



Peripersonal space in social context is modulated by action reward, but differently in males and females

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Abstract

The peripersonal space (PPS) is a multisensory representation of the near-body region of space where objects appear at hand. It also represents a buffer zone protecting the body from external threats and as such it contributes to the organization of social interactions. However, how the combination of embodied objects processing and constraints inherent to social interactions contributes to PPS representation remains an open issue. By using a cooperative task where two male ($N=22$) or female ($N=18$) participants, sharing the same action space, were requested to select a number of stimuli on a touch-screen table, we investigated the effect of non-uniform distribution of reward-yielding stimuli on selection strategy and perceptual judgments of reachability, used as a proxy of PPS representation. The probability to select a reward-yielding stimulus (50% of the stimuli) was 75% in the proximal space of one of the two confederates. Results showed that participants initially prioritized stimuli in their proximal space and were progressively influenced by the spatial distribution of reward-yielding stimuli, thus invading their confederate's action space when associated with higher probability of reward. The distribution of reward-yielding stimuli led to an increase of reachability threshold, but only when biased towards the participants' distal space. Although the invasion of others' PPS was more pronounced in male participants, the biased distribution of reward-yielding stimuli altered the reachability threshold similarly in males and females. As a whole, the data revealed that reward expectations in relation to motor actions influence both PPS exploration and representation in social context, but differently in males and females.

Introduction

In everyday life, the way we interact with the environment relies on a series of computations performed by the brain, based on the integration of information related to the body and the space in which it is embedded. This implies that the brain retains a functional representation

of the environment which depends on the current sensory-motor state as well as the outcome of previous interactions with the physical and social context (Grusser, 1983; Hall, 1966; Previc, 1998). Within this functional representation, the peripersonal space (PPS) specifies the limited space around the body dedicated to the interaction with objects located at hand-reachable distance (Bufacchi & Iannetti, 2018; Coello & Iachini, 2016; de Vignemont & Iannetti, 2015; di Pellegrino & Làdavas, 2015; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981). In relation to the linkage between PPS and action, object processing in PPS involves multisensory integration supported by a large subcortical and cortical brain fronto-parietal network implying the motor system (Brozzoli, Makin, Cardinali, Holmes, & Farné, 2011; Cléry, Guipponi, Wardak, & Hamed, 2015; Graziano, Yap, & Gross, 1994; Holmes & Spence 2004; Makin, Holmes, & Zohary, 2007; Serino, Canzoneri, & Avenanti, 2011). In line with this view, Graziano (2017) described multimodal neurons in the pre-motor cortex that discharge predominantly not only for stimuli near the body but also for more distant stimuli, so

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that 95% of these neurons code the space within reaching distance (see also di Pellegrino & Làdavas, 2015). Taking advantage of the motor nature of PPS, object perception (Costantini, Ambrosini, Tieri, Sinigaglia, & Committeri, 2010; Spence, Pavani, Maravita, & Holmes, 2004) and categorization (Blini, Desoche, Salemme, Kabil, Hadj-Bouziane, & Farnè, 2018; Iachini, Ruotolo, Vinciguerra, & Ruggiero, 2017) are facilitated when they are located in PPS.

A number of studies reported that alteration or temporary inhibition of the motor system produces shrinkage of PPS representation (Bassolino, Finisguerra, Canzoneri, Serino, & Pozzo, 2015; Bartolo, Coello, Edwards, Delépouille, Endo, & Wing, 2014; Toussaint, Wamain, Ildebidet, & Coello, 2018). Furthermore, PPS shrinks when dangerous objects (Coello et al., 2012) or unfamiliar confederates (Teneggi, Canzoneri, di Pellegrino, & Serino, 2013) are located at close distance. In contrast, extending motor abilities through tool-use was found to produce an increase in PPS representation (Bourgeois, Farnè, & Coello, 2014; Canzoneri et al., 2013; Cardinali et al., 2011; Farnè, Iriki, & Làdavas, 2005; Iriki, Tanaka, & Iwamura, 1996; Maravita, Husain, Clarke, & Driver, 2001; Maravita, Spence, Kennett, & Driver, 2002). PPS representation also extends in the presence of appealing stimuli located nearby (Coello et al., 2018) or following positive interaction with a confederate (Teneggi et al., 2013; Coello et al., 2018). Considered as a whole, these data suggest that PPS operates as an interface between perception and action and as such underlies two complementary functions: it subserves goal-directed behaviours towards non-threatening stimuli, and it supports defensive behaviours against threatening and potentially harmful stimuli (Coello, Bourgeois, & Iachini, 2012; Di Pellegrino and Làdavas 2015; de Vignemont & Iannetti, 2015; Graziano & Cooke, 2006; Hunley & Lorenco, 2018).

The defensive role of PPS makes it thus an important support in the control of social interactions. As evidence, Quesque et al. (2017) demonstrated that tool-use induces not only an enlargement of PPS (Bourgeois et al., 2014), but also an increase of the minimum comfort distance tolerated in dyadic social interactions. Furthermore, physiological responses associated with PPS invasion (Kennedy, Gläscher, Tyszka, & Adolphs, 2009) revealed to be a robust predictor of preferred comfort distance in social contexts (Cartaud, Ruggiero, Ott, Iachini, & Coello, 2018). As a consequence, individuals with enlarged self-representation of PPS reported higher rate of social anxiety (Iachini, Pagliaro, & Ruggiero, 2015; Nandrino, Ducro, Iachini, & Coello, 2017) and phobia (Lourenco, Longo, & Pathman, 2011). These results are, therefore, consistent with not only a motor function but also a defensive function of PPS (Cooke & Graziano, 2004), the latter contributing to the organisation of

object-directed actions as well as the regulation of the social life (Coello & Iachini, 2016).

In line with the defensive role of PPS, it was found that when performing a cooperative task in a shared workspace, people prioritized stimuli located in their proximal space, avoiding thus to invade others' PPS (Coello, Quesque, Gigliotti, Ott, & Bruyelle, 2018). However, despite the division of the workspace in the cooperative task, people showed an expansion of their PPS that was not observed when they performed the task alone or in the presence of a passive confederate. These findings suggest that PPS representation depends on the outcome of both self-executed and observed motor actions in a cooperative social context. They also reveal that sharing a common workspace induced a natural tendency to favour stimuli located in the proximal space, avoiding thus those located in others' proximal space. We may thus surmise that the presence of appealing stimuli in others' PPS represents a conflict situation where stimuli and space prompt different behaviours. To investigate this issue, in the present study we tested whether spatially biasing the distribution of reward-yielding stimuli towards one confederate in a dyadic cooperative task induced an invasion of the confederate's PPS. Furthermore, we tested whether such biased distribution of reward-yielding stimuli alters differently PPS representation in the two confederates. Finally, the adjustment of social space was found to be influenced by gender with shorter interpersonal distance usually judged as more comfortable in both males and females when interacting with females as compared to males (Iachini et al., 2014, 2016). Accordingly, we compared the effects of biasing the distribution of reward-yielding stimuli towards one of the confederates in both male and female dyads.

