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Report

Social Modulation of Peripersonal Space Boundaries

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Summary

The space around the body, i.e., peripersonal space (PPS), is conceived as a multisensory-motor interface between body and environment. PPS is represented by frontoparietal neurons integrating tactile, visual, and auditory stimuli occurring near the body [1-7]. PPS is plastic, because it extends by using a tool to reach far objects [8–10]. Although interactions with others occur within PPS, little is known about how social environment modulates it. Here, we show that presence and interaction with others shape PPS representation. Participants performed a tactile detection task on their face while concurrent task-irrelevant sounds approached toward or receded from their face. Because a sound affects touch when occurring within PPS [6, 10-12], we calculated the critical distance where sounds speeded up tactile reaction time as a proxy of PPS boundaries. Experiment 1 shows that PPS boundaries shrink when subjects face another individual, as compared to a mannequin, placed in far space. Experiment 2 and 3 show that, after playing an economic game with another person, PPS boundaries between self and other merge, but only if the other behaved cooperatively. These results reveal that PPS representation is sensitive to social modulation, showing a link between low-level sensorimotor processing and high-level social cognition.

Results and Discussion

In order to measure the extent of peripersonal space (PPS) representation we used an audiotactile interaction task. Subjects responded as fast as possible to a tactile stimulus administered on their face, while task-irrelevant sounds were presented, giving the impression of a sound source either approaching toward (IN sounds) or receding from (OUT sounds) their bodies. Tactile stimuli were given at five different temporal delays from sound onset, implying that they were processed when sounds were perceived at five possible different distances from the subject (ranging from D1, very far, to D5, very close; see Figure 1). We have repeatedly shown that a sound boosts tactile reaction times (RTs) when presented close to, but not far from, the stimulated body part, that is within, and not outside, the PPS [6, 10, 11]. By

administering dynamic sounds, here we measured the critical distance from the subjects' bodies, where sounds affected tactile RTs, along a continuum between near and far space: this point can be considered as the boundary of PPS representation. We tested how PPS changes as a function of the presence of (experiment 1), and the interaction with (experiment 2 and 3), others.

Experiment 1: PPS Representation as a Function of the Presence of Others

To investigate whether the presence of another person modulates PPS representation, participants (n = 18) performed the audiotactile interaction task while facing either another person (Other condition), or a mannequin (Mannequin condition) in two within-subjects conditions, run in counterbalanced order across participants. The other person and the mannequin were placed at a distance of 100 cm from the participant, i.e., close to a far loudspeaker from where approaching sounds originated and receding sounds terminated.

Mean RTs to the tactile stimulus administered at the different perceived sound distances were calculated for IN and OUT sounds and compared between the two conditions of facing the other or the mannequin, by means of an ANOVA with factors Distance (D1-D5, with D1 = farthest Distance and D5 = closest Distance), Sound (IN, OUT), and Condition (Other, Mannequin). The critical three-way interaction was significant (F[4, 44] = 2.70; p < 0.05). Thus, two separated ANOVAs were conducted for IN and OUT sounds, with the factors distance and condition. For the IN sound, the interaction Distance \times Condition was significant (F[4, 44] = 4.54; p < 0.01), suggesting that RTs were differently modulated depending on the perceived position of sound in space, as a function of whether subjects faced the mannequin or the other person. As Figure 2 shows, in the mannequin condition RTs were significantly faster when concurrent sounds were perceived at D2, D3, D4, and D5, as compared to when sounds were perceived at D1 (p < 0.001 in all cases, Newman-Keuls corrected; effect present in 14 out of 18 subjects). Thus, the estimated PPS boundaries were located between D1 and D2. In contrast, in the Other condition, RTs were faster when sounds were perceived at D3, D4, and D5, as compared to when sounds were perceived at D2 and D1 (p < 0.05 in all cases, Newman-Keuls corrected; effect present in 15 out of 18 subjects), thus indicating that PPS boundaries were located between D2 and D3, that is, in a spatial position closer to the subject as compared to the Mannequin condition. Indeed, RTs at D2 and D3 were faster in the Mannequin than in the Other condition (p < 0.05 in all cases). No change in RTs was instead found for the farthest (D1, p = 0.68) or the closest (D4 and D5, p > 0.18 in all cases) distances. No significant effects were found in the case of OUT sounds, indicating that RTs in this condition were less affected by the position of sounds in space (see Table S1 available online).

