Reshaping the Peripersonal Space in Virtual Reality

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Abstract

Peripersonal space (PPS) refers to the space around us that lies within reach, in which most of our interactions with the environment occur. However, the PPS is not a static bubble surrounding our body. Rather, it can be dynamically reshaped in size, for instance as a consequence of the use of tools extending the arm's reach. Here we employed a visuo-tactile detection task in an immersive VR environment to measure the size of participants' PPS before and after different kinds of tool training. A short training period in which participants *pulled* objects from the Extrapersonal space (EPS) towards themselves via a tool was effective in enlarging the PPS, a result that nicely complements previous studies carried out in real life studies. However, no significant change in PPS size was achieved via training with other motor routines such as pulling, hammering or shooting, each of which involving a different kind of interaction between the agent and the targets. Taken together, our results suggest that the reshaping of the PPS is a complex phenomenon in which the kind of motor routines exploited to interact with the surrounding objects, plays a critical role.

Introduction

The space around us can be divided based on what lies within our reach or outside of it. This distinction is of primary importance for defining efficient motor plans that allow us to interact with the environment. The area surrounding our body, which is known as the *Peripersonal space* (PPS), was first described in monkeys, with the discovery of multi-modal neurons that only fire if a stimulus is placed near the body of the animal [1]. These neurons are located in the ventral premotor cortex F4 [2] and have receptive fields that surround the monkey's hand and move with it [1]. Interestingly, the electrical stimulation of these neurons elicits defensive-like movements in monkeys, as if the animals are trying to protect the part of the body where the receptive fields of the stimulated neurons are located [3]. The PPS can thus be conceptualized as a system specifically dedicated to the perception of stimuli that are in the immediate surroundings of the body and that may indicate potential risk or interest. In line with that, it has been proposed that the activity of brain areas in which PPS neurons are located aims at maintaining a margin of safety around the body [4].

Neuropsychological studies with neglect patients provide evidence for the presence of a specific area in the human brain dedicated to the perception of stimuli in the PPS. Hemineglect, or simply neglect, is a condition resulting from brain damage that leads to the inability to attend to stimuli presented in the contralesional hemifield [5]. In some cases, neglect patients fail to report the presence of a stimulus presented in the controlesional side when a competing stimulus is simultaneously shown in the ipsilesional side, a phenomenon known as "extinction" [6]. Ladavas et al. [7] demonstrated that the extinction effect also occurs cross-modally: the reduction in sensitivity to a tactile stimulus triggered on the controlesional hand induced by an ipsilesional touch was rather identical to that yielded by a visual stimulus displayed around the ipsilesional hand, suggesting the existence of a cross-modal visuo-tactile extinction. However, this effect was significantly reduced when the visual stimulus was presented outside of the patient's PPS, indicating that the deficit in the combination of visual and tactile information in neglect was more pronounced within the PPS. A dissociation between PPS and the Extrapersonal space (EPS) is also found in pseudo-neglect, an attentional deficit presented by neurologically healthy individuals. When asked to bisect a horizontal line, most people tend to provide leftward-biased responses [8]. Interestingly, this attentional bias attenuates progressively with distance. When asked to perform the bisection task in EPS, individual responses shift rightward instead of leftward [9], [10].

While the general definition of the size of the PPS is straightforward, its precise measurement poses some challenges. In animal models, the border between PPS and EPS can be measured with accuracy using in-vivo single-cell recording [1]. However, in humans a non-invasive behavioral approach has to be adopted. One of the most widely used methods to capture the boundary between PPS and EPS is the audio-tactile detection task pioneered by Canzonieri et al. [11]. In this task, participants are presented with a looming auditory stimulus that creates the illusion of an approaching sound source. Following a predetermined delay, a tactile stimulus is delivered to the hand as a vibration and participants are instructed to react to this as fast as possible, while ignoring the auditory stimulus. If the vibration is delivered when the sound is perceived as being in the PPS, participants are faster to react than when the sound is perceived as being in the EPS. Thus, the operational definition of PPS using this auditory-tactile detection task can be summarized as the maximum distance from the participant’s body at which the auditory stimulus can still facilitate the detection of the tactile stimulus. Notably, one of the characteristics of PPS neurons is that they are multimodal [1] and thus capable of firing for both visual and auditory impulses. This has opened up to the possibility of measuring detection facilitation within the PPS with visual instead of auditory stimuli.

