-social intentions, sharing actions does not necessary entail a task facilitation, particularly when requiring inter-individual motor coordination, as shown in our previous studies performed in monkeys (Visco-Comandini et al. 2015) and in human subjects at different ages (Satta et al. 2017).

Coordinating with a partner, seen under this light, can be intuitively defined as effortful. But what do we exactly mean with that? In the literature two forms of effort have been addressed: physical and cognitive effort. Physical effort in the context of reaching movements has been defined as the negative utility associated with a given motor action, independent from other costs, such as success chances and reward delay (Morel et al. 2017). This definition, though, could apply also to the concept of cognitive effort, and therefore cannot be considered sufficiently discriminative. A critical feature that has been pointed out to be a typical sign of physical effort, in contraposition to mental effort, is that it implies a metabolic cost (Westbrook & Braver 2015). Moreover, physical effort can be easily assessed by manipulating force application. A positive definition and measure of cognitive effort, instead, remains still challenging, given its intrinsic experiential nature, which makes it a more elusive, not directly measurable construct (Kool & Botvinick 2018). Here, we chose to consider it as the computational expense necessary to exert proactive control over the own motor output, which is deemed to be a key feature of voluntary action (Braver et al. 2012). On this wake, computational cost has been further defined as a function of the amount of information required to update ones’ prior knowledge to solve a task (Zénon et al. 2018). The behavioral and neural

correlates of cognitive and physical effort have been studied with the aim of demonstrating their different nature. The collected evidence so far supports the hypothesis of physical and cognitive effort to be two distinct action features which influence decision making and reward evaluation processes in a differential manner (Apps et al. 2015, Białaszek et al. 2017), being supported by - at least partially - distinct neural circuitries (Varrazzani et al. 2015, Chong et al. 2017).

Here we argue that the coordination cost paid by our animals can be classified as a type of cognitive effort. In fact, the amount of force necessary to reach the target was always the same across action types. Yet, a higher degree of fine cognitive control on the force application was requested when cooperating with the partner. In line with Westbrook and Braver's (2015) conceptual framework, the best measure of cognitive effort can be obtained by assessing the subject avoidance behavior towards a certain task. In our experiments, monkeys were able to show their perceived cost of acting together in two steps: first, they showed a stronger avoidance of those choice contexts in which the choice between only two joint action was possible; second, they tended to prefer solitary action, when coordinating actions with the partner was not sufficiently rewarded.

The cognitive effort of exerting a finer control on own actions, though, is amplified when applied within a social context. Moreover, it has been argued that goal directed behavior depends both on capacity and motivation: having the skills to perform a task, in fact, does not imply the will to perform it. This same concept has been applied to intentional social behavior (Conteras-Huerta et al. 2020). Whether to act together or not was not just a matter of capacity for our monkeys: as we observed, in fact, the size of the reward offered to act together did not just influence their propensity to choose to coordinate with the partner, but also their success rates. The avoidance of the joint action type, hence, cannot be considered as a simple measure of task difficulty, but also as an index of monkeys' willingness to face the effort of acting together with the partner.

When deciding to act together, the cost of coordinating with their partner was evident from a decrease in performance, both in the contexts of the classical paradigm established in our lab (*training* task) and in the new task developed to give the chance to choose whether to act alone or together. These results are in line with the previous research conducted in our lab, which showed that the cost implied by coordinating action with a partner was always reflected in a significantly reduced success rate exhibited by the dyads when performing joint action,

compared to solitary action (Visco-Comandini et al., 2015; Ferrari-Toniolo et al., 2019). Moreover, our two monkeys exhibited a change in their motor profiles, consisting in an increase of reaction times and a reduction of cursor movement velocity. It has been shown that non-human primates are able to modify their motor profiles and successfully coordinate their action in order to achieve a common goal (Visco-Comandini et al., 2015; Ferrari-Toniolo et al., 2019). In agreement with the literature, our monkeys moved their cursors significantly slower when acting together, trading off their execution speed to gain the higher accuracy needed to successfully coordinate with their mate. This behavior can be framed in the well-established psychophysical concept of speed-accuracy tradeoff (Fitts, 1954). Differently from what observed so far on dyads of monkeys engaging in a joint action (Visco-Comandini et al., 2015; Ferrari-Toniolo et al., 2019) and from the results shown in our control task, when the monkeys chose a joint target between two alternative offers, movement onset was no longer anticipated. This retardation in initiating the movement was systematically associated to the TOGETHER condition, both in the control and SOLO vs TOGETHER choice contexts. Moreover, when choosing individual action over joint action, reaction times did not differ from the ones observed in the SOLO vs SOLO choice contexts. Given these results, we argue that movement onset retardation, as evident when monkeys decided to act together, cannot be explained by a mere higher computational cost required by choosing between two different types of actions. We hypothesize, hence, that in this case our monkeys did not recur to the well-known strategy of reducing their reaction times in order to increase inter-individual temporal synchronization when acting together. Our suggestion is that taking more time before acting together could be explained in this case as an alternative strategy aimed at guessing the partner's intention to share action.

Experiment 3: Neural correlates of choosing joint action over solitary action - an EEG study on non-human primates

Background

The existence of internal models of one's own and the other's action has been hypothesized by several authors, but how these models are formed and coded at the neural level has not been clarified yet. In origin, Wolpert's theory of social motor control was based on the first critical evidence emerging from studies conducted on human and non-human primates that showed how the same brain areas that were demonstrated to be clearly involved in motor control were active also during the observation of others' actions (Gallese et al. 2003). As suggested, the recruitment of the motor system could be crucial to allow a form of sensorimotor translation necessary to read motor intentionality when sharing actions (Rizzolatti & Sinigaglia 2010). On the wake of Wolpert's work, Keller et al. (2016) postulated the existence of joint internal model as a combination through complementary integration and segregation processes of self and other's internal models.

Only recently the idea emerged that those internal models, which are involved in performing joint action tasks, are not the same as those implied in observing an action independent from our own. Along this line it was proposed that the execution of a joint action task implies the formation of a dyadic motor plan, that is the active prediction of the own and partner's action effects. This postulate, which is known as "Dual Route hypothesis" has been supported by the evidence that visuomotor interference emerges only in non-interactive contexts (i.e., when action is observed), while no top-down inhibition is evident during motor interaction (Sacheli et al. 2018).

The neural basis of the formation of such dyadic motor models are still object of speculation, and only recently some promising results have emerged. Shared goal representation has been found to be encoded by the left anterior intraparietal sulcus in humans (Sacheli et al. 2015). A selective involvement of the human left ventral premotor cortex has been identified for the ability to generate motor predictions of the partner's behavior to achieve a common goal (Sacheli et al. 2019). A similar evidence of predictive coding of the partner's behavior in the

context of inter-individual motor coordination has been shown in monkeys' dorsal premotor cortex (Ferrari-Toniolo 2019).

Except for few recent fMRI (Sacheli et al. 2015, Sacheli et al. 2019, Abe et al. 2019) and invasive neurophysiological experiments (Haroush and Williams 2015, Ferrari-Toniolo et al. 2019a, Ong et al. 2020), most of the existing studies aimed at revealing the neural basis of social behaviors, have been conducted by mean of electroencephalography (EEG) methods. One of the main turning points in this line of research was the introduction of the so-called 'hyperscanning' method, first introduced as a method for dual fMRI recordings (Montague et al. 2020). This approach was acquired fast enough by the scientific community to implement simultaneous EEG recording systems and, it led to interesting new findings. It has been consistently demonstrated, for example, that of successful coordination between individual can be traced back to an increase of inter-brain synchronization, particularly on the alpha band and in centro-parietal domains associated to sensorimotor control (Konvalinka et al. 2014, Novembre et al. 2016, Novembre et al. 2017, Jahng et al. 2017, Hu et al. 2018, Kawasaki et al. 2018; Washburn et al. 2019, Cho et al. 2020). Amongst these, three main studies that have focused specifically on investigating the difference in brain activity between solitary and joint action stand out (Kourtis et al. 2013, Kourtis et al. 2019, Astolfi et al. 2020).