A sound localization experiment (Figure S1) excluded that the differential effect found for IN and OUT sounds was due to differences in the way subjects localized the two sound sources at corresponding temporal delays (see Supplemental Information and Figure S1). Rather, the stronger spatially dependent

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Physical Distance

Figure 1. Experimental Paradigm

Participants responded to a tactile stimulus on their face, while task-irrelevant sounds either approached toward (IN sounds) or receded from (OUT sounds) their face. On each trial, the tactile stimulus was delivered at one out of five possible different delays from sound onset, so that it was processed when the sound was perceived at a different distance from the subject's body (from D1, very far, to D5, very close; see Figure S1 for results from a sound localization experiment).

effect shown for the IN sound is coherent with previous findings showing higher relevance of looming stimuli for PPS neurons [12–15]. A further control experiment (experiment S2) demonstrated that the social modulation of audiotactile interaction shown in experiment 1 was specifically related to a representation of PPS, because no spatial modulation of multisensory integration due to the presence of the Other was found in an audio-visual interaction task not directly related to the body and the space around it (See Supplemental Information and experiment S2, as described in the Table S2 legend).

In sum, these findings show that PPS representation shrank when the far space was occupied by another person, as compared to when it was occupied by an artificial body-like object, suggesting that one's own PPS accommodates in the presence of others. Previous studies highlighted the behavioral function of PPS representation, which has been conceived as a space of interaction critical for triggering defensive [7, 16] or approaching [1, 17] behaviors. Most studies on PPS tested subjects processing artificial stimuli in neutral environments in absence of cospecifics. This is surprising, because the others often represent the most behaviorally relevant stimuli in the environment. Few previous findings suggest a "social" component in PPS representation. In monkey, bimodal neurons in the posterior parietal cortex respond to tactile stimuli on the animal's body and to visual stimuli presented close to the experimenter's body [18]. Homologous areas in humans respond to tactile stimuli on one's own face and to visual stimuli approaching another person's face [19]. Thus, some PPS neurons process events occurring not only within one's own PPS but also within the PPS of others. Heed et al. [20] recently showed that multisensory integration is modulated as a function of the presence and activities of others within one's own PPS. The present data extend

previous findings by showing that the presence of others also in the extrapersonal space shapes PPS representation, such that the presence of others structures the representation of space around oneself. As Deleuze said: "The other is neither an object in my field of perception, nor a subject who perceives me: it is first and foremost a structure of the perceptual field, without which this field as an ensemble would not function as it does" (see [21], pp. 356–357).

The role of others in modulating spatial representation is particularly evident if PPS is conceived as a space of interaction. The following experiments show that not only the presence of others but also the nature of interaction with others shapes PPS representation.

Experiments 2 and 3: PPS Representation as a Function of Interaction with Others

In experiment 2, a new group of 32 participants performed the audiotactile interaction task facing another subject, before and after performing with her an economic game with material gains. Each participant played the game once: subjects were randomly assigned to two between-subjects conditions, in which the other player (i.e., an actor previously unknown to the participant) was instructed to choose a game strategy yielding either equal payoffs (Cooperative game condition), or unequal payoffs (Noncooperative game condition) (see Figure 2 legend). Participants' ratings, acquired at the end of the experimental session, showed that the actor's strategy resulted in a positive valuation of Cooperative (fair) partners and in a negative valuation of Noncooperative (unfair) partners (see [22]) (see Supplemental Information and Table S3). In order to test how PPS representation varied before and after the game, as a function of the partner's game behavior, we ran an ANOVA on mean tactile RTs with the within-subjects factors of Distance (D1-D5), Sound (IN, OUT), Session (before and after the game), and the between-subjects factor Condition (Cooperative and Noncooperative). The four-way interaction was significant (F[4, 120] = 2.45; p < 0.05). Thus, we conducted two separate ANOVAs, one for each Condition.