However, PPS should not be considered as a static bubble that surrounds one's body. Not only the PPS has been reported to show different characteristics between healthy and clinical populations [12], [13], but it has also been shown to be malleable to environmental conditions. For instance, as the size of the PPS is robustly based on the extension of our reach, if our reach changes, the PPS gets modulated accordingly. Peripersonal neurons tuned to a specific area within the surrounding space have been shown to quickly reshape their receptive fields to accommodate changes in the extent of the reaching area. Indeed, when monkeys are trained to use a stick to retrieve food from a distance, the receptive field of PPS neurons becomes longer [14]. In humans, there have been reports of amputees [15] and wheelchair users [16] having a smaller PPS compared to controls, whereas blind cane users [17] and long-term computer mouse users [18] have a larger PPS when holding their cane or mouse respectively. Also elite athletes show a remapped PPS. For instance, experienced tennis players exhibit larger PPS when they hold their racket [19], with a similar effect also being found in fencers holding their sword [20].

While modulation resulting from long-term conditioning induces a stable and durable reshaping of the PPS, there have also been reports of PPS reshaping after a short training session. For instance, after performing a task in which participants use the tip of a cane to find objects scattered on the floor, an extension of the PPS was reported. This effect was similar to blind cane-users, however the remodulation in the healthy participants was transient [17]. Indeed, when participants were retested the day after the training, the PPS extension had disappeared. This result supports the idea that the duration of the training is proportional to the stability of the remapping. Indeed, this brief extension of PPS as a result of a short tool-use training has been observed under several different conditions [15], [18], [21], [22]. An enlargement of the PPS has also been observed while walking on a treadmill [23], suggesting that the illusion of moving forward, even when there is no overall displacement, increases the perception of what can be considered within reach. However, as the expansion of PPS has been achieved via quite different motor routines, it is not clear which aspect of the training triggers the reshaping. Is it the forward motion of a body part, the proprioceptive feedback of reaching with a tool, or the motion of the body induced by walking?

Virtual Reality (VR) set-ups offer an ideal environment to study which aspect of the training plays a key role in inducing the reshaping of the PPS as it allows to design ecologically-plausible looming visual stimuli. Indeed, previous reports suggest that PPS can successfully be investigated with VR [24]–[26]. As it has been demonstrated for the audio-tactile task, if the vibration is delivered when the virtual visual stimulus is perceived as being close to the participants body, reaction times (RTs) to the vibration are significantly reduced, and in some cases almost halved [24].

However, some concerns have been presented on whether measuring the PPS in VR provides a true representation of the PPS in the real world. Specifically, Ferroni et al. [27] asked participants to perform a short training in which they had to move small objects from point A to point B with a horizontal dragging motion, with both A and B being landing points placed in EPS. This task triggered an enlargement of the PPS when the task was performed in the real world. However, this was not the case when the same routine was executed in a VR environment. Even though this result seems to question the usefulness of VR environments to study modulations of the PPS, it is important to note that a large variability of the effectiveness of the motor training has also been reported for experiments carried out in real world, so a more systematic investigation is needed to reach a definitive conclusion.

In our study we attempted to induce a reshaping of PPS in a VR environment by carrying out four different types of training. The first group of participants (Experiment 1) was trained using the most widely used task to induce a reshaping of the PPS: pulling an object closer to one's body with the use of a tool. In a different condition, the same participants were instead instructed to perform a similar motor routine but with the opposite goal: to push an object away from their bodies into the EPS. In Experiment 2 we aimed to determine whether crossing the PPS/EPS border, as in the push-pull conditions in Experiment 1, is essential for reshaping the PPS or whether any repetitive hand movement with a tool can induce such a reshaping. To this end, participants had to repeatedly hit a target in the EPS using a hammer. To further explore this issue, in a final condition, participants were required to interact with the target in the EPS without any direct "physical contact" as they were required to shoot the target with a toy-gun. The first assessment in validating the VR as a tool to investigate PPS would be to replicate the PPS expansion as a consequence of training that involved pulling movements, as this training is the one of the most widely used in previous literature. Then, in case the PPS malleability is bidirectional, we would expect to reduce the PPS space as a consequence of pushing. Finally, with the hammering and shooting conditions, we aimed to investigate whether crossing the PPS/EPS border (hammering) or direct physical contact with a target (shooting) during training is essential for modulating the size of the PPS.

Results

Experiment 1

Data Preprocessing

As there is an extensive literature showing that during a visuo-tactile or audio-tactile detection task participants RTs decrease as the irrelevant stimulus approaches [15], [23]–[26], we looked for a decrease or increase in RTs in the Baseline condition as a function of visual stimulus distance at which a tactile vibration was delivered. For each participant, we measured the linear regression (Eq. 1) and then correlated the variance explained by the linear model (R^2) with the slope of the fit (*b* in Eq. 1). As expected, we found a strong correlation between the two (Pearson's $r = 0.95$, $p < 0.001$). Data in Fig. 2 show that participants with the steepest slope, indicating a steeper increase in RTs as a function of visual stimulus distance, also had the highest goodness of fit. Furthermore, there is a clear cluster of participants who had both a very poor goodness of fit ($R^2<0.1$) and a very flat slope ($b < 0.1$), suggesting that not only RTs did not increase but also did not follow a linear trend in general (Fig. 2, datapoints within dotted rectangle). In other words, these participants showed no reduction in RTs as the incoming stimulus was approaching, but the variance of the whole dataset was poorly accounted for by a linear model indicating poor performance in general. For this reason, this cluster of 8 participants was excluded, leaving a dataset of 33 participants for further analyses.