The literature on monkeys' EEG is scant, and very few studies have attempted to use this method, mostly to study auditory and visual evoked responses (e.g., Van der Marel et al., 1984, Gil-da-Costa et al. 2013, Ito et al. 2015, Sandhaeger et al. 2019), and key cognitive processes related to stimulus awareness and prediction, such as the well-known mismatch negativity (Glover et al. 1991, Paller et al. 1992). Despite intracranial recordings allow a more direct measure and better spatial resolution, EEG recordings can bring the advantage of providing a widespread measure of brain activity, which can help understanding how the brain is modulated by the phenomenon inquired on a larger scale. Moreover, and specifically in the present case, the advantage of using this method is that it allows us to have a better comparison with the human literature and apply similar techniques of analysis, such as inter-brain synchronization estimation. Secondly, this could give insight to guide chamber location for intracranial recordings.

For these reasons, we conducted an hyperscanning EEG experiment by simultaneously measuring brain activity from two monkeys while they were choosing between acting alone or jointly with a partner.

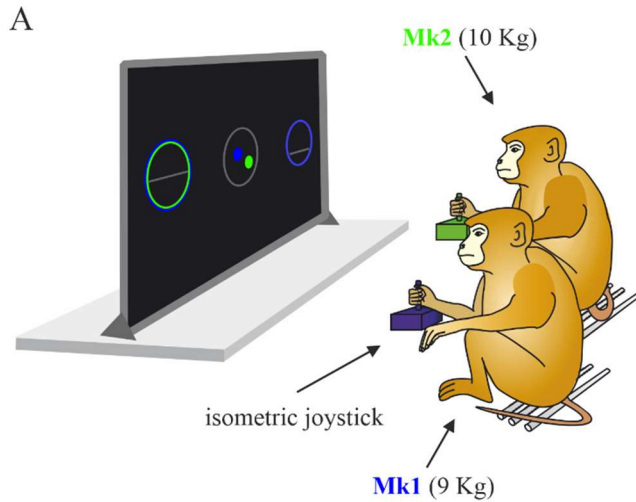
Methods

Animals

Two male rhesus monkeys were used for the experiment (*Macaca mulatta*): Monkey M, 9 Kg; Monkey T, 10 Kg. In the present work, Monkey M will be addressed as Mk1, while Monkey T will be addressed as Mk2. Animal care and housing procedures were in conformity with European (EU Directive 63-2010) and Italian (DL. 26/2014) laws on the use of nonhuman primates in scientific research. During the early stages of behavioral training (namely, about 2 years before recording) each monkey underwent surgery for headpost implantation. In preparation to surgery, they were first pre-anesthetized with ketamine (10 mg/kg, i.m.), and then completely anesthetized with a mix of Oxygen/Isoflurane (1–3% to effect). A titanium headpost was implanted on the skull under aseptic conditions. Before continuing with the training, the animals were put at cage rest to fully recover for at least a week, while undergoing standard post-operative treatment with antibiotics and pain killers. After approximately six months post-implantation, they were both successfully trained to head fixation.

Experimental setup

The experimental setup is illustrated in Figure 1A. Both monkeys were trained to control a cursor (diameter: 0.6 degrees of visual angle; DVA) displaced on a black screen by applying a dynamic force on an isometric joystick (ATI Industrial Automation, Apex NC) in the two dimensions of the horizontal plane (sampling frequency: 1 kHz). The applied force was proportionally converted into a movement of the cursors on the x and y axis on the vertical plane of the monitor. The NIH-funded software package REX was used for task control and behavioral data collection. Monkeys were required to always use the same arm to perform the task while the other arm was gently restrained. In both cases the joystick was controlled with the left hand, since both monkeys showed a preference in using their left limb at the early stages of their training. Both monkeys were additionally trained to work while having their head fixated in a natural, comfortable position by mean of a clamping mechanism acting on their headpost implant. Both monkeys were placed in a soundproof chamber, seated side-to-side on two primate chairs in front of a 40-inch monitor (100 Hz, 800-600 resolution, 32-bit color depth; monitor-eye distance: 150 cm). A security distance of at least 60 cm was always guaranteed to prevent physical contact. The orientation and structure of the chair minimized



B

Choice contexts	A/B	B/A
S_1 vs T		
S_2 vs T		
Controls	S_1 vs S_1	
	S_2 vs S_2	
	T vs T	

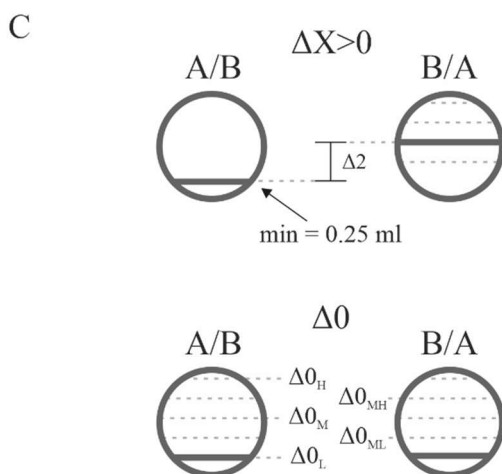


Figure 1. Experimental setup and task conditions.

(A) Two monkeys were placed in a darkened, sound-attenuated chamber and seated side-to-side on primate chairs in front of a common monitor. Both monkeys exerted a force on an isometric joystick to displace a colored visual cursor from a central control position toward a target located at one of eight possible locations on the screen, at 45° intervals on a circumference at 8 DVA radius.

(B) The action type condition were combined to form five possible choice contexts: two SOLO vs TOGETHER choice contexts, in which each monkey got to play as a ruler and choose between acting alone or with the partner; three control contexts, in which the monkeys could choose between two targets of the same action type (two SOLO options for Mk1, two TOGETHER options).

(C) the reward condition was defined by five classes of relative difference ($\Delta 0, \dots \Delta 4$). When the reward difference was higher than 0 ($\Delta X > 0$), the payoff was obtained by summing to an established minimum reward (0.025ml), 1, 2, 3 or 4 units of reward difference ($u = 0.30\text{ml}$). The payoff absolute value of the $\Delta 0$ class was instead randomly assigned between the five possible reward levels: $r_{min}(\Delta 0L)$, $r_{min} + 1u(\Delta 0ML)$, $r_{min} + 2u(\Delta 0M)$, $r_{min} + 3u(\Delta 0MH)$, $r_{min} + 4u(\Delta 0H)$.

also visual contact. During data collection eye movements were monitored and sampled at 1 kHz through an infrared oculometer (Arrington Research) and stored together with joystick force signals and key events.

Behavioral task

The task adopted was almost identical to the test task used in the previous experiment. The two monkeys were again called to choose between acting alone (SOLO condition) or jointly (TOGETHER condition) to gain a fluid reward. In the SOLO action type, monkeys obtained the expected reward by moving their cursor alone, while in the TOGETHER one the animals had to reciprocally coordinate their forces to bring jointly their cursors into the selected target and gain their reward. As a control, monkeys were required to choose between two SOLO or two TOGETHER options with different payoff. The five choice contexts used in the task are recapitulated in Figure 1B.

Target position and presentation order were well balanced throughout a pseudo-randomized design to control for any potential biasing effect on behavior. The choice was made by moving the cursor from a central target to the peripheral target associated to the chosen option.

Each choice option was associated to a certain amount of reward on a trial-by-trial basis (Fig. 1C). The unit of reward difference was of 0.30 ml and the payoff associated to each option was calculated as follows:

$$Rew = r_{min} + u \times d$$

Where r_{min} is the minimum absolute reward amount necessary to maximize the chances that monkeys will engage the trial, u is the unit of reward difference and d is the delta size. The value of r_{min} was 0.25ml as empirically computed from monkeys' behavior. When $d = 0$, namely when the two offers did not differ in their associate payoff, the value of the reward assigned to the two options was randomly picked from the set of all possible combination of reward levels obtainable, which were: r_{min} ($\Delta 0_L$), $r_{min}+1u$ ($\Delta 0_{ML}$), $r_{min}+2u$ ($\Delta 0_M$), $r_{min}+3u$ ($\Delta 0_{MH}$), $r_{min}+4u$ ($\Delta 0_H$).