In the Noncooperative game group, for the IN Sound, the main effects of Distance (F[4, 60] = 21.63, p < 0.00001) and Session (F[1, 15] = 13.12; p < 0.01) were significant, but not the two-way interaction (p = 0.10). Both before and after the game, RTs recorded when sounds were perceived at the farthest distances (i.e., D1 and D2) were significantly slower than those for sounds at the closest distances (i.e., D3, D4, and D5, p < 0.001 in all cases, Newman-Keuls corrected), thus suggesting that PPS boundaries were located approximately at the same spatial range as in experiment 1, in the Other condition. RTs for all sound distances were speeded up after the Noncooperative game as compared to before the game. Importantly, the critical point where sounds affected RTs did not change before and after the game (see Figure 3A). In the case of the OUT sounds, only a significant effect of Session (F[1, 15] = 7.82; p < 0.05) was found, showing, again, a general speeding effect in RTs after the Noncooperative game (see Table S1).

A different pattern of results was found in the Cooperative game condition. In case of IN sounds, the two-way interaction Distance × Session was significant (F[4, 60] = 4.20; p < 0.01). As Figure 3B shows, before the game, RTs varied as a function of the position of sounds in space, with slower RTs for the farther distances (D1 and D2), as compared to the closer distances (D3, D4, D5; p < 0.001 in all cases, Newman-Keuls corrected). Thus, the estimated boundary of PPS was located between

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Figure 2. PPS Boundaries as a Function of the Presence of Others in Experiment 1

Participants performed the audiotactile interaction task in two experimental conditions, facing either a mannequin (Mannequin condition), or another person (Other condition). The other person was an actor, a female, of approximately the same age as the participants, unknown to the participants. Two different actors took part in the experiments, one for each half of participants, in order to avoid any idiosyncratic effect due to the actor's appearance. The actors were requested to keep a neutral expression during the experiment and to look toward the participant's face, without any specific instruction about eye contact.

The figure shows mean RTs at different perceived sound distances (for the IN sound; see Table S1 for the OUT sound), corresponding to different times of tactile stimulus delivery, when participants faced the other person or the mannequin (error bars represent SEM). RTs at the different temporal delays have been fit with a sigmoid function. The sigmoid central point curve was computed as a measure of the temporal delay, i.e., the distance, at which sounds start affecting RTs and was analyzed in order to quantify PPS boundaries. The sigmoid central point was higher in the Other (1,566 ms, black vertical line) as

compared to the Mannequin (1,384 ms; dashed vertical line) condition (t[15] = -1.6; p < 0.05, one-tailed; two subjects were not included in the analysis due to bad fitting), meaning that PPS boundaries were closer to the participants when they faced the other person than when they faced the mannequin. See Supplemental Experimental Procedures for the sigmoid fitting analysis.

D2 and D3. On the contrary, after the game, PPS boundaries between near and far space vanished; there was no significant difference between RTs at any sound distance (p > 0.12 in all cases). Such an effect was due to faster RTs associated to sounds perceived at the farthest distances (i.e., D1 and D2) after the game as compared to before the game (p < 0.001 in all cases). No change in RTs was instead found for closest sound distances (D3, D4, and D5; p > 0.20 in all cases). Thus, after the Cooperative interaction, audiotactile integration increased for stimuli presented at the space occupied by the Other (far distances), and not for stimuli presented within one's own PPS (close distances). As a consequence, there were no more detectable PPS boundaries between the self and the other after the game, suggesting that the participant's PPS had extended as far as to include the space around the partner. No significant effect of Session (p = 0.19) or Interaction (p = 0.86) was found for the OUT sound (see Table S1).

In order to demonstrate that PPS representation extended after a fair interaction with the other, in experiment 3 we tested a new group of 20 subjects. Before and after they had played the economic game in the Cooperative condition, PPS boundaries were measured over a wider spatial range, as compared to experiment 2 (see Figure 4). Near and far loudspeakers were separated by 2 m, the participant was placed at the location of the near loudspeaker, whereas the actor was placed at 1 m from the participant, thus midway between the two loudspeakers. Seven, instead of five, temporal delays were used, so that sounds were perceived at seven different locations. IN sounds only were presented. Temporal delays were chosen so that the last five delays (D1-D5) corresponded to time intervals used in the previous experiments, whereas D-1 and D-2 occurred earlier along in the trial. In this way, when the tactile stimulus was administered at D-2 and D-1 the sound was perceived at further locations, as compared to the other intervals, beyond the actor.