Size of PPS before and after training

Individual and average RTs for each visual stimulus distance are plotted in Fig. 3 for the three conditions. In all three conditions, when the size of the PPS was measured using the Baseline Task there was a clear influence of stimulus distance on RTs, with longer distances triggering the slowest response. RTs, averaged across participants, ranged between 250 ms and 310 ms, in line with previous reports [26].

Hollow circles represent individual reaction times, vertical bars depict average reaction times ± S.E.M. In all three conditions there is an evident increase in RTs as the distance of the visual stimulus from the participant increases when the tactile vibration is delivered.

To test whether the PPS of participants had changed as a result of the training performed in the Push and Pull conditions, individuals RTs for the trials in which the ball was launched from the central monster (80% of all trials) were pooled together and analyzed at the group level. To make the three conditions easier to compare with each other, average RTs were normalized between 0–1 using Eq. 2. To determine the exact border of the PPS in the three conditions average RTs were plotted as a function visual stimulus distance and fit with a sigmoid function (Eq. 3). The point of maximum slope of the fit (x0) can be considered as the border of the PPS [26].

Aggregate sigmoid functions for the three separate conditions are plotted together in Fig. 4A. The PPS appears to be the smallest in the Baseline Condition (red curve) with a size of 1.26 m, while the PPS appears to get enlarged as a result of both the Pull (green curve) and the Push training (blue curve), yielding a PPS measuring 1.58 m and 1.46 m respectively. The size of the PPS in the Baseline condition is very similar (only a difference of 1 cm) to the one previously found by Buck et al. [24] using the same paradigm in VR.

The significant difference between the aggregate data for each condition was quantified by the bootstrap sign test. On each one of the 12,000 iterations, separately for each condition, the data were sampled with the replacement (as many independent samples as the full dataset) and fit with a sigmoid function, to estimate the border of the PPS. For the Push condition (Fig. 4B) there was a slight trend of PPS enlargement after training, as shown by the peaks of the distribution that were rather spread apart. However, this trend did not reach statistical significance ($p = 0.09$). For the Pull condition (Fig. 4C), the same trend of a PPS enlargement after training was observed but this time modulation was quantitatively higher and was found to be statistically significant ($p = 0.03$). These results suggest that, in line with several previous reports, the Pull Training yielded a significant enlargement of the PPS of around 20% (0.32 m of difference between the two conditions). The Push training, despite including a motor routine in the opposite direction (from PPS to EPS), also showed a tendency to induce an enlargement of the PPS, suggesting that modulation of the PPS is not selective for the actions towards the participant's body. However, as changes in PPS size in the push condition failed to reach statistical significance, it seems that motor routines in which elements within the PPS are moved further away to the EPS cannot change the size of PPS.

Experiment 2

Data Preprocessing

In the second experiment, we tested for the very first time the role of training motor routines that (a) did not involve a crossing of the PPS/EPS border or (b) did not include a direct, physical contact between the observer and the target in EPS. As a preliminary step, and similarly to Experiment 1, individual RTs were fitted with a linear function to test for linear increase as a function of visual-stimulus distance. Also in this case, we found a strong correlation between the variance explained by the linear model (R^2) and the Regression Slope (b in Eq. 1). The two values were strongly correlated with each other (Pearson's $r = 0.49$, $p = 0.003$) and again we found a small cluster of participants (within the dotted rectangle of Fig. 5) who exhibited both a very low goodness of fit and a very flat slope. As these participants that provided noisy and stereotypical responses were excluded from the subsequent analyses, resulting in a total of 28 participants in the final dataset.

Size of PPS before and after training

Average RTs plotted as a function of distance in the three conditions are plotted as a function of visual stimulus distance in Fig. 6. Experiment 2 confirms the validity of the Baseline Task as a tool to measure the border of PPS, given that RTs steadily increase as the distance of the approaching visual stimulus at which vibration is delivered increases. Furthermore, average RTs are in line with Experiment 1, ranging from 250 ms to 320 ms.

To test whether the Hammer and Toy-Gun training had any influence on the size of the PPS, all trials in which the ball was launched from the central monster (80% of all trials) were pooled together and analyzed at a group level. First, average reaction times were normalized between 0–1 using Eq. 2. Then, average RTs as a function of visual stimulus distance were fitted according to Eq. 3 (see Methods) and the point of maximum slope (x0) was taken as the border of PPS.