The time course of the task was the same of the one adopted in the Test tasks (*Experiment 2*) with just few changes in epochs' duration, introduced *ad hoc* to adapt it to neural recordings (Figure 2). Each trial was characterized by two main phases: the instruction phase (IP) and the choice phase (CP). During the IP, the animals were informed of the two options offered for that specific trial displayed in sequence on a central (i.e., spatially neutral) position of the screen. Each option (A and B) was presented for 800ms, followed by a delay of 500ms. After this, the two cursors and a grey central target appeared, and each monkey placed the cursor inside that target and hold it for a center holding time (CHT) of 800-1100ms. Only then the two same

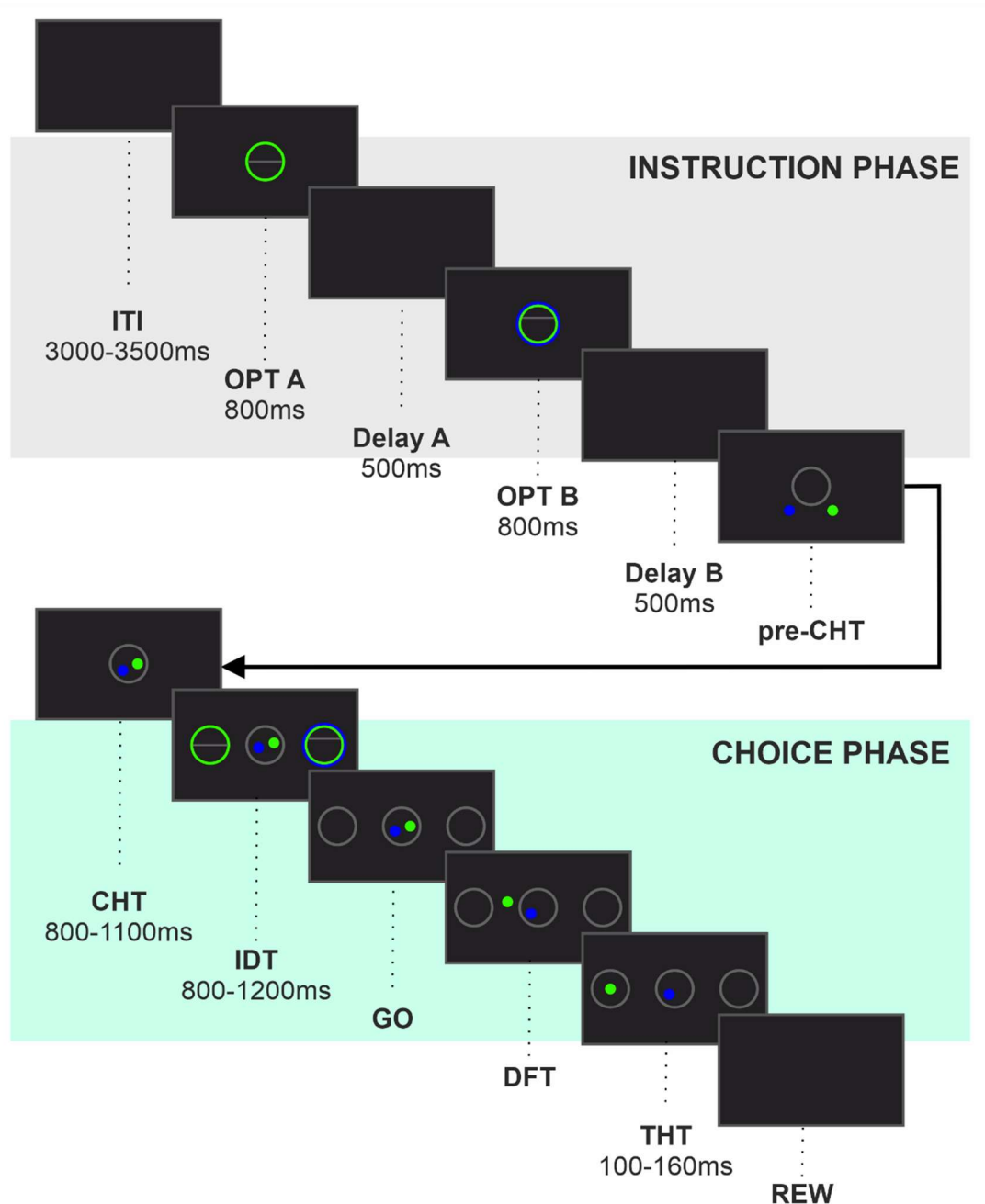


Figure 2. Task time course. Each trial was characterized by two main phases: the instruction phase (IP) and the choice phase (CP). During the IP, the animals were informed of the two options offered for that specific trial, displayed in sequence in a central (i.e., spatially neutral) position of the screen. Each option (A and B) was presented for 800ms, followed by a delay of 500ms. After this, the two cursors and a grey central target appeared, and each monkey was trained to place the cursor inside that target and hold it in there for a center holding time (CHT) of 800-1100ms. Only then, the two options appeared again, one displaced on the left and the other on the right (in a randomized way), at 8 DVA from the center. After a predictable instruction delay time (IDT) of 800-1200ms, the two options disappeared, leaving in their place only two neutral grey circles, and the monkeys were allowed to move their cursors from the central target towards one or the peripheral targets (dynamic force time, DFT), accordingly to the choice made, or to defect the trial, if the options were deemed to be not worth the effort. The movement had to be performed within a time-window of 2000ms, otherwise the trial was aborted. Once one target was reached and the cursor/s kept inside it for a short target holding time (THT, 100-160ms), one or both monkeys – depending on the action type of the selected target – received the chosen amount of reward, (REW).

options appeared again, one displaced towards the left and the other towards the right (in a

randomized way) at 8 DVA from the center. After a varying instruction delay time (IDT) of 800-1200ms the two options disappeared and being replaced by two neutral grey circles. The monkeys were allowed to move their cursors from the central target towards one or the peripheral targets (dynamic force time, DFT), accordingly to the choice made, or to defect the trial, if the options were deemed to be not worth the effort. Once one target was reached and the cursor/s kept inside for a short target holding time (THT, 100-160ms), one or both monkeys – depending on the action type of the selected target – received the chosen amount of reward (REW).

The total number of trials collected was 16010 trials (33 sessions), with an average of 485 trials per session.

Behavioral indexes

Choice rates

Choice Rates (CRs) have been calculated for each SOLO vs TOGETHER choice context, negative, null, and positive reward delta, and i session, as follows:

$$CR_{CC,\Delta X,i} = \frac{n_{chosen\ option}}{n_{engaged\ trials}} \times 100$$

Where $-4 \leq \Delta X \leq 4$ and n stands for ‘the number of’

The two options were considered as different objects (i.e., SOLO and TOGETHER), so that for each of them the following question was asked: How often has this action type been chosen (CR) when its reward is lower ($-\Delta 4, -\Delta 3, -\Delta 2, -\Delta 1$), equal ($\Delta 0$), or higher ($+\Delta 1, +\Delta 2, +\Delta 3, +\Delta 4$) than the reward associated to the other one? Hence, in this case:

$$CR_{SOLO,-\Delta X} + CR_{TOGETHER,+\Delta X} = 100\%$$

$$CR_{SOLO,+\Delta X} + CR_{TOGETHER,-\Delta X} = 100\%$$

Indifference point and reward discrimination

Median choice rates across reward deltas were fitted to the following logistic curve:

$$y_{fit} = y_{min} + \frac{y_{max} - y_{min}}{1 + 10^{(\rho - x) \times \eta}}$$

Where:

- y_{fit} is the fitted curve
- y_{min} is the minimum choice rate
- y_{max} is the maximum choice rate
- $x = -\Delta 4, -\Delta 3, -\Delta 2, -\Delta 1, \Delta 0, +\Delta 1, +\Delta 2, +\Delta 3, +\Delta 4$

- ρ is the delta at which the choice rate is 50%
- η is the sigmoid steepness

Logistic curve's parameters were estimated by a machine learning algorithm. Sigmoid's ρ value represented the indifference point between the two offers, while the steepness η was considered as an index of monkey's ability to discriminate between offered payoffs.