An ANOVA with the factors Distance and Session (before and after the game) showed a significant two-way interaction (F[6, 114] = 2.21; p < 0.05): at D1, RTs after the game were faster than before the game (p < 0.05; p > 0.10 for all other comparisons, Newman-Keuls corrected), confirming that, after the Cooperative interaction, audiotactile integration increased for sounds presented at the position occupied by the Other. Crucially, RTs were modulated by the spatial location of sounds both before and after the game. However, the critical point where sounds began affecting tactile RTs was located at a further distance after the game than before the game (see Figure 3 and legend for statistical analysis). These results, together with those from experiment 2, indicate that PPS boundaries extended, after the Cooperative interaction, to include the space occupied by the Other.

In sum, the present study shows that PPS representation not only is sensitive to the presence of others but also is shaped by interactions with others and, more specifically, by valuation of other people's behavior during the interaction. Previous evidence shows a link between PPS representation and individuals' emotional states (e.g., claustrophobic fear [24]). Results from the present study are new in showing a direct link between PPS representation and feelings generated by interaction with others.

After an unfair, uncooperative interaction, subjects were generically faster to respond to tactile stimuli, independently from the position of concurrent sounds in space. Such a general speeding effect seems not directly related to spatial processing and is likely to depend on increased arousal following a socially unacceptable behavior of the other [25]. Prior evidence indicates that perceived unfairness of treatment arouses negative emotions [26, 27], increases skin conductance responses [28], and activates the insula [29] and the amygdala [30], brain areas consistently implicated in mediating negative emotional reactions and modulating arousal.

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A Non-cooperative game condition



Time of tactile stimulation (ms) - Perceived sound distance

Figure 3. PPS Boundaries when Facing a Noncooperative or a Cooperative Other in Experiment 2 Participants performed the audiotactile task before and after playing a one-shot bargaining game with a human partner via a computer interface. There were two game conditions, Cooperative and Noncooperative condition; half of the participants were randomly assigned to the Cooperative condition and the other half to the Noncooperative condition. The game was a modified version of the mutual advantage game [23], in which two human players interact with each other to earn real stakes. In the game, the participant moved always first by choosing either to earn €7 for herself, giving €3 to the confederate, and the game was over; or to cooperate, putting the confederate on the move. The confederate could either reciprocate cooperation, taking an option paying €10 to both players (Cooperative game condition); or defect, earning €7 for herself and giving €3 to the other player (Noncooperative game condition) (see Table S3). The figure shows mean RTs at different perceived sound distances (for the IN sound; see Table S1 for the OUT sound), corresponding to different times of tactile stimulus delivery (error bars represent SEM). (A) and (B) show, respectively. the results from the Noncooperative game condition and from the Cooperative game condition, before and after the game. RTs at the different temporal delays have been fit with a sigmoid function. In the Noncooperative game group, RTs were generically faster at any sound distances after the game than before the game. but PPS boundaries did not shift. The central sigmoid central point did not differ between the two sessions (before the game = 1,467 ms, black vertical line; after the game = 1,443 ms, dashed vertical line; t[13] = 0.32, p = 0.76; two subjects were excluded due to bad fitting). In the Cooperative game group. RTs were faster after the game than before the game only at the farthest sound distances (D1 and D2), that is at the space occupied by the cooperative other. See Supplemental Experimental Procedures for the sigmoid fitting analysis.

processed in order to implement defensive behavior [7] shifted beyond the space occupied by the cooperative other.