Method

Participants

Forty healthy participants voluntarily took part in the experiment (22 males and 18 females, 18–35 years old, $M = 22.53$ years, $SD = 3.40$ years). Participants were recruited in pairs and were not acquainted with their confederate. Each dyad was made up of two male or female participants in order to avoid any possible effect of gender difference in the cooperative task (Iachini et al., 2015). They all had normal or corrected-to-normal visual acuity and were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971; mean laterality quotient = 0.81, $SD = 0.26$). They had no prior detailed information about the hypothesis of the study and gave their informed consent prior to the beginning of the experiment. The protocol received approval by the Institutional Ethics Committee (Ref. Number 2017-7-S52) and was conducted according to

the ethical principles of the Declaration of Helsinki (World Medical Association, 2013).

Apparatus and stimuli

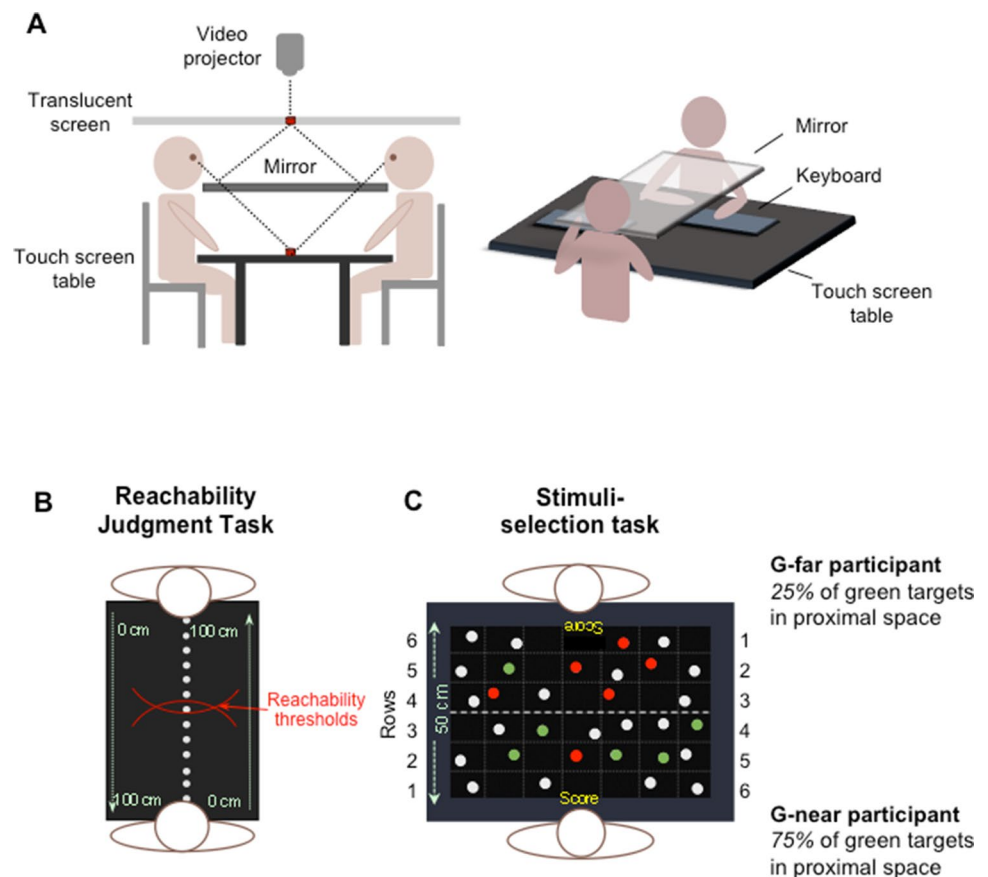
Experimental material, paradigm and procedure were the same as used by Coello et al. (2018). Figure 1a provides a schematic illustration of the experimental apparatus. Two participants sat facing each other at opposite sides of a 40" touch-screen table (Samsung SUR40, 109.5 × 70.74 cm). The touch-screen table was placed in the middle of a steel structure, that supported a 30 cm × 100 cm movable rectangular mirror placed 34 cm above the touch-screen table, and a 200 × 150 cm horizontal translucent screen placed 34 cm above the mirror. A video projector (Infocus 3926D) mounted on the ceiling and connected to a computer (Dell 7010) projected a 161 × 118 cm image on the mirror, through the translucent screen located 79 cm below the video projector. Depending on the task, participants were requested to process the stimuli projected on the mirror (reachability judgment task), or directly displayed by the touch-screen table (stimuli-selection task).

In the *reachability-judgment task*, 51 grey stimuli (1 cm-diameter dots), ranging from 0 cm to 100 cm away from the head position of the participants (mean inter-target distance

of 2 cm), were projected at the level of the touch-screen table, by the way of the optical projection of the image displayed on the mirror through the translucent screen (Fig. 1b). The stimuli were randomly displayed for 250 ms and presented four times each, for thus a total of 204 trials (51 distances × 4 repetitions). While performing the task, a black sheet covered the touch-screen table in order to avoid any luminous source that could interfere with the perception of the visual stimuli.

In the *stimuli-selection task*, 32 grey stimuli (2.7 cm-diameter dots) were randomly displayed on the black background of the 40" (1920 × 1080 px) touch-screen table (active area of 88.56 × 49.81 cm) according to a non-visible distribution grid (Fig. 1c). The grid was composed of 42 non-visible cells (6 rows × 7 columns) that covered the whole touch-screen table. When positioned at the centre of the cells, the inter-stimuli distance was 12.65 cm (274 px) along the *x* axis and 8.30 cm (180 px) along the *y* axis. In each block of stimuli selection, the 32 grey stimuli were displayed at random locations [from 0 to 60 pixels from the centre in the (*x*, *y*) directions] in randomly selected cells, thus leaving 10 cells empty. The configuration of the set of stimuli changed in each block, which gave the feeling of a sequence of random distributions. Participants selected each stimulus by touching it on the screen with the right index

Fig. 1 a Schematic illustration of the experimental apparatus. b Stimuli used in the reachability judgment task. c Stimuli used in the stimuli-selection task. According to the group, the probability of selecting a (green) reward-yielding stimulus was 75% in the participant's or his/her confederate's proximal space



finger, resulting in a stimulus' colour change. If the stimulus turned to green (50% of the stimuli), a sound of clinking coins was played and participants gained one point (reward-yielding stimulus). If the stimulus turned to red (50% of the stimuli), a buzzing sound was played and participants gained no point (no reward-yielding stimulus). The probability to select a green reward-yielding stimulus was differently distributed according to the location of the participants in the dyads. For 50% of the participants (G_{near}), the probability of selecting a reward-yielding stimulus was 75% in the near space (rows 1, 2, 3) and 25% in the far space (rows 4, 5, 6). For the other 50% of the participants (G_{far}), the probability of selecting a reward-yielding stimulus was 75% in the far space (rows 4, 5, 6) and 25% in the near space (rows 1, 2, 3, see Fig. 1c). Participants belonging to the G_{near} or G_{far} group were randomly placed in either side of the touch-screen table. Each dyad performed 34 blocks of stimuli selection, each block including 12 selections of stimuli (alternatively 6 per participant). Two digital counters were displayed along the proximal edge of the touch-screen table, in the middle, so that each participant of the dyads could check for the score accumulated throughout the task.