Sigmoid functions on aggregate data across participants for the three separate conditions are plotted in Fig. 7A. As it is clear from inspection, the size of the PPS was the biggest in the Baseline Condition (red curve) with a size of 1.20 m. This result is very close to the size of PPS found in the Baseline Condition of Experiment 1 (1.26 m). Indeed, there was no statistically significant difference between the Baseline conditions of two experiments ($p = 0.27$), as tested with the same bootstrapping procedure implemented in Experiment 1.

At odds with Experiment 1, the two trainings employed in Exp. 2 did not induce any significant changes of the size of PPS. Both conditions yielded a slight shrinkage of the PPS, that was more pronounced in the Hammer condition (0.96 m) than in the Gun Condition (1.04 m) and in contrast with the enlargement reported for the pulling effect of Exp. 1. However, as already mentioned, neither the use of the hammer (Fig. 7B) nor that of the toy-gun induced a significant change on the size of the PPS (Fig. 7C), suggesting that when the items we interact with do not cross the PPS/EPS border (hammer) or when no physical contact is established between objects in the PPS and EPS (toy-gun), no significant change in the PPS size occurs.

Discussion

In this study we investigated the effects of a brief tool-use training on the extension of the PPS in a VR setting. Across two experiments, participants had their PPS measured before and after performing four different types of tool-training. The task we chose to measure the size PPS was the visuo-tactile detection task, which has been shown before to be a valid tool for determining the size of the PPS in humans [26]. In the Baseline condition of both experiments we found that the extension of PPS before any training was 1.28 m and 1.20 m respectively. This result is reassuring in terms of validation of the visuo-tactile paradigm in VR as it almost perfectly replicates previous findings [24], [25].

In Experiment 1, the size of PPS was measured after two kinds of training: the Pull training in which participants had to pull marbles from their EPS to their PPS and the Push training in which participants had to push marbles away from their PPS into their EPS. We found that the Pull training triggered a significant enlargement of the PPS of more than 20% after only 10 minutes of activity. This result is in line with previous reports that used a similar training motor routine in animal models [14], brain-damaged patients [28]–[30], and healthy controls [15], [31]. However, this is the first time in which an expansion of the PPS is achieved in VR via tool-use training, thus providing key evidence for the effectiveness of using VR environments to measure and modulate the PPS. Furthermore, even though the Push training in which the interaction with the objects was carried out in the opposite direction (from PPS to EPS), we found a trend for an expansion of the PPS (around 15%) but this effect was quantitatively less robust and failed to reach statistical significance. To further investigate how different motor routines during training can modulate the PPS size, in Experiment 2 we designed two new training actions. In one condition, participants had to use a hammer to hit a blob avatar that was moving sideways in the EPS, while in the other condition they had to use a toy-gun to shoot the avatar placed in the far space. Although we did observe a slight shrinkage of the PPS, none of the two types of training had any significant effect on the size of the PPS.

Considering the results of Experiment 1, one might speculate that the direction of motion during the training is crucial, with the Pull routine requiring to move objects from the EPS to the PPS being the only kind of motion capable of remapping PPS. Indeed, there have been previous reports of action specificity on the extension of the PPS suggesting that different action kinematics might yield different effects. For instance, Brozzoli et al. [32] compared the effects of a grasping and a pointing action on visuo-tactile interactions. They found that during the approaching phase of the moment, the Grasping action led to a stronger cross-modal congruency effect compared to the pointing action, in which participants approached the target without touching it. Results from Experiment 2 seem to suggest that it might be also possible to induce a shrinkage of PPS, even though the kind of training we leveraged on (hammering and shooting), failed to induce a significant change in PPS. A reduction of the PPS size might be related to the need to become more conservative in terms of defensive behavior. As participants were asked to use weapons to hit the blob avatar, this might have triggered the implicit belief of having to defend themselves from the avatar. Indeed, it has been established that carrying out a defensive behavior for a prolonged period of time can trigger a shrinkage of PPS. For instance, expert boxers exhibit an anomalous Hand Blink Reflex (HBR) compared to controls [33]. The HBR is a subcortical response at the brainstem level, elicited by the electrical stimulation of the median nerve at the wrist and recorded from the orbicularis oculi muscles. HBR dramatically increases when the stimulated hand is statically positioned inside the PPS surrounding the face [34]. However, when boxers assume the guard position, the HBR is heavily suppressed, even though the affected limb is stationarily positioned within the PPS. This might be because boxers perceive themselves as protected from danger while they are in the guard position, thus shrinking their PPS. Similarly, we might speculate that participants in Exp. 2 in which two kind of fight-related actions were involved (hammering and shooting), might have been prompted to activate a defensive behavior to be adequately defend themselves from the avatar, and this, in turn might have reduced the size of their PPS.