The present findings highlight a strong relationship between basic sensorimotor functions and complex social representations. They are consistent with approaches to cognition

Instead, after a fair, cooperative interaction, PPS boundaries between the self and the other merged. Such effect can be interpreted in the light of the nature of the interaction experience. According to Bakan, cooperative interactions are characterized by the concept of communion: "communion arises from strivings to integrate the self in a larger social unit through caring for others" [31]. The change in PPS representation found following the cooperative interaction seems to reflect Bakan's definition, grounded at the level of sensory-motor processes underlying spatial representations. As a consequence of cooperative, communal interaction, the boundaries of space within which external stimuli are more efficiently suggesting that mental processes are situated and embodied in our physical experiences [32–36]. In this view, high-level social and cognitive representations (e.g., cooperation) are immersed or recoded into the physical and perceptual experiences of the body, thereby providing concrete and rich feelings that facilitate prediction, evaluation, and social behavior.

Experimental Procedures

Participants

Seventy students, all females, to avoid effects due to gender differences, participated in experiment 1 (n = 18), experiment 2 (n = 32), and experiment

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Time of tactile stimulation (ms) - Perceived sound distance

Figure 4. Shift of PPS Boundaries after the Cooperative Interaction in Experiment 3

Participants played the economic game as in experiment 2, in the Cooperative condition only. PPS boundaries were measured before and after the game by means of a modified version of the audiotactile interaction task, as shown at bottom of the figure. Mean RTs at the seven different perceived sound distances, before and after the game, are reported (error bars represent SEM). RTs at the different temporal delays are fit with a sigmoid function. The sigmoid central point curve was computed as a measure of the temporal delay, i.e., the distance at which sounds start affecting RTs, and was analyzed in order to quantify PPS boundaries. The sigmoid central point was lower after the game (1,731 ms, black vertical line) than before the game (1,911 ms, dashed vertical line); (t[19] = 2.10; p < 0.05, onetailed), indicating that PPS boundaries extended toward the space occupied by the cooperative other.

3 (n = 20) (see Supplemental Experimental Procedures). All subjects gave their informed consent to participate in the study, which was approved by the Ethical Committee of the Department of Psychology, University of Bologna. The study was run in accordance with the Declaration of Helsinki.

PPS Task

Apparatus and Stimuli

During the experiment, subjects were comfortably seated beside a table, which the audiotactile apparatus was mounted on. This consisted of (a) two loudspeakers (hidden from view), one placed close to the participants' right cheek (at \sim 5 cm), the other one placed at a distance of \sim 100 cm from the near loudspeaker, thus far from the participant; and (b) a constant-current electrical stimulator controlling a pair of neurological electrodes, attached on the participant's right cheek.

Auditory stimuli were samples of pink noise of 3,000 (Experiments 1 and 2) or 4,000 (experiment 3) ms duration, whose intensity was manipulated in order to generate two kinds of sounds: IN sounds gave the impression of a sound source moving from the far to the near loudspeaker, i.e., toward the subject; OUT sounds gave the impression of a sound source moving in the opposite direction, i.e., receding from the subject [37, 38]. During each trial, either an IN or an OUT sound was presented, while, in ~77% of the trials, subjects also received a tactile stimulus on their right cheek. The remaining trials were catch trials with auditory stimulation only. Subjects were asked to respond vocally as fast as possible to the tactile target, when present, trying to ignore concurrent sounds. Tactile RTs were recorded. (See Supplemental Experimental Procedures.)

Design and Procedure

The tactile stimulus was delivered at different temporal delays from the onset of the auditory stimulus, so that touch was processed when the sound was perceived at different locations with respect to the subject's body (see Figure 1A and Supplemental Information).

In experiment 1, participants performed the audiotactile interaction task in two experimental conditions, facing either a mannequin (Mannequin condition) or another person (Other condition).

In experiment 2 and experiment 3, participants performed the audiotactile task before and after playing a modified version of the mutual advantage game [23]. Subjects were confronted either with a fair and cooperatively acting confederate or with a confederate who was unfair and acted not cooperatively. At the end of the experiment, participants were asked to fill a questionnaire assessing their feelings about the game and to complete the Davis's Interpersonal Reactivity Index (IRI) [39] (see Supplemental Information). Finally, they purchased different products, according to the monetary outcome earned during the game, and were debriefed.

Supplemental Information

Supplemental Information includes one figure, three tables, and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2013.01.043.

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