Successes rates

For each condition c – whether imposed or chosen – and i session we have computed the success rate as follows:

$$SR_{c,i} = \frac{n_{\text{successful reaching}}}{n_{\text{chosen option}}} \times 100$$

Where n stands for 'the number of'

Reward gain optimization indexes

The percentage of trials in which the highest reward was chosen (HRCR) was computed for each i session and within each choice context, as follows:

$$HRCR_{CC,i} = \frac{n_{\text{high reward chosen trials}}}{n_{\text{total trials CC}}} \times 100$$

The percentage of reward effectively gained (EGR) by each monkey out of the total maximum amount of reward offered was computed for each i session and within each choice context as follows:

$$EGR_{CC,i} = \frac{\text{total reward gained in CC}}{\text{total maximum reward offer in CC}} \times 100$$

A theoretical EGR was also computed as the maximum reward that monkeys could gain by choosing systematically only one action type. This ideal value was adjusted by weighing it for the actual reward that the monkeys were able to get in the choice control contexts as follows:

$$\text{Threshold}_{\text{SOLO1,Mk}} = \frac{ASO_{S1 \text{ vs } S1}}{100} \times \text{max}$$

$$\text{Threshold}_{\text{SOLO2,Mk}} = \frac{ASO_{S2 \text{ vs } S2}}{100} \times \text{max}$$

$$\text{Threshold}_{\text{TOGETHER}} = \frac{ASO_{T \text{ vs } T}}{100} \times \text{max}$$

Where max is the maximum amount of reward obtainable theoretically by always choosing the same action type (either SOLO or TOGETHER).

$\text{Threshold}_{\text{SOLO}}$ was used to indicate the effort minimization threshold, namely the weighed maximum reward that monkeys could gain by choosing systematically only SOLO action type.

Threshold_{TOGETHER} was used to indicate the effort maximization threshold, namely the weighed maximum reward that monkeys could gain by choosing systematically only TOGETHER action type.

As a more general index of monkeys' predisposition to choose TOGETHER's option we also computed the sharp choice rate of TOGETHER condition within SOLO vs TOGETHER choice contexts, for each *i* session:

$$CR_{CC,i} = \frac{n \text{ TOGETHERchosen}}{n \text{ choice-made trials}} \times 100$$

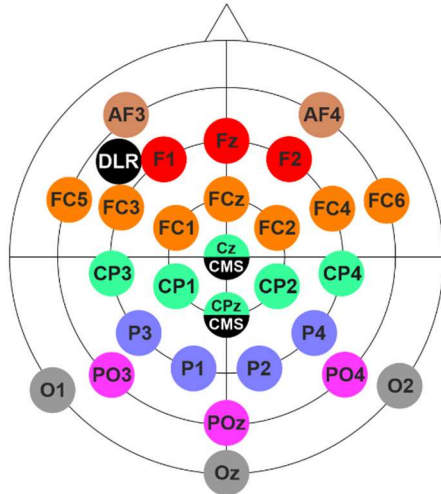
EEG recording

A dual EEG system (ActiveTwo, BioSemi, Amsterdam, The Netherlands) was adopted, to allow simultaneous recordings from both animals (Figure 3A). The software ActiView (version 6.05) was used for data acquisition. The electrophysiological activity of monkeys' brains was recorded from two sets of 26 active electrodes (BioSemi, Amsterdam, The Netherlands), mounted on a tailored headcap made by EasyCap (EASYCAP GmbH, Herrsching, Germany) with an electrode configuration re-adapted from the standard the 10-10 system to match monkey's anatomy. The incoming signal was digitized at a sample rate of 2048 Hz. The Common Mode Sense (CMS) active electrode was used as a reference, and the Driven Right Leg (DRL) passive electrode was used for grounding. The EEG cap configuration is represented in Figure 3B. Cz and CPz electrodes were excluded, since once was used to allow the headpost implant to pass through the cap and the other one was used for the CMS electrode. A customized safety box was used to make cap fastening easier, safer, and more comfortable for the animals and to contain the risk of the monkeys grabbing the cap and the electrodes during the preparatory and recording phases. The component was custom-designed by mean of a CAD software (Autodesk Fusion 360) and 3D printed in Poly(dodecano-12-lactam), a very resistant yet flexible material (Fig. 3C).

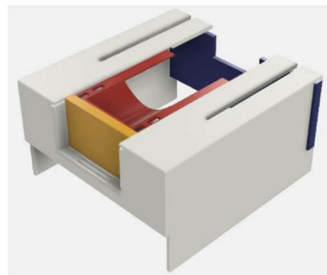
A



B



C



3D printing

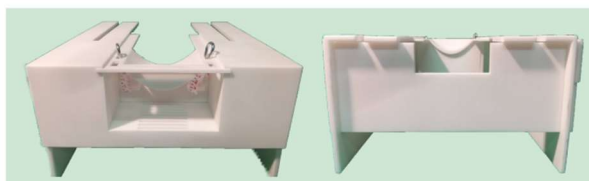


Figure 3. EEG recordings implementation.

(A) A dual EEG system was adopted, to allow simultaneous recordings from both animals. (B) The EEG cap configuration consisted of a re-adaptation of the 10-10 system to monkey’s anatomy. A total of 26 electrodes were used for signal recording. Two additional electrodes (CMS and DRL) were used for referencing and grounding. (C) A customized safety box was modeled, and 3D printed and used to facilitate cap mounting procedures and keep the animals, the experimenter, and the equipment safe.

EEG preprocessing

All data were preprocessed offline using Matlab R2019a (MathWorks, MA, USA), with the open-source toolboxes FieldTrip (Oostenveld et al. 2011; <https://www.fieldtriptoolbox.org/>). A bandpass filtering between 1 and 90 Hz was applied to EEG data. An additional notch filter (48–52 Hz, Butterworth, third order) was used to reduce data contamination due to power line

noise. Continuous data files were segmented to include the entire length of each trial and downsampled to 1000 Hz, to match eye and cursor signals' sampling rate. Each signal segment was visually inspected. Bad trials (namely, with evident transient artifacts due to monkeys' movements or other technical issues) were discarded, and noisy channels were replaced by interpolation. Cz and CPz channels, which were replaced by the headpost implant and the CMS electrode during the recordings were always interpolated. All channels were re-referenced to the common average. Independent component analysis (ICA) was applied to identify and remove signal components reflecting eye blinks and lateral eye movements (Jung et al., 2000). Our analysis was focused on the time-window during which the dyad had to make a decision between the two options, as presented simultaneously in their action space before the final go cue was provided. Therefore, the segment of signal covering the entire trial length was re-epoched from -200ms before to 800ms after the beginning of the IDT (see trial time course in Fig. 2). All epochs with an average signal exceeding 50 μ V were excluded. This additional check was applied to remove those artifacts that eluded the previous qualitative artifact rejection.

Statistical analysis

EEG and behavioral data were analyzed using Matlab R2019a (MathWorks, MA, USA), with FieldTrip (Oostenveld et al. 2011; <https://www.fieldtriptoolbox.org/>) and Letswave (Version 7; <https://www.letswave.org/>) toolboxes.

To assess the normality of samples Shapiro-Wilk test was used. When samples were not normally distributed, non-parametric statistical test were applied.