One of the key contributions of the present study is that it has successfully investigated PPS manipulations in a VR environment, as previous studies have questioned the possibility to do so. For instance, as mentioned in the Introduction, Ferroni et al. [27] found that the same kind of training that triggered an expansion of PPS in a real life setting did not achieve the same result in VR, which prompted them to conclude that the PPS in VR might be characterized by different properties. One possible explanation to reconcile these findings might be in terms of the differences between the experimental paradigm implemented here and in Ferroni et al. [27]. In their paradigm, during the training phase participants had to move an object from point A to point B with both points being located in the EPS. This means that participants never had to move objects closer to or further away from them, with no transitions between PPS and EPS. On the other hand, in the Pull training of the present study, the only condition that was successful in inducing a significant enlargement of the PPS, objects were moved from EPS to PPS to establish a clear connection between the two spaces. Considering this, it is surprising that the opposite movement, Push, did not provide any significant result and even more interesting it’s that, nevertheless, the tendency found was towards an enlargement of the PPS. If the direction of motion is crucial to the reshaping, one might have expected a constriction of the size of the PPS. Going back to the comparison between the present study with that of Ferroni et al. [27], it is clear that the condition more similar across the two studies is the Hammer training, in which participants had “physical contact” with the targets but without moving the objects between the PPS and the EPS. Notably, in Ferroni et al. [27] such training yielded a weak tendency to shrink the PPS, suggesting that the two kinds of training taken into account, might trigger similar PPS reshaping. These results, in combination with those from the present study, strongly suggest that the type of motor routine carried out during the training, plays a fundamental role in PPS reshaping.

From the current results it is clear that pulling objects towards oneself has a special role in the representation of PPS, which could possibly be derived from the evolutionary relevance of pulling objects closer in order to interact with them. Future studies should aim at investigating two main experimental questions. First, it should be determined whether it is possible to trigger a reshaping with any other kind of tool training while considering variables such as the cinematic of the training actions or the training duration. Subsequently it would also be crucial to test the lifespan of the expansion effect triggered by the tool training, to determine whether changes in the PPS are transient phenomena or are long lasting. Finally, as the present study revealed that reliable and accurate measurements of PPS can also be achieved in VR, future studies should take further advantage of this technology to investigate PPS in more ecological settings and situations.

Methods

Participants

A total of 46 participants took part to Experiment 1- Push & Pull (mean age: 21.43 ± 3.85, 37 females, 1 author). 33 participants took part to Experiment 2 – Hammer & Gun (mean age:22.12 ± 3.37, 24 females, 1 author). All participants had normal or corrected to normal vision and gave written informed consent. The study was approved by the Cyprus National Bioethics Committee (Protocol Number: EEBK EP 2018.01.138) and was in accordance with the ethical standards of the 1964 Declaration of Helsinki. Participants were also asked to abstain from caffeine for at least two hours prior to the experiment to control for possible effects induced by stimulants on RTs [35]. Due to technical failure of hardware, complete behavioral datasets from 6 participants were not collected and were thus excluded from further analyses, leaving a total of 41 participants for Experiment 1 and 32 participants for Experiment 2.

Apparatus

The VR environment was built in Unity Game Engine (version 2020.3.29f1) using C# version 7.3. The blob avatar and the tools animations were imported from the Unity Asset Store. The virtual environment was presented to participants using the HTC Vive ProEye headset, that features a resolution of 2880 by 1600 pixels and a refresh rate of 90Hz. All data was analyzed using Matlab 2020b (The Mathworks, Inc., Natick, MA, USA).

Measurements of PPS – Baseline Task

To measure the size of the PPS we used the visuo-tactile detection task first proposed by Serino [26]. The experiment took place in a neutral virtual room in which three blob avatars were positioned at a distance of 2.5 m away from the observer, either straight ahead (at 0°) or at an eccentricity of 30° to the left or to the right of the observer (Fig. 1A). The avatars remained still for the whole duration of the task apart from an idle animation: slight up-and-down bouncing on the spot and blinking of their only eye. Participants were instructed to stand still inside a small circle which ensured a fixed distance (2.5m) from the blob avatars, to fixate on the central blob avatar, and to pull the trigger on the controller each time they felt a vibration. On each trial, one of the avatars (the central avatar on 80% of the trials) launched a semi-transparent bubble with a diameter of 10cm that travelled horizontally at a constant speed of 75cm/s towards the participant. The vibration could be delivered when the bubble was at 2.25, 1.75, 1.25, 0.75 or 0.25 meters from the participant. In total we collected 20 repetitions for each distance in Experiment 1 and 15 repetitions for each distance in Experiment 2 for to optimize the duration of the Task. On top of that, 15 trials for each of the two control conditions were added: (1) tactile only, in which the vibration was delivered without a bubble being launched, and (2) the bubble travelled the whole distance with no vibration being delivered. The control conditions ensured that the appearance of the ball did not trigger a stereotypical response. This meant that on each PPS measurement the participant was presented with a total of 140 trials for Experiment 1 and 105 trials for Experiment 2, with a single block lasting approximately 10 minutes.