Procedure

To begin with, participants of each dyad completed the written consent and the Edinburgh Handedness Inventory (Oldfield, 1971). The two participants were then seated in a dark room at opposite sides of the touch-screen table (inter-head distance of 1 m) and received the instructions relating to the two tasks. The experimental session was composed of three subsequent phases: 1) A pre-test phase in which participants performed the reachability judgment task; 2) a test phase in which participants performed the stimuli-selection task; 3) a post-test phase in which participants performed the reachability judgment task again. The whole experimental session lasted about one hour.

In the *reachability judgment task* (pre-test and post-test phases), the two participants of the dyads were requested to estimate if the stimulus presented could be reached or not with the right hand, but without performing any actual movement. The participants saw the same stimulus but performed the task individually, providing thus simultaneously reachable/unreachable responses on different keyboards with their left index and middle fingers. Following a short practice session (5 stimuli), each participant judged the reachability of 204 stimuli in both sessions (pretest and posttest). Inter-stimuli interval lasted 1.5 s, during which participants provided their responses. A short break period of 60 s was provided halfway in each session.

In the *stimuli-selection task*, the mirror, the two keyboards and the black sheet covering the touch-screen table were removed. In order to highlight the cooperative aspect

of the stimuli-selection task, the latter was presented to participants as a game that had to be played together. The aim was to get a maximum score by cooperatively cumulating as many points as possible by finding as many green (reward-yielding) stimuli as possible. For this purpose, they alternatively selected with their right finger 12 stimuli out of the 32 displayed on the screen. Participants in the G_{near} group always performed the first selection in order to standardize the procedure. Overall, each participant selected a total of 204 stimuli leading to a total of 408 stimuli per dyad (2 participants \times 6 stimuli \times 34 blocks of trials). Participants had no right to verbally or visually communicate during the whole experiment. At the end of the experiment, participants responded to two individual social characteristics questionnaires. First, the Interpersonal Reactivity Index-IRI (French version, Gilet, Mella, Studer, Grünh, & Labouvie-Vief, 2013), assessing through four subscales cognitive empathy (Perspective Taking, Fantasy) and affective empathy (Empathic Concern, Personal distress). Second, the Social Value Orientation- SVO- Slider Measure (French version, Murphy, Ackermann, & Handgraaf, 2011), assessing people's prosocial tendency, which has been found to influence the propensity to cooperate (Zeelenberg, Nelissen, Breugelmans, & Pieters, 2008). Finally, we checked in a post-experiment debriefing that none of the participants were aware of the hypotheses tested, which was the case.

Data and statistical analysis

Matlab software (R2017a) was used for the implementation of the tasks as well as for data collection and analysis. Statistical analyses were carried out with R version 3.3.2 (R Core Team, 2017) and R Studio version 1.0.136. Concerning the *reachability judgment task*, the perceived boundary of PPS (reachability threshold) was determined using the maximum likelihood fit procedure based on second-order derivatives (quasi-Newton method) to obtain the logit regression model that best fitted the dichotomous responses (reachable/unreachable) provided by participants for each of the 51 distances of stimuli (Bourgeois & Coello, 2012). The logit regression model was obtained by employing the following equation:

$$Y = \exp^{(\alpha+\beta X)} / (1 + \exp^{(\alpha+\beta X)}).$$

In this model, X relates to the distance at which the stimulus has appeared while Y corresponds to the answer given by the participants. Reachability threshold corresponds to $(-\alpha/\beta)$, which defines the critical value of X marking the transition between the response "reachable" and "unreachable", i.e. the boundary of PPS. Individual reachability thresholds were corrected according to the actual arm length by subtracting arm length (cm) to the critical value of X . Reachability thresholds were computed

separately for pretest and posttest. A reachability threshold in the posttest similar to that in the pretest (posttest-pretest difference = 0) indicated no change of PPS representation. A higher reachability threshold in the posttest (posttest-pretest difference > 0) indicated a shift of reachability threshold away from the participant (i.e., extension of PPS representation), while a lower reachability threshold (posttest-pretest difference < 0) denoted a shift of reachability threshold towards the participant (i.e., shrinkage of PPS representation). We analysed the perceived change of reachability thresholds (posttest-pretest difference) through a Session (Pretest, Posttest) × Group (G_{near} , G_{far}) × gender (male, female) analysis of variance (ANOVA), with Group and Gender as between-subject factors. The goodness of fit of the logistic regression was estimated through McFadden's pseudo- R squared.

Concerning the *stimulus-selection task*, we computed the number of stimuli selected in the distal space (rows 4–6 for G_{near} and G_{far}) for each participant and for each block. For the data analyses described hereafter, non-parametric statistical tests were used as the number of comparisons did not allow the validation of the necessary assumptions (normality, homoscedasticity) to use parametric tests. Specifically, we applied permutation-based ANOVA following Manly's method (Manly, 2007), setting the number of permutations at 99,999. Post-hoc comparisons were assessed through permutation tests based on 9999 Monte-Carlo resampling, using the `independence_test` function of the `coin` package implemented on R (Hothorn, Hornik, Van De Wiel, & Zeileis, 2008).

First, we calculated the average number of distal stimuli selected, *all blocks* considered together, in order to assess the general tendency to invade the confederate's space. Statistical analyses were carried out using a permutation-based ANOVA with Group (G_{near} , G_{far}) and Gender (Female, Male) as between-subject variables. Second, we compared the average number of distal stimuli selected in *the first and last three blocks* to account for an eventual change in selection strategy during the selection task. We applied permutation-based ANOVA with Block (First, Last) as within-subject variable, and Group (G_{near} , G_{far}) and Gender (Male, Female) as between-subject variables. Third, in order to assess the precise moment at which a change in the participants' strategy occurred, we compared the number of distal stimuli selected across all blocks in G_{near} and G_{far} , taking gender into account. We performed permutation-based multiple comparisons for each block of trials, comparing first G_{near} versus G_{far} 's performances, and males' versus females' performances separately for G_{near} and G_{far} . We further conducted linear regression analysis and applied F test to test the overall significance of the model, in order to account for any global change in the performance across blocks, depending on the gender.

Furthermore, in line with Coello's et al. (2018) analysis, we calculated for each participant (1) the difference between posttest and pretest reachability estimates, (2) the average amplitude of selection actions toward the stimuli across all blocks and (3) the number of rewards obtained in the distal space. Correlations between the two latter variables and the individual posttest-pretest difference in reachability threshold were tested (Spearman's rank correlation coefficient), considering gender and group together, in order to evaluate whether the reported change of PPS representation was related to the amount of rewards obtained rather than to the amplitude of motor performances. In addition, we applied a z test to compare the observed percentage of reward-yielding stimuli selected in G_{near} and G_{far} to the percentage that participants would have obtained if they had only selected stimuli located in their respective proximal space.

Finally, in order to analyse the results at the IRI scale, we computed the score obtained by the participant at each of the four subscales of the questionnaire: the Perspective Taking and Fantasy subscales (relating to cognitive component of empathy) and the Empathic Concern and Personal Distress subscales (accounting for the affective component of empathy). The Perspective Taking subscale evaluates the ability to adopt other people's psychological point of view. The Fantasy subscale measures the inclination to get involved in fictional situations and to identify with fictional characters in books, play or movies. The Empathic Concern subscale refers to the propensity to be concerned and feel compassion for other people. The Personal distress subscale measures the tendency to experience distress or discomfort in response to others' emotional distress. As concerns the SVO-Slider Measure, we analysed the first six primary items (discarding the nine secondary items as being less essential according to our hypotheses and not calculable for every participant). The score at the SVO-Slider Measure is provided in angle expressed in degrees: an angle less than -12.04° indicates the tendency to be competitive; between -12.04° and 22.45° the propensity to be individualist; between 22.45° and 57.15° the tendency to be prosocial; and greater than 57.15° the propensity to be altruistic. In order to test the differences in individual social characteristics between females and males, we statistically compared the scores at the four IRI subscales and at the Primary Items using the Mann-Whitney U test for two independent samples, with Gender (Female, Male) as between-subject factor.