Kruskal-Wallis test was performed to compare Success rates across imposed and chosen conditions (7 groups: S1 vs S1, S2 vs S2, T vs T, S1 chosen in S1 vs T, T chosen in S1 vs T, S2 chosen in S2 vs T, T chosen in S2 vs T). Kruskal-wallis test was performed to compare the rate at which monkeys chose the highest reward within a trial (HRCR) between choice contexts (5 groups: S1 vs S1, S2 vs S2, T vs T, S1 vs T, S2 vs T). In addition, the reward gained by both monkeys within the SOLO vs TOGETHER choice contexts was compared to the computed maximum reward that they could have gain by choosing systematically only the individual action type (i.e., the effort minimization threshold) by mean of a Wilcoxon rank test, performed four times, namely for each monkey as taking part as a ruler in his own SOLO vs TOGETHER choice contexts, or as taking part as a partner when the other monkeys was playing the ruler's

role. In order to spot the inter-independence of monkeys' propensity to choose to act together across sessions, the Choice Rates of TOGETHER action type in SOLO vs TOGETHER choice contexts, as computed for the two monkeys, were correlated across sessions by mean of the Spearman's rank correlation.

Because of time constraints we will report only some preliminary results obtained by the analysis of the data recorded on Mk1. In the context of these analysis, the choice contexts used were re-labeled as following: SOLO (to indicate S_1 vs S_1), OBS (to indicate S_2 vs S_2), TOGETHER (to indicate T vs T), OBS SOLO chosen (when Mk1 observed S_2 vs T choice context, before Mk2 chose SOLO condition) SOLO chosen (when Mk1 chose SOLO over TOGETHER in S_1 vs T choice context), OBS TOGETHER chosen (when Mk1 observed S_2 vs T choice context, before Mk2 chose TOGETHER condition) TOGETHER chosen (when Mk1 chose TOGETHER over SOLO in S_1 vs T choice context).

A one-way ANOVA was performed for each epoch of interest. This analysis was performed twice for all electrode: first, to compare the neural activity across control choice contexts (3 levels: OBS, SOLO, and TOGETHER); second, to compare the neural activity across SOLO vs TOGETHER choice contexts as split depending on whether Mk1 was making a choice or observing Mk2's choice contexts and on the chose made after the time-windows of interest (4 levels: OBS SOLO chosen in S_2 vs T, SOLO chosen in S_1 vs T, OBS TOGETHER chosen in S_2 vs T, TOGETHER chosen in S_1 vs T).

Results

The cost of acting together

In order to replicate our findings about monkeys' action type preference (see *Experiment 2*), we evaluated the subjective cost of acting TOGETHER as evident from their choice behavior. In agreement with what has been already reported, a shift of the indifference point of the curves fitted to the choice rates revealed that TOGETHER condition was considered costlier than

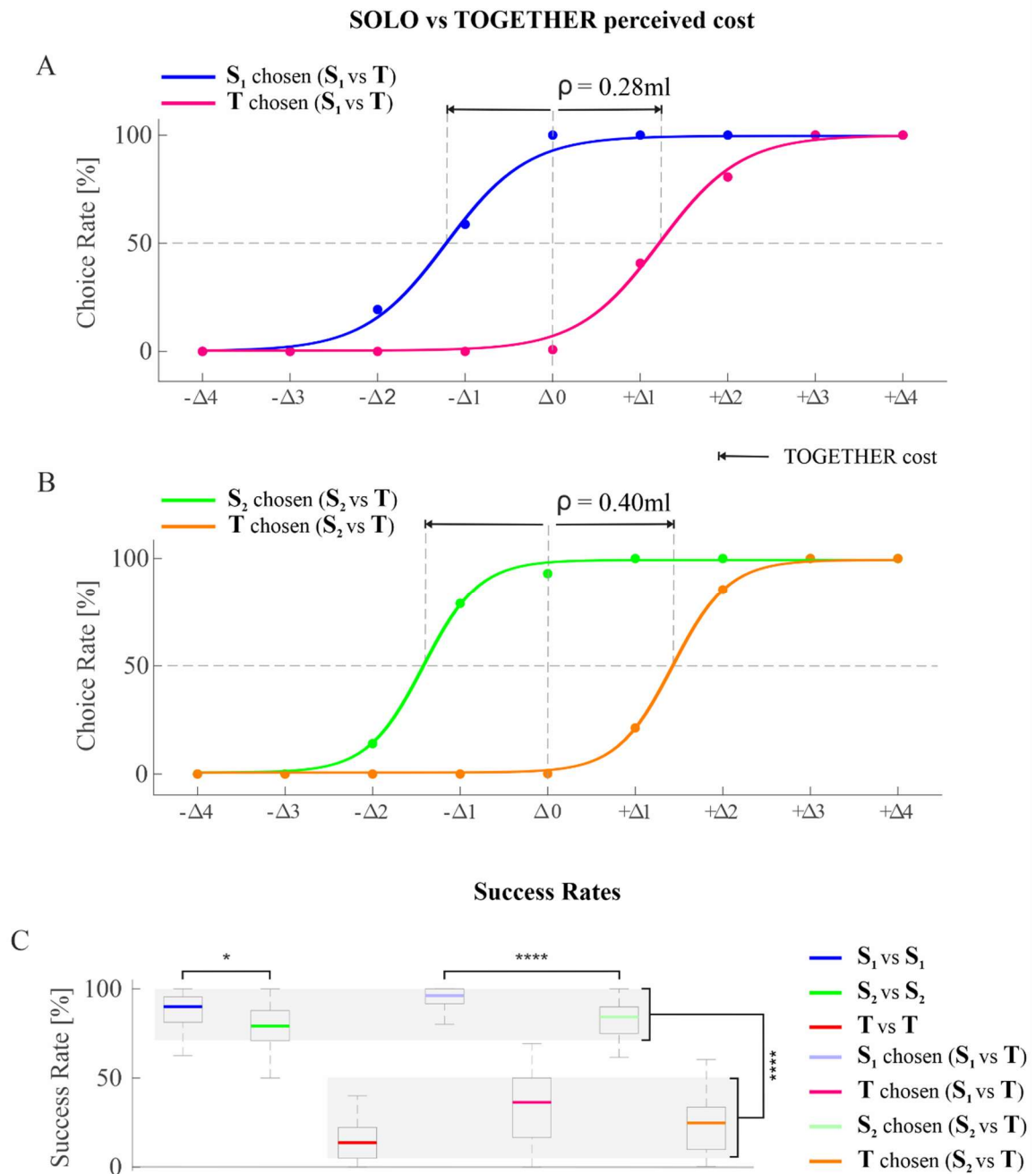


Figure 4. Subjective cost of actin together as evident from choice behavior and task performance. (A-B) Sigmoid functions fitted to monkey’s choice rates for SOLO and TOGETHER conditions within SOLO vs TOGETHER choice contexts for the test task. The perceived cost of acting together emerged as a shift of the indifference point between the two action types offered, which was of $\rho = 0.28\text{ml}$ for Mk1 and $\rho = 0.40\text{ml}$ for Mk2. **(C)** Median success rates (SRs) were compared across imposed and chosen conditions (Kruskal Wallis test, $p < 0.05$). SRs in all TOGETHER groups were significantly higher when SRs in SOLO conditions. Moreover, Mk1’s SOLO SRs were higher than Mk2’s.

SOLO’s. In this case, Mk1’s perceived cost was of $\Delta = 0.28\text{ml}$ (Fig. 4A), while Mk2’s was of $\Delta = 0.40\text{ml}$ (Fig. 4B).

As already observed in the previously analyzed behavioral dataset (*Experiment 2*) a decrease in performance was evident whenever the two monkeys performed an action together. This

result was confirmed by the analysis of the behavior acquired during our EEG recordings. In fact, a significant difference in Success Rates (SRs) emerged when comparing all groups obtained by the combination of choice context and the action type performed (Kruskal-Wallis test; $\chi^2(6) = 521.27$, $p = 2.19 \cdot 10^{-109}$; Fig. 4C). SRs in TOGETHER condition were always significantly lower than SOLO's, as revealed by post hoc analysis (Dunn-Šidák test). In this case, Mk1's individual SRs were higher than Mk2's, both when the SOLO action type was imposed ($p = 0.0253$) or chosen ($p = 3.10 \cdot 10^{-6}$). No significant difference was found between success rate of TOGETHER's groups.