Experiment 1 – Push & Pull

Pull Training

The participant was positioned in the same non-descriptive white room used for the Baseline Task described above, with only one blob avatar placed at 2.5 m directly in front of them (Fig. 1B). The blob avatar did not move except for the idle animation. On each trial a small round marble appeared on the floor between the participant and the blob avatar at a maximum distance of 1.5 m and an eccentricity of 0°, 30° or 60° on the left or the right respectively, at one of five possible positions. Participants were instructed to use a shovel (1.45 m long) to pull the marble into a circle of 70 cm radius, with participants standing in its center. Once the marble had been successfully dragged into the circle, the next trial was initiated. Each participant completed a total of 200 trials, with 40 trials for each possible eccentricity. The whole block lasted approximately 10 minutes.

Push Training

The methods were identical to those for the Pull training, except that participants were instructed to perform a pushing routine. Specifically, on each trial they had to use the shovel to push the marble away from them into a circle of 70cm radius positioned around the blob avatar, instead of pulling it towards them as in the previous condition. This task used in Experiment 1 aimed at testing whether the direction of action while using a tool plays a role in reshaping the PPS (Fig. 1C).

Experiment 2 – Hammer & Gun

Hammer Training

In this condition participants were positioned in the same non-descriptive white room with a single blob avatar standing at 2.5 m and moving from left to right completing a semi-circular trajectory reaching a maximum of 30° of eccentricity on each side at a speed of 2.618 m/s (Fig. 1D). Participants were equipped with a hammer bridging the distance between their extended arm and the blob avatar and were instructed to hit the avatar on the head. Each successful hit was signaled by both a vibration of the controller and a back-and-forth rocking motion of the avatar (as if it was reacting to the hit). Furthermore, to make the task more engaging, a green life-bar representing the remaining energy left of the avatar was positioned above it. On each successful hit, the life-bar decreased, reaching 0 after 200 successful hits. Each participant performed three blocks of this training in succession, with a total duration of about 10 minutes (same as in previous trainings).

Toy-Gun Training

Participants had to use a yellow toy-gun to hit the blob avatar that moved along the same trajectory described for the hammer training. Every time the trigger was pulled the controller vibrated and each successful hit was signaled by a back-and-forth movement of the blob avatar (similar to the hammer training). The bullet travelled towards the target at a speed of 2.618 m/s. The same life-bar used for the hammer training was used here as well. Each participant completed 3 blocks of 200 trials. (Fig. 1E).

Procedure

Independently of the experiment and the order of conditions, the experimental session began with presenting participants with a 7-trial sample of the Baseline Task in order to familiarize them with the procedure.

Participants performed the Baseline Task to measure the extension of their PPS three times in each experiment: once without having performed any training (Baseline Condition) and once after each training session (Push Condition and Pull Condition for Experiment 1 or Hammer Condition and Gun Condition in Experiment 2). The order of conditions was counterbalanced across participants. Between each condition participants removed the VR headset and took a 15-minute break to ensure that any remaining effect induced by training wore off before beginning the next condition of the experiment.

Data Analysis

To measure the size of the PPS we pooled together trials from all participants in which the bubble was released by the central monster (80% of all trials) and analyzed them at the group level. During the data preprocessing all trials in which participants failed to pull the trigger or pulled the trigger before the vibration, were excluded. To further ensure that we only considered genuine responses to the tactile stimulus, we also excluded trials in which the RTs were unreasonably fast (< 100 ms-possibly indicating a reaction to the release of the bubble and not the vibration) or slow (> 1000 ms-possibly indicating lack of attention) or fell beyond 3 standard deviations from the average individual RTs for each possible distance. In practice, this led to the rejection of less than 1% of all trials.

There have been various reports in the literature showing that RTs in a visuo-tactile or audio-tactile detection task are expected to increase as a function of increasing irrelevant stimulus distance [15], [23]–[26]. For this reason, in a preliminary analysis we plotted individual RTs against visual stimulus distance and fitted them with the linear function (Eq. 1):

$$y\left(x\right)=ax+b$$ Eq. 1

In order to make RTs easier to compare among conditions, average RTs at the group level were normalized between 0 and 1 (Eq. 2)

$$z_i=\frac{(x_i-min(x))}{max(x)-min(x)}$$ Eq. 2

To compute the exact PPS border in each condition, average RTs at the group level were plotted against visual stimulus distance and fitted with a sigmoid function (Eq. 3) as suggested by Serino et al. [26]. Fitting parameters were set to anchor the sigmoid curve between 0 and 1, and x0 was restricted between 0.25 and 2.25 m.

$$y\left(x\right)=\frac{y_{min}+y_{max}e^{(x-xc)/b}}{1+e^{(x-xc)/b}}$$ Eq. 3

Statistical significance was tested using the bootstrapping method [36]. On each repetition (12,000 iterations) and separately for each condition, the data were sampled with replacement (as many independent samples as the full dataset) and fit with the sigmoid function described above, whose peak yielded an estimate of the size of PPS. As an additional step to ensure that each tested distance was represented equally in the new re-sampled dataset, each tested distance was resampled an equal number of times, thus preventing a possible unbalanced dataset. For Experiment 1, each distance was resampled on average 532 times in each new dataset while in Experiment 2 each distance was resampled on average 323 times. PPS size distributions for each condition were tested for significance separately using a Bootstrap t-test [36].