For parametric ANOVA designs, the normality assumption was verified using the Shapiro-Wilk test and checking the skewness and kurtosis values of the distributions. The homogeneity of the variance-covariance matrix was verified using the Box's M test and the sphericity assumption was verified using Mauchly's sphericity test. Effect sizes were indexed using partial Eta-squared (η_{2p}). Post-hoc comparisons were performed using Tukey's HSD test.

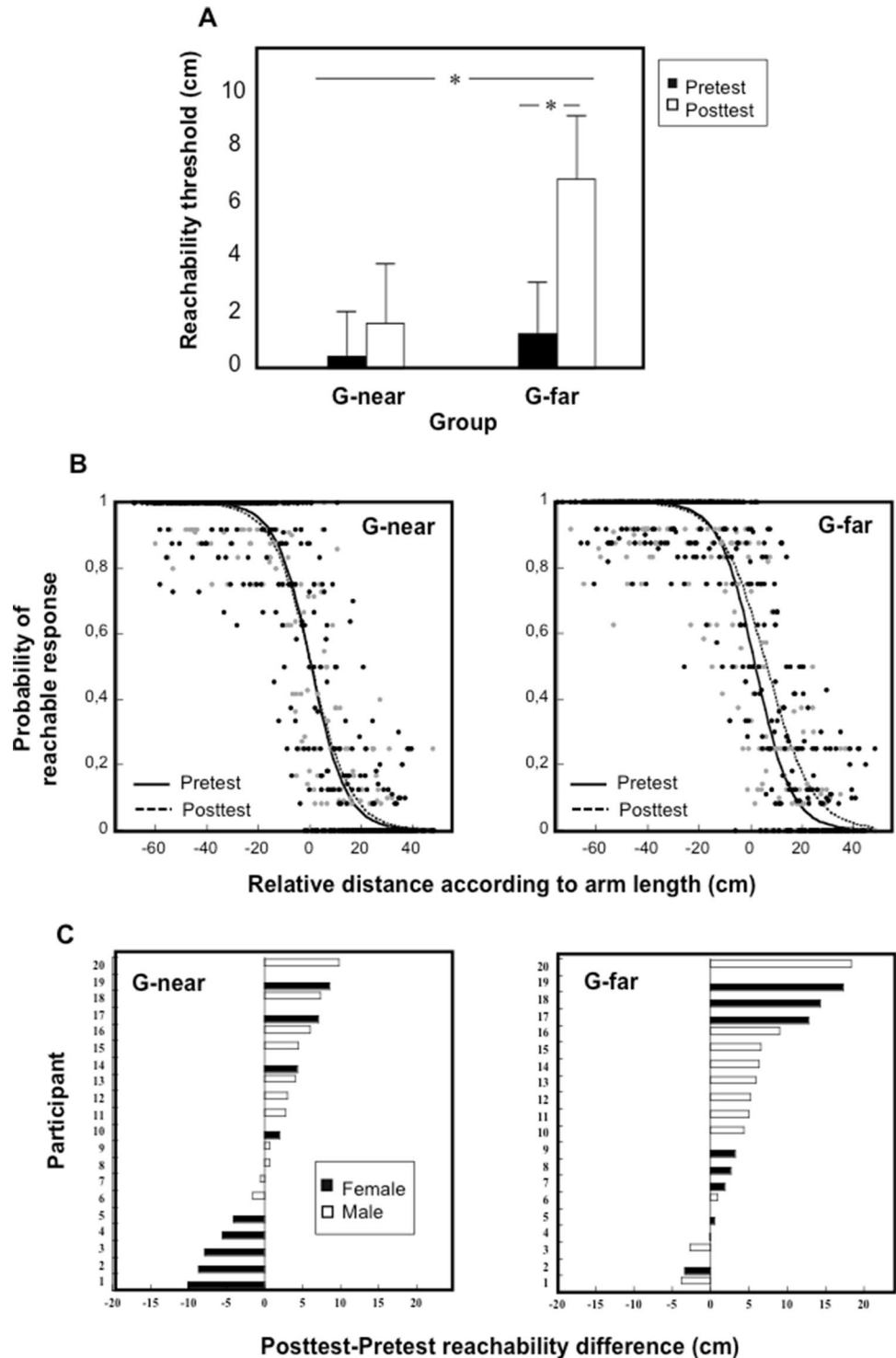
Significance threshold was set at $\alpha=0.05$ for all statistical tests and at $\alpha=0.10$ for tests validating the assumptions necessary to the application of parametric tests (normality, sphericity, homogeneity of variance–covariance matrices).

Results

Reachability judgment task

As concerns the goodness of fit in logistic regressions, MacFadden's pseudo-R squared was on average 0.62 (SD=0.16).

Fig. 2 **a** Mean relative pretest and posttest reachability threshold according to arm length (cm) as a function of the Group (G_{near} , G_{far}). Error bars represent standard errors. Stars indicate significant differences between groups in the posttest–pretest reachability threshold change ($*p < 0.05$). **b** Group logit fit as function of Group (G_{near} , G_{far}) and Session (Pretest, Posttest). Dots represent individual answers for both female and male participants. **c** Individual posttest–pretest differences of reachability threshold (cm) as a function of the Group (G_{near} , G_{far}). Positive and negative signs indicate, respectively, an expansion and shrinkage of PPS representation



In the pre-test, participants overestimated their actual reachability threshold on average by 1.28 cm ($SD=6.70$ cm), which corresponded to an overestimation of arm-length of 2% ($M=72.50$ cm, $SD=5.00$ cm). Statistical analysis revealed a significant Session \times Group interaction ($F(1, 36)=5.19, p=0.029, \eta^2p=0.13$, see Fig. 2a). Pairwise comparisons showed that reachability threshold increased in the posttest relative to the pretest in G_{far} (pretest: $M=1.21$ cm, $SD=7.74$ cm and posttest: $M=6.37$ cm, $SD=9.40$ cm, $p=0.003$) but not in G_{near} (pretest: $M=0.45$ cm, $SD=6.77$ cm and posttest: $M=1.45$ cm, $SD=8.97$ cm, $p=0.878$, see Fig. 2b). Neither the Gender principal effect ($F(1, 36)=0.52, p=0.475$) nor the interaction effects Gender \times Group ($F(1, 36)=1.32, p=0.258$), Session \times Gender ($F(1, 36)=1.16, p=0.288$) and Gender \times Group \times Session ($F(1, 36)=1.94, p=0.172$) were significant. These results suggest that the reachability threshold was not statistically different between females and males in G_{near} (females:

$M=-0.78$ cm, $SD=5.81$ cm and $M=-2.37$ cm, $SD=8.75$ for pretest and posttest, respectively; males: $M=1.45$ cm, $SD=7.59$ cm and $M=4.58$ cm, $SD=8.22$ cm for pretest and posttest, respectively) as well as in G_{far} (females: $M=1.62$ cm, $SD=6.47$ cm and $M=7.11$ cm, $SD=8.30$ cm, for pretest and posttest, respectively; males: $M=0.87$ cm, $SD=8.95$ cm and $M=5.76$ cm, $SD=10.57$ cm, for pretest and posttest, respectively). Figure 2c shows individual posttest–pretest reachability threshold differences as function of gender and group.