To check whether also in this case the two monkeys' choice strategy was aimed at increasing the chances of gaining the higher reward possible from each trial, we computed how often monkeys aimed at the maximum offer of the trial in control and SOLO vs TOGETHER choice contexts (Fig. 5A). The comparison between trial optimization rates, showed a significant difference across choice contexts (Kruskal-Wallis test; $\chi^2(4) = 90.63$, $p = 9.67 \cdot 10^{-19}$). Post hoc analysis (Dunn-Šidák test, Tab. 1) showed that in the SOLO vs TOGETHER choice contexts the animals effectively aimed at the higher offer similarly to when they were choosing alone between two individual actions. In the T vs T choice context, instead, this tendency was found significantly lower when compared to all the other choice contexts. Moreover, in this case Mk1's trial optimization was significantly higher even than the other conditions in which at least a SOLO option was offered. We investigated then if the optimization strategy adopted could be effective to optimize the reward that monkeys could gain during a session from SOLO vs TOGETHER trials. To clarify this point, we compared the actual percentage of reward gained out of the total amount offered within a session (EGR index) in SOLO vs TOGETHER trials with the effort minimization threshold (i.e., the maximum reward that monkeys could gain by choosing systematically only one action type: either SOLO or TOGETHER; Fig. 5B). The maximum reward gainable by choosing only one action type was theoretically around 70%. The actual maximum gain that monkeys could have get by choosing always TOGETHER targets over SOLO ones was very low (median: 10%), while the actual maximum gain that they could have get by choosing always to act alone was between 45% and 60% depending on each monkey's individual ability to perform the center out task (when choosing between two SOLO targets) and to hold the target in the center (when the partner was choosing between two SOLO targets). By comparing the actual percentage of the reward gained out of the total amount offered within a session (EGR) in SOLO vs TOGETHER with these thresholds, only in S₁ vs T choice context monkeys' gain was significantly exceeding the amount that they could have

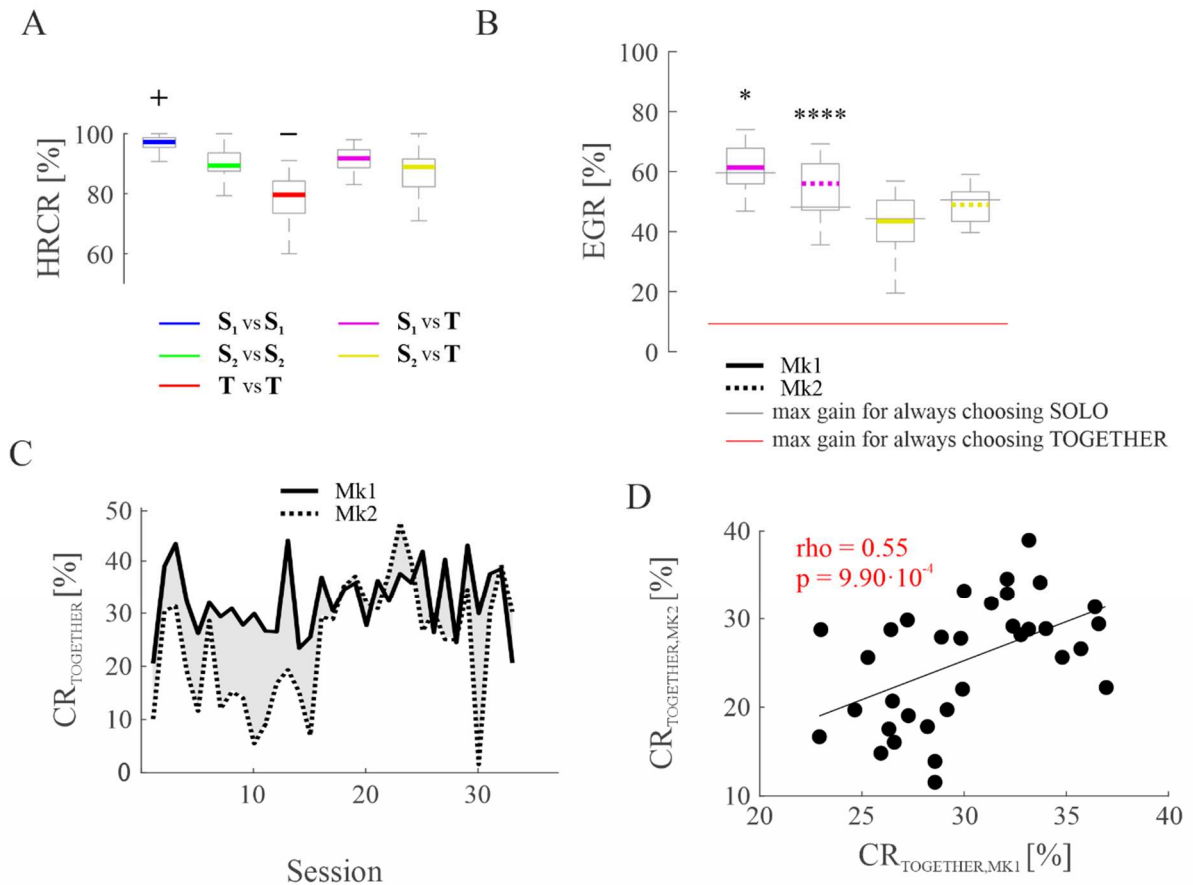


Figure 5. Reward gain optimization strategy. (A) Median high reward choice rate (HRCR) was compared across choice contexts (Kruskal-Wallis test, $p < 0.05$), showing a lower tendency to aim for the higher reward in T vs T choice contexts, compare to the two other control choice contexts. (B) The median effective gain rate (EGR), indicating the reward gained by both monkeys within the SOLO vs TOGETHER choice contexts, were compared to the effort minimization threshold, defined as the weighed maximum reward that they could have gain by choosing systematically only the SOLO action type (Wilcoxon rank test, $p < 0.05$). A higher EGR was evident only in the S₁ vs T choice context, for both the ruler (Mk1) and the partner (Mk2) (C) The rate at which TOGETHER condition was chosen over SOLO's by each monkey in each session (CR_{TOGETHER}) within SOLO vs TOGETHER choice contexts. is represented (D) A correlation between Mk1 and Mk2 TOGETHER choice rates in SOLO vs TOGETHER choice contexts emerged.

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$

gain by ignoring completely all TOGETHER's targets (Wilcoxon test: SOLO1 vs TOGETHER Mk1: $Z = 2.15$, $p = 0.0312$; SOLO1 vs TOGETHER Mk2: $Z = 3.49$, $p = 4.86 \cdot 10^{-4}$). When Mk1 was playing as a ruler, both monkeys managed to gain around 2-7% more than what they could have gotten by choosing systematically the SOLO option. Instead, when Mk2 was designed as the ruler, there was no evident convenience of the "aim at the higher" choice strategy showed by the monkeys, compared to the "always choose the safest and easier option" strategy.

Since we demonstrated that monkeys estimated similarly the cost of acting together and adopted similar choice strategies, we wonder if an interdependence between monkeys'

Choice contexts compared		P value
SOLO 1 vs SOLO 1	SOLO 2 vs SOLO 2	$1.48 \cdot 10^{-4}$
	SOLO 1 vs TOGETHER	0.0114
	SOLO 2 vs TOGETHER	$1.44 \cdot 10^{-7}$
SOLO 2 vs SOLO 2	SOLO 1 vs TOGETHER	0.9630
	SOLO 2 vs TOGETHER	0.8644
SOLO 1 vs TOGETHER	SOLO 2 vs TOGETHER	0.1464
TOGETHER vs TOGETHER	SOLO 1 vs SOLO 1	0
	SOLO 2 vs SOLO 2	$1.11 \cdot 10^{-5}$
	SOLO 1 vs TOGETHER	$2.69 \cdot 10^{-8}$
	SOLO 2 vs TOGETHER	0.0041

Table 1. Dunn-Šidák test for multiple comparison of choice contexts' high reward choice rate (HRCR).

predisposition of acting together could be observed also in this case. Monkeys' $CR_{TOGETHER}$ in SOLO vs TOGETHER choice contexts seemed to vary congruently across sessions (Fig. 5C). In fact, a significant correlation between Mk1 and Mk2's $CR_{TOGETHER}$ was found (Spearman correlation: $\rho = 0.55$, $p = 9.90 \cdot 10^{-4}$; Fig.5D). The propensity to choose to reach a target together when playing as a ruler, thus, was reciprocally influenced by the attitude of the partner to choose this condition when it was his turn to play the same role.