Declarations

Authors Contribution

I.P., Methodology, Investigation, Analyses, Writing-Original Draft, Writing-Review and Editing. KM: Methodology, Investigation, Analyses, Writing-Review and Editing. SA: Methodology and Software. MA: Methodology, Writing-Review and Editing, Supervision. RA: Methodology, Analyses, Writing-Review and Editing, Supervision.

Data Availability Statement

Data for the main findings of this study are available at: 10.5281/zenodo.8072114.

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References

1. G. Rizzolatti, C. Scandolara, M. Matelli, and M. Gentilucci, "Afferent properties of periarcuate neurons in macaque monkeys. II. Visual responses," *Behav Brain Res*, vol. 2, no. 2, pp. 147–163, Mar. 1981, doi: 10.1016/0166-4328(81)90053-x.
2. M. Gentilucci, L. Fogassi, G. Luppino, M. Matelli, R. Camarda, and G. Rizzolatti, "Functional organization of inferior area 6 in the macaque monkey," *Exp Brain Res*, vol. 71, no. 3, pp. 475–490, Jul. 1988, doi: 10.1007/BF00248741.
3. M. S. A. Graziano, C. S. R. Taylor, and T. Moore, "Complex movements evoked by microstimulation of precentral cortex," *Neuron*, vol. 34, no. 5, pp. 841–851, May 2002, doi: 10.1016/s0896-6273(02)00698-0.
4. M. S. A. Graziano and D. F. Cooke, "Parieto-frontal interactions, personal space, and defensive behavior," *Neuropsychologia*, vol. 44, no. 6, pp. 845–859, 2006, doi: 10.1016/j.neuropsychologia.2005.09.009.
5. G. Vallar, "Spatial hemineglect in humans," *Trends Cogn Sci*, vol. 2, no. 3, pp. 87–97, Mar. 1998, doi: 10.1016/s1364-6613(98)01145-0.
6. E. De Renzi, *Disorders of space exploration and cognition*. Chichester ; New York: J. Wiley, 1982.
7. E. Làdavas, G. di Pellegrino, A. Farnè, and G. Zeloni, "Neuropsychological evidence of an integrated visuotactile representation of peripersonal space in humans," *J Cogn Neurosci*, vol. 10, no. 5, pp. 581–589, Sep. 1998, doi: 10.1162/089892998562988.