Stimuli selection task

For a descriptive purpose, we calculated the frequency of stimuli selected at each location, by dividing the number of times each cell with a stimulus was selected on the touchscreen table by the number of times this cell contained a stimulus. Figure 3a, b shows the frequency of stimuli

Fig. 3 **a** Density maps of the targets selected by the participants in G_{near} and G_{far} in the stimuli-selection task. The rectangles represent the distribution grid composed of 42 cells. The frequency of selection of a given stimulus location is associated with a colour bar ranging from blue (rare selection) to red (frequent selection). The plots represent participants' performances according to their position on the touchscreen table: rows 1, 2 and 3 correspond to G_{near} 's proximal space and rows 4, 5, 6 to G_{far} 's proximal space. **b** Density maps of the stimuli selected by male and female participants in G_{near} and G_{far} . The red bar indicates the participants' location

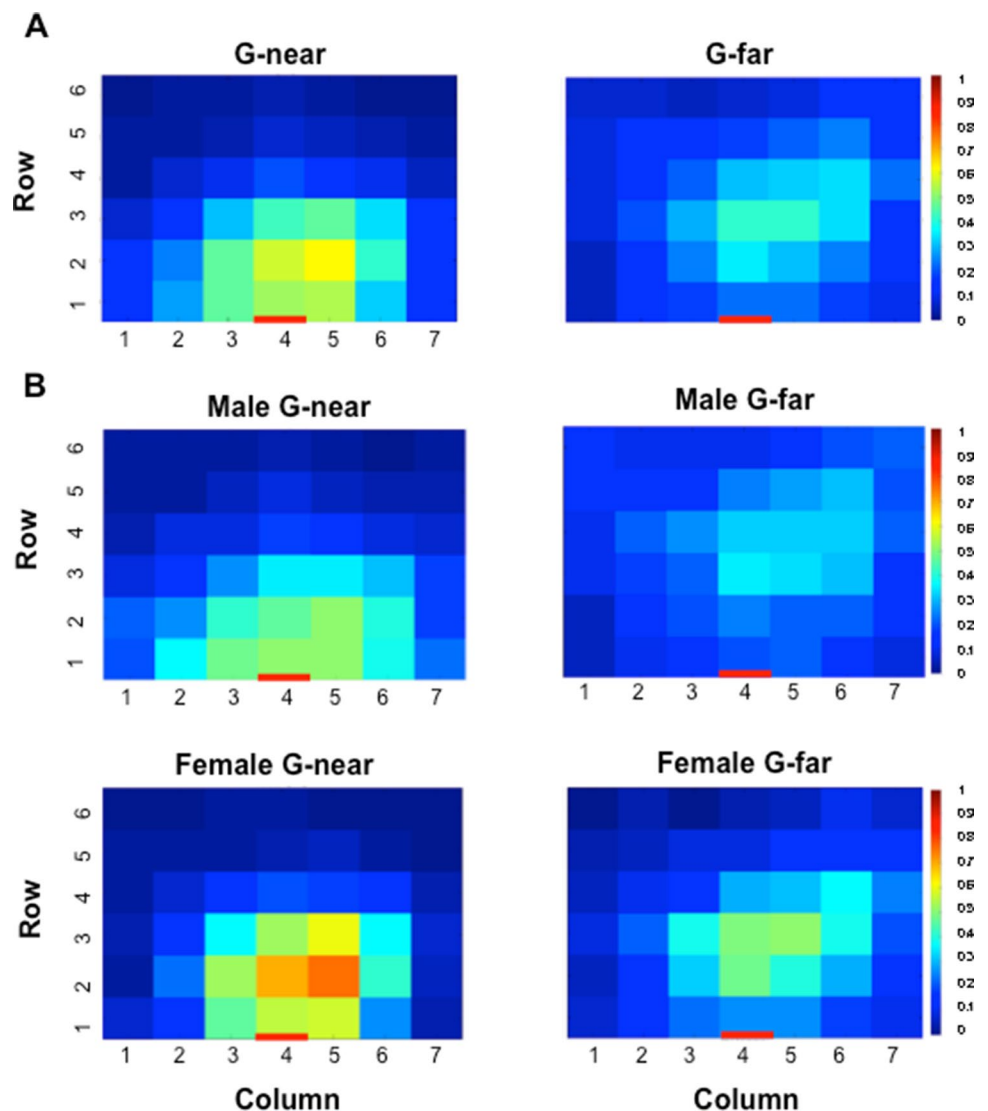


Table 1 Number of stimuli selected during the stimuli-selection task by all participants in each row as a function of the Group (G_{near} , G_{far}), the Gender (Female, Male) and percentage of stimuli selected in the proximal area (rows 1–2), the central area (rows 3–4) and the distal area (rows 5–6)

Group	Gender	Row					
		1	2	3	4	5	6
G_{near}	Female	488	615	487	176	50	20
			60%		36%		4%
G_{near}	Male	751	690	476	192	91	44
			64%		30%		6%
G_{far}	Female	278	431	529	351	173	74
			39%		48%		13%
G_{far}	Male	258	347	470	493	419	266
			27%		43%		30%

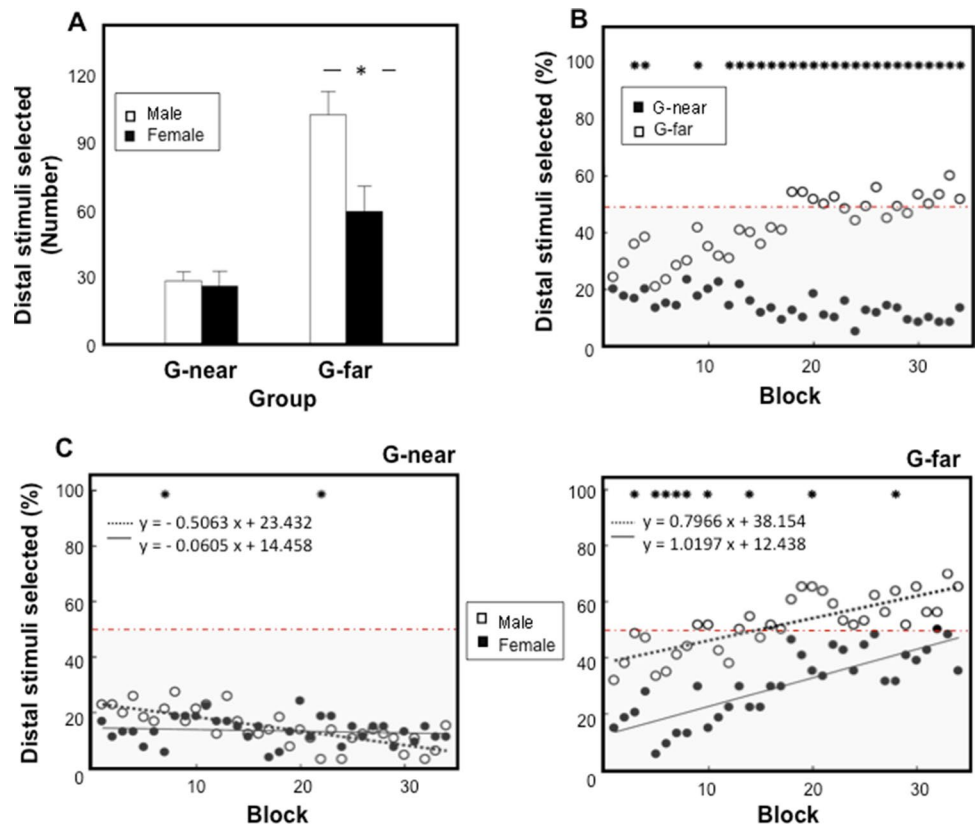
The percentages are calculated in relation to the total number of stimuli selected, equal to 1836 for females (6 stimuli × 34 blocks × 9 participants) and to 2244 for males (6 stimuli × 34 blocks × 11 participants)