Choosing and predicting others' choice in the brain

The waveform of the signal recorded from the CPz electrode is represented (Fig. 6A). This channel was chosen as a representative of the response evoked by the comparison of the two options on the screen. Three epochs of interest were selected: a first, brief epoch comprising a quick negative response between 65 and 75ms after the stimulus appearance. A second time-window, in which the response for the three choice contexts started to depart, at around 120-160ms. A third, wider window, in which a positive, slower response modulated by the choice context factor was observed. The topographies of the baseline activity and of these three time-windows are represented in Figure 6B. During the first epoch of interest (65-75ms) we observed a rapid response characterized by an occipital negativity, which was invariant across choice contexts. In the second topography (120-160ms), the polarity of the recorded scalp activity was inverted with a stronger centro-frontal negativity observed in the OBS choice

ANOVA was performed for each epoch and electrode (F values and significant tests are represented on the topographies in Fig. 6C). The statistics confirmed that while there was no difference between choice contexts during the baseline and the first quick negative response (65-75ms), a significant difference emerged for CPz and FC6 channels during the early stages of the long, positive modulation. Moreover, around the higher and wider positive pick (250-350ms), the activity recorded from several centro-parietal electrodes seem to be strongly modulated by the three choice contexts.

Once established that Mk1 brain activity was modulated by the action type to be performed in the three control choice contexts (i.e., OBS, SOLO and TOGETHER), we wondered if the neural activity in the SOLO vs TOGETHER choice contexts could reflect similar processes with an additional distinction between the action type chosen or expected to be chosen by the partner (Fig. 7). To clarify this point, we compared four types of conditions: two cases in which Mk1 was expected to choose between acting alone or together divided second to the choice made (i.e., SOLO chosen or TOGETHER chosen) at the end of the instruction delay time (IDT); two cases in which Mk1 was expected to anticipate Mk2 choice between acting alone or together, divided second to the choice made (i.e., observed SOLO chosen or observed TOGETHER chosen) at the end of the IDT. The same time-windows of interest were found and highlighted on CPz waveform (Fig. 7A). The topographies for these four groups (Fig. 7B) show a similar occipital negativity around 65-75ms followed by a polarity inversion during which a mild *choice context x choice* effect starts to emerge, particularly with a higher similarity of SOLO chosen and TOGETHER chosen topographies. Finally, a strong positivity spreading along the z axis was evident in all the three groups in which Mk1 was either choosing actively to act alone or together (SOLO chosen and TOGETHER chosen) or predicting that Mk2 would have choose to act together. Interestingly, the same strong positivity was not observed when Mk1 could predict that Mk2 would have choose to work alone. Again, the statistics (one-way ANOVA, Fig. 7C) confirmed no significant difference during the early stages of the evoked response (baseline and 65-75ms time-window), while an effect of the *choice context x choce* factor emerged on PO4 and CP2 channels during the 120-160ms period, spreading toward many centro-parietal channels and two frontal ones during the high, prolonged positive response at 250-230ms.

Monkey 1 - SOLO vs TOGETHER choice contexts

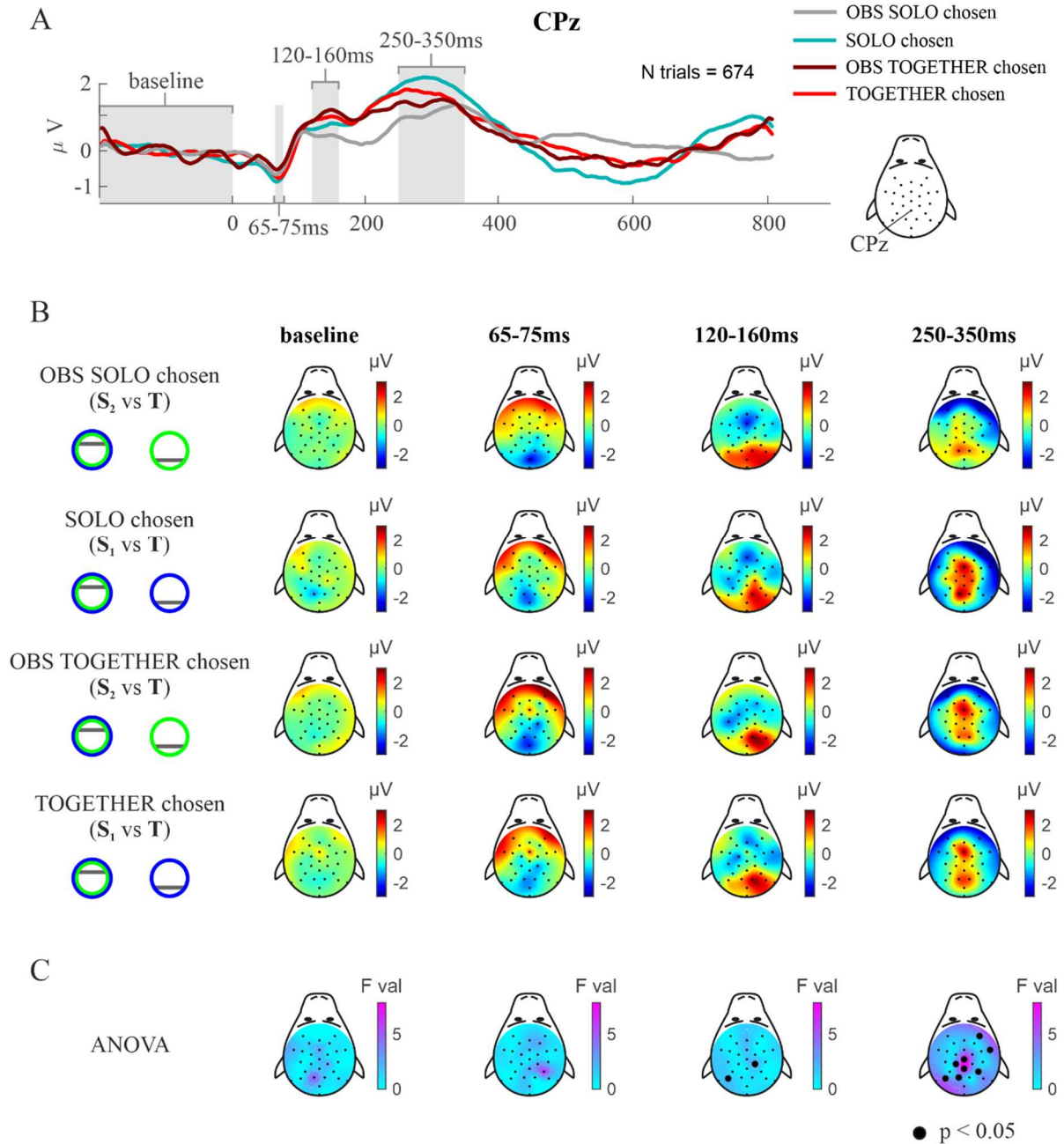


Figure 7. Mk1's ERPs modulation in SOLO vs TOGETHER choice contexts (A) The waveform of the signal recorded during the IDT epoch from channel CPz within each control choice contexts is represented, divided second to the role of Mk1 (ruler or partner/observer) and to the choice made at the end of the IDT (SOLO chosen or TOGETHER chosen). Four time-windows are highlighted: the baseline preceding the comparison of the two offers; a first, quick negative response with a peak at 65-75ms; the time point (120-160ms) in which the selected task features modulate the ERP, as evident from the divergence of the four waveforms; the highest and wider positive peak observed between 250-350ms. (B) the topographies of the four time-windows are represented for each role x choice combination (OBS SOLO chosen, SOLO chosen, OS TOGETHER chosen and TOGETHER chosen). (C) F value of the one-way ANOVA (4 levels: OBS SOLO chosen, SOLO chosen, OBS TOGETHER chosen, TOGETHER chosen; $p < 0.05$) performed for each electrode in the time-window of interest is represented. Significant differences are highlighted by a black dot.