selected at each location according to the group and gender and offers a visualization of the areas of the touch-screen table where participants acted predominantly. Table 1 shows the number of stimuli selected by females and males, in both G_{near} and G_{far} , as well as their percentage relative to the total number of stimuli selected, after pooling rows 1–2 (proximal area), rows 3–4 (central area) and 5–6 (distal area).

In order to better account for the invasive behaviour characterising the participants, we contrasted the number of distal stimuli (localised beyond the middle of the table) selected in G_{near} and G_{far} , taking into account the gender.

Permutation-based ANOVA revealed a significant Group ($p < 0.001$) principal effect. Post-hoc comparisons showed that as a whole, the number of distal stimuli selected in G_{far} ($M = 86.25$, $SD = 40.76$) was broader than the number of distal stimuli selected in G_{near} ($M = 28.65$, $SD = 16.84$, $z = -4.30$, $p < 0.001$). The Gender principal effect was also significant ($p = 0.011$), as well as the Group × Gender interaction ($p = 0.023$, see Fig. 4a). Post-hoc comparisons relating to the interaction revealed that in G_{near} , no statistically significant difference emerged between males and females ($M = 29.73$, $SD = 14.24$ and $M = 27.33$, $SD = 20.41$,

Fig. 4 **a** Number of distal stimuli selected on average by males and females in G_{far} and G_{near} . Error bars represent standard errors. Stars indicate significant differences ($p < 0.05$). **b** Percentage of distal stimuli selected across the 34 blocks in G_{far} and G_{near} . The two groups diverged consistently from the 12th block on. **c** Percentage of distal stimuli selected across the 34 blocks by male and female participants in G_{far} and G_{near} . For G_{far} and G_{near} . The regression equations express the linear relationship between the blocks and the percentage of distal stimuli selection is displayed. Stars indicate significant differences revealed by permutation tests. The grey area in the graph represents the proximal area on the touch-screen table, and the horizontal red dotted line indicates when the stimuli are equivalently selected in the proximal space and in the distal space



respectively, $z = -0.31$, $p = 0.763$), the former crossing the middle line 15% of the time and the latter 13%. In G_{far} , male participants selected on average more distal stimuli than female participants ($M = 106.27$, $SD = 34.91$ and $M = 61.78$, $SD = 34.62$, respectively, $z = -2.43$, $p = 0.012$), crossing the middle of the screen and invading their confederate's space 52% of the time compared to 30% in females.

Regarding the change of selection performance between the beginning and the end of the stimuli-selection task, statistical analysis showed a significant Block \times Group interaction ($p = 0.001$). As revealed by post hoc comparisons, the number of distal stimuli selected was, on average, statistically higher in the last blocks compared to the first blocks in G_{far} ($M = 3.30$, $SD = 1.73$ and $M = 1.78$, $SD = 1.63$, respectively, $z = -2.62$, $p = 0.004$), but not in G_{near} ($M = 0.06$, $SD = 0.78$ and $M = 1.08$, $SD = 0.92$, respectively, $z = 0.19$, $p = 0.445$). Furthermore, statistical analysis revealed a gender principal effect ($p = 0.021$), with males globally selecting more distal stimuli than females ($M = 2.19$, $SD = 1.73$ and $M = 1.32$, $SD = 1.23$, respectively, $z = -2.42$, $p = 0.017$). This effect was modulated by neither the Group nor the Block (Gender \times Group \times Block: $p = 0.593$, Gender \times Group: $p = 0.057$, Gender \times Block: $p = 0.456$).

When analysing the change of selection performance across all the blocks, permutation tests showed that G_{near} and G_{far} 's strategy diverged consistently from the 12th block (see Fig. 4b). Concerning the gender effect (see Fig. 4c), in G_{near} regression analysis revealed that male participants selected progressively more proximal stimuli across the blocks ($R = -0.75$, $F(1,32) = 41.73$, $p < 0.001$), which was not observed in female participants ($R = -0.13$, $F(1,32) = 0.53$, $p = 0.473$). However, no specific pattern in the change of strategy across block emerged from permutation tests when contrasting males and females. Within G_{far} , regression analysis showed that both female and male participants selected more distal stimuli across blocks (respectively, $R = 0.78$, $F(1,32) = 51.77$, $p < 0.001$ and $R = 0.82$, $F(1,32) = 65.15$, $p < 0.001$), although only male participants consistently selected an average of more than 50% of the stimuli in the distal space (see Fig. 4c). In line with these results, permutation tests revealed that male participants' strategy statistically differed from the female participants' one from the third block on and repeatedly all along the blocks. This suggested a tendency for male participants to invade their confederate's space sooner and more consistently than female participants. All Z and p values for each block permutation test are reported in Table 2.

In agreement with the design of the experiment, and participants' natural preference for proximal space, results showed that the number of reward-yielding stimuli obtained depended on the group, with G_{near} obtaining 2840 (70%) and G_{far} 2095 (51%) reward-yielding stimuli. This distribution was statistically different from the theoretical distribution

(75% for G_{near} and 25% for G_{far}) that would result if participants had selected stimuli only in their proximal space ($z = -7.38$, $p < 0.001$ for G_{near} , $z = 26.85$, $p < 0.001$ for G_{far}).

Relation between change in reachability threshold, reaching actions' amplitude and amount of rewards obtained

Correlation analysis indicated that the reported change of PPS representation was related to the amount of rewards obtained rather than to the change in the characteristics of the motor activity. Indeed, when correlating the posttest–pretest difference of reachability threshold to the number of rewards obtained by each participant, gender and group considered together, Spearman's correlation coefficient between the two variables was 0.33 ($p = 0.039$) when considering the rewards obtained after selecting stimuli in the distal space. In contrast, when correlating the posttest–pretest difference in reachability threshold to the average amplitude of the selection actions, the Spearman's correlation coefficient between the two variables was 0.29 and not significant ($p = 0.067$).