Discussion

The aim of the present work was to study the electrophysiological activity as recorded from two non-human primates' brains while choosing to act alone or together.

Subjective cost and choice strategies

In agreement with what has already been observed from the results shown in the second section of this thesis (*Experiment 2*), the two monkeys demonstrated to be able to subjectively evaluate the cost of inter-individual motor coordination and to use this information to decide between acting alone or together. Moreover, in coherence with the previous findings, both animals aimed at optimizing their trial-contingent gain while taking the cost of acting together into account. A fair trade was established also in this case, so that the tendency to choose to act together to gain a more convenient reward was reciprocally modulated in a dynamic fashion.

First steps towards an understanding of neural basis of choosing joint action

The neural activity recorded from Mk1 was analyzed in order to move towards the understanding of the correlates of acting alone or together. Particularly we focused on the IDT epoch, namely a time-window of 800ms during which the two animals were able to see the two offers at the same time, displaced on opposite sides of the screen, right before being able to make their choice.

Our findings supported the interpretation of a two-steps modulation of brain activity evoked by the salient stimulus presented at the beginning of the IDT epoch: an early, quick visual response, which was invariant across choice contexts; a later, slower cognitive response, which was modulated by the action type subsequently chosen by the animal or by his partner.

The C1 wave is the evoked visual response with the earliest onset, which peaks at around 80-100ms and is known to originate from area V1 (Luck 2014). The neural response observed in Mk1 showed a modulation similar to this component, with a negativity at around 65-75ms followed by a polarity inversion with a quick, rising slope. This response seemed to be anticipated of about 20ms, when compared to the standard equivalent in humans in agreement with the notion that ERP component latencies in monkeys are typically 25% shorter

(Woodman, 2012) The inversion of polarity following the observed C1-like response resembles the P1 component another wave that is believed to originate from occipital areas, which is modulated by arousal and characterized by a positive peak around 100-130ms (Luck 2014). An analogue of this component has been already found in monkeys (Van der Marel et al. 1984). This first components of the visual evoked potential were not found to be significantly modulated by the choice contexts, nor by the action type preferred, as to be expected.

After about 120ms from stimulus onset, the observed ERP seemed to be modulated by task related cognitive factors. Particularly at around 250-300ms a higher positive peak was observed, which could resemble the P300 component described in the literature on human EEG. This wave has been associated to several cognitive functions such as updating of representations, strategic response, task difficulty or stimulus classification and decision-making (Kourtis et al. 2013, Luck 2014). This same component has been found and studied on monkeys as well in the attempt of modeling well-known EEG biomarker of severe human psychopathologies such as schizophrenia (Glover et al. 1991, Paller et al. 1992).

Previous pioneering evidence collected on humans (Kourtis et al. 2013) suggests that, when acting together, the amplitude of the P300 component during the planning phase is increased in frontal domains and decreased in the parietal ones when compared to individual action. In partial agreement with these findings the action type to be chosen seemed to modulate the amplitude of the P300-like component in Mk1, as it can be observed in the CPz waveform. Yet, our data included also decisional aspects and provide information about cognitive and motor processes underlying choices or predicted choices about future action in a social context, which are missing in Kourtis et al. (2013).

At this level of data analysis, it is still difficult to interpret the meaning of the observed modulation of the slow and wide response observed on Mk1 brain from about 100ms up to 400ms. Nevertheless, the results emerged by comparing the time locked responses observed within the four possible scenarios characterizing the SOLO vs TOGETHER choice context (i.e., OBS SOLO chosen, SOLO chosen, OBS TOGETHER chosen, TOGETHER chosen) allowed us to move a step closer towards a better understanding of the modulation found when comparing the neural activity observed across control choice contexts. Mk1's response during the IDT epoch was not just modulated by the meaning of the visual scene presented: if that would have been the case no difference would have emerged when the monkey was observing a SOLO vs TOGETHER choice contexts in which Mk2 was designed as the ruler depending

on the choice expected. On the contrary, Mkl response was strongly modulated by the choice (SOLO or TOGETHER) expected from the partner. This type of modulation cannot be read as a mere mirror-like activity aimed at predicting the other's action. In fact, this response does not only include information about the partner's intention but is also integrates the meaning that it has for the single individual.

Future directions

The results presented so far constitute only the tip of the iceberg of a wide amount of information that can be extracted from the collected data.

One of the first factors that we will have to examine in depth is the modulation of reward on neural activity and its interaction with the choice made in control as well as SOLO vs TOGETHER choice contexts. Several studies have already investigated value-based decision making in human and non-human primates (e.g. Padoa-Schioppa & Assad 2006, Levy & Glimcher, 2011, Rich & Wallis 2016, Pisauro et al. 2017, Setogawa et al. 2019), also with a particular focus on value embodiment in action planning processes (e.g. Roesch & Olson 2004, Pastor-Bernier & Cisek 2011, Cai & Padoa-Schioppa 2014, Suriya-Arunroj & Gail 2015) and cost-benefit analysis processes (e.g., Hosokawa et al. 2013, Apps et al. 2015). To date, though, none has addressed the neural basis of choosing between acting alone or together via EEG recordings in non-human primates.

As a further step, the difference between action types should be also investigated during the execution phase of cursor's movement. In this regard, it would be interesting to study inter-brain synchronization particularly in the frequency domain and to look for signs of cortical workload while comparing SOLO and TOGETHER performed actions. Some previous results for example have shown a higher degree of alpha power in centro-posterior sites as an index of self-other integration and segregation (Novembre et al. 2016). Moreover, we could compare the representation of partner's action while coordinating compared when the partner is acting alone. Co-acting has been shown to elicit more intense representation of other's action compared to mere observation (Menoret et al. 2014). More in general, the newest methods of hyperscanning data analysis developed in the recent years (Czeszumski et al. 2020) could be applied to the instruction (IDT) and execution (DFT) phases in order to assess synchronicity, similarity, network properties and information flow across brains.

A focused analysis should be conducted also during the instruction phase in order to see how the sequential instruction is decoded by the two monkeys in contrast to the simultaneous instruction provided right before making their decision. We know in fact from the analysis conducted on their behavior (*Experiment 2*) that they were able to take this information into account. It has been demonstrated that sequential evaluation of options is neutrally segregated from the actual selection phase (Yoo et al. 2020), which we chose to focus on as a first step in our analysis. Frontal asymmetry, which has been pointed out to be a marker of approach-avoidance tendencies towards a stimulus (Kelley et al. 2017) could emerged during the instruction phase.

Conclusions

We started from the notion that rhesus monkeys are capable of coordinating actions with a mate by paying the cost that it entails. On the wake of this premise, we demonstrated that giving the time to prepare to act together can reduce such a cost and foster the monkeys' successful coordination. Such an improvement in the dyad's performance can be explained by the advantageous recourse to a "We-representation" which might selectively foster joint action.

Going a step further we demonstrated that monkeys can be willing to engage in a joint task depending on an integrated evaluation of different kinds of factors related to the advantages and disadvantages of sharing their actions with others. Particularly we noticed that the cost of acting together was finely estimated by both our subjects and used to make economic decisions. Most importantly we demonstrated an inter-dependence of monkeys' propensity to choose to act with the partner, which could be interpreted as a dynamic behavioral adjustment aimed at establishing a fair distribution of costs and benefits for both coordinating partners.

At last, we started to investigate the neural underpinnings of the demonstrated capability to make decisions about sharing actions in a social context using EEG. Our work shows promising preliminary results that might help bridging the gap between existing neurophysiological literature on social neuroscience based on human and non-human primates.

Taken all together our findings show that non-human primates are an excellent model for studying the neural underpinnings of motor-cognitive and social aspects entailed by sharing actions with others.

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