Individual social characteristics measures

As concerns the results in the IRI scale, statistical analysis did not show any significant difference between female and male participants at the Perspective Taking subscale ($U = 710$, $p = 0.214$; $M = 25.7$, $SD = 4.07$ for females and $M = 25.1$, $SD = 4.20$ for males), at the Fantasy subscale ($U = 718$, $p = 0.238$; $M = 26.8$, $SD = 5.37$ for females and $M = 26.2$, $SD = 5.64$ for males) and at the Empathic Concern subscale ($U = 774$, $p = 0.433$; $M = 26.0$, $SD = 4.17$ for females and $M = 26.0$, $SD = 3.55$ for males). On the contrary, statistical analysis showed a significant gender difference at the Personal Distress subscale ($U = 234$, $p < 0.001$) with females reporting a higher score than males ($M = 25.2$, $SD = 4.22$ and $M = 18.6$, $SD = 4.79$, respectively).

As concerns the results at SVO-Slider Measure, four participants (3 females and 1 male) resulted individualistic (angle comprised between -12.04° and 22.45°) while the rest of participants resulted prosocial (angle comprised between 22.45° and 57.15°). Furthermore, males showed higher angles than females ($M = 35.0$, $SD = 7.37$ and $M = 31.1$, $SD = 9.92$, respectively), resulting statistically more prosocial than females ($U = 610$, $p = 0.037$).

Discussion

The aims of the present study were to investigate (1) how two face-to-face confederates actively explore a shared space when the constraints related to actions' outcome prompt the invasion of one of the confederate's space; (2) how does such

Table 2 Detailed results of multiple comparisons based on permutation tests (z , p , % of distal stimuli) for G_{far} versus G_{near} , Females versus Males in G_{far} , Females versus Males in G_{near}

Block	G_{far} versus G_{near}				Females versus Males— G_{far}				Females versus Males— G_{near}			
	z		p		Distal stimuli (%)		z		p		Distal stimuli (%)	
	G_{far}	G_{near}	G_{far}	G_{near}	Females	Males	G_{far}	G_{near}	Females	Males	Females	Males
1	0.47	0.711	24.17	20.00	-1.14	0.276	14.81	31.82	-0.58	0.648	16.67	22.73
2	1.39	0.203	29.17	17.50	-1.35	0.201	18.52	37.88	-1.35	0.246	11.11	22.73
3	2.42	0.017	35.83	16.67	-2.18	0.033	20.37	48.48	-0.93	0.495	12.96	19.70
4	2.18	0.033	38.33	20.00	-1.31	0.214	27.78	46.97	-1.91	0.078	12.96	25.76
5	1.12	0.328	20.83	13.33	-2.44	0.015	5.56	33.33	-1.51	0.162	7.41	18.18
6	1.21	0.287	23.33	15.00	-2.13	0.036	9.26	34.85	-0.54	0.636	12.96	16.67
7	1.90	0.071	28.33	14.17	-2.10	0.043	12.96	40.91	-2.81	0.004	5.56	21.21
8	0.79	0.493	30.00	23.33	-2.17	0.027	12.96	43.94	-0.95	0.380	18.52	27.27
9	2.94	0.004	41.67	17.50	-1.72	0.110	29.63	51.52	0.25	0.830	18.52	16.67
10	1.75	0.097	35.00	20.00	-2.49	0.013	14.81	51.52	-0.34	0.835	18.52	21.21
11	1.16	0.299	31.67	22.50	-1.80	0.070	18.52	42.42	-0.06	1.000	22.22	22.73
12	2.09	0.042	30.83	14.17	-1.34	0.202	22.22	37.88	0.46	0.740	16.67	12.12
13	2.16	0.038	40.83	21.67	-1.45	0.157	29.63	50.00	-0.96	0.383	16.67	25.76
14	2.65	0.008	40.00	15.83	-2.24	0.027	22.22	54.55	-0.22	0.854	14.81	16.67
15	2.81	0.004	35.83	11.67	-1.77	0.095	22.22	46.97	-0.15	1.000	11.11	12.12
16	2.93	0.004	41.67	13.33	-1.47	0.176	29.63	51.52	0.30	0.860	14.81	12.12
17	3.08	0.001	40.83	9.17	-1.20	0.239	29.63	50.00	-1.50	0.208	3.70	13.64
18	3.98	0.000	54.17	12.50	-1.08	0.308	46.30	60.61	-1.30	0.259	5.56	18.18
19	4.35	0.000	54.17	10.00	-1.78	0.081	40.74	65.15	0.95	0.381	12.96	7.58
20	3.52	0.000	51.67	18.33	-2.26	0.028	35.19	65.15	1.20	0.256	24.07	13.64
21	3.63	0.000	50.00	10.83	-1.82	0.086	33.33	63.64	0.08	1.000	11.11	10.61
22	3.98	0.000	52.50	10.00	-0.96	0.385	44.44	59.09	2.20	0.023	18.52	3.03
23	3.59	0.000	48.33	15.83	-0.83	0.443	42.59	53.03	0.59	0.693	18.52	13.64
24	3.84	0.000	44.17	5.00	-1.03	0.344	35.19	51.52	1.02	0.459	7.41	3.03
25	3.63	0.000	49.17	12.50	-0.55	0.608	44.44	53.03	0.71	0.578	14.81	10.61
26	4.26	0.000	55.83	11.67	-1.06	0.320	48.15	62.12	-0.13	1.000	11.11	12.12
27	3.12	0.002	45.00	14.17	-1.64	0.114	31.48	56.06	0.13	1.000	14.81	13.64
28	3.72	0.000	49.17	13.33	-2.32	0.021	31.48	63.64	0.36	0.854	14.81	12.12
29	4.18	0.000	46.67	9.17	-0.88	0.423	40.74	51.52	-0.56	0.771	7.41	10.61
30	4.46	0.000	53.33	8.33	-2.02	0.051	38.89	65.15	1.36	0.301	12.96	4.55
31	4.12	0.000	50.00	10.00	-1.01	0.377	42.59	56.06	-0.20	1.000	9.26	10.61
32	4.28	0.000	53.33	8.33	-0.44	0.715	50.00	56.06	1.66	0.184	14.81	3.03
33	4.70	0.000	60.00	8.33	-1.61	0.133	48.15	69.70	0.82	0.611	11.11	6.06
34	3.62	0.000	51.67	13.33	-1.95	0.060	35.19	65.15	-0.47	0.713	11.11	15.15

behaviour alter participants’ PPS representation; and (3) whether the observed experimental effects are modulated by the participants’ gender. For this purpose, we probed participants’ PPS representation through a reachability judgment task before and after taking part in a stimuli-selection task performed cooperatively with a confederate. The experimental manipulation consisted in increasing for one participant and decreasing for the other participant of a dyad the probability to select a reward-yielding stimulus when acting in the proximal space.

The first important result obtained in the present study concerns the impact of the biased spatial distribution of the

reward-yielding stimuli on the exploration of the shared action space. Initially, participants spontaneously selected stimuli in their respective proximal space, confirming thus previous observations (e.g., Coello et al., 2018). Afterwards, the selection behaviour changed across the blocks of trials: without being aware of it, participants were attracted by the area in which the probability of selecting a reward-yielding stimulus was higher. Specifically, they progressively acted more distally when the probability to select a reward-yielding stimulus was higher in the distal space, and more proximally when the probability to select a reward-yielding stimulus was higher in the proximal space. As discussed

before (Coello et al., 2018) and supported by the correlation analysis, this indicates that participants were sensitive to the probability of performing a successful action in relation to the distribution of reward-yielding stimuli, reflecting thus non-conscious learning of environmental regularities. Accordingly, these results expand the findings of previous studies on reward effect on attention (Anderson, 2013; Chelazzi, Perlato, Santandrea, & Della Libera, 2013; Jiang, Swallow, Won, Cistera, & Rosenbaum, 2015) and ocular control (Camara, Manohar, & Husain, 2013; Hickey & van Zoest, 2012) to object-oriented manual actions.

A remarkable outcome of the present study was that participants invaded the space of their confederate when the probability of succeeding an action was higher in the confederate's proximal space. Such invading behaviour was not fully expected. Indeed, it was not observed in our previous study (Coello et al., 2018), where the probability to select a reward-yielding stimulus was equally spread across the whole action space. This observation was in line with the assumption that in a social context, for a defensive purpose, people tend to adjust the representation of their own PPS so as to avoid interfering with others' PPS (Coello & Iachini, 2016; Fujii, Hihara & Iriki, 2007; Kennedy et al., 2009; Szpak et al., 2015; Teneggi et al., 2013), except when the confederate has a passive attitude (Coello et al., 2018). Moreover, Coello et al. (2018) showed that when participants performed the stimuli-selection task alone, the behavioural adaptation leading them to act in the distal space (when associated with more reward-yielding stimuli) occurred rapidly, i.e. within the first 20 stimuli selections. In the present study, instead, the change of strategy occurred consistently following approximately 85 stimuli selections. The fact that behavioural adaptation in the present study required more action repetition indicated that the social context interfered with the optimisation of the stimuli selection strategy. Specifically, the propensity to avoid others' PPS appeared here to be in conflict with the natural spatial exploration for reward search in the cooperative stimuli-selection task. As a consequence, selecting reward-yielding stimuli in the distal space was delayed when this required invading others' PPS. In the same vein, previous studies in monkeys showed that the brain regions involved in motor related visual processing (namely, pre-frontal and parietal cortices) adapted their response properties according to the social context: neuronal activity depended on whether the location of two monkeys enabled them to reach for the same food item, and was also modulated by the social status of the monkeys, by discarding the stimuli near the more dominant monkey (Fujii et al., 2007; Fujii, Hihara, Nagasaka, & Iriki, 2009). This suggests that the same object can be included or not in the PPS, depending on its value and the social context.

The second important result of the present study concerns the gender difference that emerged in relation to the

invasion behaviour, with males invading their confederate's space more often than females. One possible explanation could rely on the difference in arm length between males and females, the former having longer arms than the latter. However, this interpretation can be ruled out, because our analysis was based on the number of times participants acted beyond the middle of the touch-screen table, which corresponded to 25 cm, a distance that was largely within an arm's reach for both males and females. The gender effect might thus rely on other variables, such as higher order social factors. Previous research highlighted indeed differences in the regulation of social distance depending on gender (Fisher, & Byrne, 1975; Iachini et al., 2016). For instance, when assessing comfortable interpersonal distance between males and females, it was found that male–male pairs prefer larger inter-personal distances than female–female pairs (Bailey, Hartnett, & Gibson, 1972; Iachini et al., 2016). This was supposed to be in relation with the females' tendency to be more affiliative (Uzzel, & Horne, 2006) and empathic (Christov-Moore et al., 2014), and more sensitive to non-verbal behaviour (Sokolov, Krüger, Enck, Krägeloh-Mann, & Pavlova, 2011), resulting in shorter interpersonal distances (Bailenson, Blascovich, Beall, & Loomis, 2001; Baxter, 1970; Hartnett, Bailey, & Gibson, 1970; Liebman, 1970; Patterson & Edinger, 1987). Moreover, studies in social psychology revealed that whereas females are more inter-personally oriented, males are more group-oriented (Baumeister & Sommer, 1997; Gabriel & Gardner, 1999), and engage more frequently in competitive between-group interactions than females (Pemberton, Insko, & Schopler, 1996; Vugt, Cremer, & Janssen, 2007). These differences could provide a possible interpretative framework to account for the gender effect observed in the present study. We can indeed speculate that females would invade less their confederate's space because they are potentially more sensitive to PPS intrusion's consequences, which is in line with females' higher Personal Distress score obtained in the IRI scale. In contrast, males would neglect this aspect and invade other's PPS because this constitutes a more appropriate cooperative strategy to get a higher score. This is in line with males' higher prosocial tendency revealed by the SVO-Slider Measure test. Furthermore, differences were reported in previous studies concerning reward sensitivity in males and females, with females outperforming males in tasks associated with immediate compared to delayed rewards (e.g., Byrne & Worthy, 2015). This suggests that males' behaviour in the present study cannot be simply explained by a better environmental learning than females. Considering these results, it would be interesting to analyse in a further study how male and female participants would behave in a situation where dyads have to compete instead of cooperate.

Finally, a third important result concerns the change of PPS representation following the stimuli-selection task

performed in a shared space. Participants for whom the probability of obtaining a reward was higher in the distal space showed an increase of their PPS representation. On the contrary, participants for whom the probability of obtaining a reward was higher in their proximal space did not show any specific change of PPS representation. This indicates that PPS representation depends not only on the body state and the action system but also on action outcome, confirming thus previous empirical findings (Coello et al., 2018, 2012). Indeed, in Coello et al. (2018), participants who had a 75% chance of selecting a reward-yielding stimulus in their proximal or distal space showed instead a decrease (−2.49 cm) or increase (+2.35 cm) of PPS, respectively. An increase of PPS was also observed in a cooperation context when the distribution of reward-yielding stimuli was unbiased (+3.19 cm). In the present study, we found a broader effect of cooperation context on PPS when reward-yielding stimuli were biased towards the distal (+5.16) rather than the proximal space (+1.01 cm). It is worth noting that the change of PPS was related to the amount of reward obtained and not the change in movement amplitude in the stimuli selection task. Taken as a whole, these results suggest that the information drawn from observing successful actions of conspecific combined with the biased distribution of reward-yielding stimuli modulated the effect of sharing action space with confederates on PPS representation. More specifically, participants having 75% of reward-yielding stimuli located in their distal space would show a higher increase of PPS representation because the effect of the reward distribution and of sharing an action space with someone else would add up. On the contrary, for participants having 75% of reward-yielding stimuli located in their proximal space, these two effects would have combined and canceled. Thus, the decrease of PPS representation induced by the presence of more reward-yielding stimuli in the near space would have been counterbalanced by the social context. Assuming that this interpretation is correct, this would confirm that PPS representation depends on the outcome of both self-generated and observed motor actions as suggested in previous study (Coello et al., 2018). Finally, no statistically significant difference emerged between males and females, even though they appeared to behave differently in the stimuli-selection task. Further studies could enrich these results by analysing, for instance, a situation where one participant is observing while the other is acting in a reward-biased action space.

In conclusion, the present study revealed that (1) expected rewards in the environment in relation to motor actions combine with social interaction context; (2) these factors influence both PPS representation and exploration, prompting people to invade others' space, and (3) this interaction would work differently between males and females. Taken as a whole, our results enrich the theoretical debate on PPS representation, providing evidence in favour of the idea that

PPS representation stems from the integration of multiple factors including the agent with his/her physical characteristics and possibilities to act in the environment, the stimuli's value and the interaction with other individuals within a shared space. Furthermore, it paves the way for new research avenues in relation to gender differences in acting within PPS and adjusting its representation in social interaction contexts.

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