8. M. E. McCourt and G. Jewell, “Visuospatial attention in line bisection: Stimulusmodulation of pseudoneglect,” *Neuropsychologia*, 1999, doi: 10.1016/S0028-3932(98)00140-7.
9. M. R. Longo and S. F. Lourenco, “Bisecting the mental number line in near and far space,” *Brain and Cognition*, vol. 72, no. 3, pp. 362–367, Apr. 2010, doi: 10.1016/j.bandc.2009.10.016.
10. M. E. McCourt and M. Garlinghouse, “Asymmetries of Visuospatial Attention are Modulated by Viewing Distance and Visual Field Elevation: Pseudoneglect in Peripersonal and Extrapersonal Space,” *Cortex*, vol. 36, no. 5, pp. 715–731, Jan. 2000, doi: 10.1016/S0010-9452(08)70548-3.
11. E. Canzoneri, E. Magosso, and A. Serino, “Dynamic Sounds Capture the Boundaries of Peripersonal Space Representation in Humans,” *PLOS ONE*, vol. 7, no. 9, p. e44306, Sep. 2012, doi: 10.1371/journal.pone.0044306.
12. G. Di Cosmo *et al.*, “Peripersonal space boundary in schizotypy and schizophrenia,” *Schizophrenia Research*, vol. 197, pp. 589–590, Jul. 2018, doi: 10.1016/j.schres.2017.12.003.
13. J.-P. Noel *et al.*, “Visual-Tactile Spatial Multisensory Interaction in Adults With Autism and Schizophrenia,” *Frontiers in Psychiatry*, vol. 11, 2020, Accessed: May 26, 2023. [Online]. Available: https://www.frontiersin.org/articles/10.3389/fpsyt.2020.578401
14. A. Iriki, M. Tanaka, and Y. Iwamura, “Coding of modified body schema during tool use by macaque postcentral neurones,” *Neuroreport*, vol. 7, no. 14, pp. 2325–2330, Oct. 1996, doi: 10.1097/00001756-199610020-00010.
15. E. Canzoneri, S. Ubaldi, V. Rastelli, A. Finisguerra, M. Bassolino, and A. Serino, “Tool-use reshapes the boundaries of body and peripersonal space representations,” *Exp Brain Res*, vol. 228, no. 1, pp. 25–42, Jul. 2013, doi: 10.1007/s00221-013-3532-2.
16. M. Scandola, S. M. Aglioti, C. Bonente, R. Avesani, and V. Moro, “Spinal cord lesions shrink peripersonal space around the feet, passive mobilization of paraplegic limbs restores it,” *Sci Rep*, vol. 6, no. 1, Art. no. 1, Apr. 2016, doi: 10.1038/srep24126.
17. A. Serino, M. Bassolino, A. Farnè, and E. Làdavas, “Extended multisensory space in blind cane users,” *Psychol Sci*, vol. 18, no. 7, pp. 642–648, Jul. 2007, doi: 10.1111/j.1467-9280.2007.01952.x.
18. M. Bassolino, A. Serino, S. Ubaldi, and E. Làdavas, “Everyday use of the computer mouse extends peripersonal space representation,” *Neuropsychologia*, vol. 48, pp. 803–811, 2010, doi: 10.1016/j.neuropsychologia.2009.11.009.
19. M. Biggio, A. Bisio, L. Avanzino, P. Ruggeri, and M. Bove, “This racket is not mine: The influence of the tool-use on peripersonal space,” *Neuropsychologia*, vol. 103, pp. 54–58, 2017, doi: 10.1016/j.neuropsychologia.2017.07.018.
20. M. Biggio, A. Bisio, L. Avanzino, P. Ruggeri, and M. Bove, “Familiarity with a Tool Influences Peripersonal Space and Primary Motor Cortex Excitability of Muscles Involved in Haptic Contact,” *Cereb Cortex Commun*, vol. 1, no. 1, p. tgaa065, 2020, doi: 10.1093/texcom/tgaa065.
21. N. P. Holmes, G. A. Calvert, and C. Spence, “Extending or projecting peripersonal space with tools? Multisensory interactions highlight only the distal and proximal ends of tools,” *Neuroscience Letters*, vol. 372, no. 1–2, pp. 62–67, 2004, doi: 10.1016/j.neulet.2004.09.024.

22. I. Patané, T. Iachini, A. Farnè, and F. Frassinetti, “Disentangling Action from Social Space: Tool-Use Differently Shapes the Space around Us,” *PLOS ONE*, vol. 11, no. 5, p. e0154247, May 2016, doi: 10.1371/journal.pone.0154247.
23. J.-P. Noel *et al.*, “Rapid Recalibration of Peri-Personal Space: Psychophysical, Electrophysiological, and Neural Network Modeling Evidence,” *Cereb Cortex*, vol. 30, no. 9, pp. 5088–5106, Jul. 2020, doi: 10.1093/cercor/bhaa103.
24. L. Buck, S. Park, and B. Bodenheimer, “Determining Peripersonal Space Boundaries and Their Plasticity in Relation to Object and Agent Characteristics in an Immersive Virtual Environment,” Mar. 2020, pp. 332–342. doi: 10.1109/VR46266.2020.1581103473496.
25. H.-S. Lee *et al.*, “Altered Peripersonal Space and the Bodily Self in Schizophrenia: A Virtual Reality Study,” *Schizophr Bull*, vol. 47, no. 4, pp. 927–937, Jul. 2021, doi: 10.1093/schbul/sbab024.
26. A. Serino *et al.*, “Peripersonal Space: An Index of Multisensory Body–Environment Interactions in Real, Virtual, and Mixed Realities,” *Frontiers in ICT*, vol. 4, 2018, Accessed: Jan. 06, 2023. [Online]. Available: https://www.frontiersin.org/articles/10.3389/fict.2017.00031
27. F. Ferroni *et al.*, “The Remapping of Peripersonal Space in a Real but Not in a Virtual Environment,” *Brain Sciences*, vol. 12, no. 9, Art. no. 9, Sep. 2022, doi: 10.3390/brainsci12091125.
28. S. Bonifazi, A. Farnè, L. Rinaldesi, and E. Làdavas, “Dynamic size-change of peri-hand space through tool-use: Spatial extension or shift of the multi-sensory area,” *Journal of Neuropsychology*, vol. 1, no. 1, pp. 101–114, 2007, doi: 10.1348/174866407X180846.
29. A. Farnè and E. Làdavas, “Dynamic size-change of hand peripersonal space following tool use,” *NeuroReport*, vol. 11, no. 8, p. 1645, Jun. 2000.
30. A. Maravita, K. Clarke, M. Husain, and J. Driver, “Active Tool Use with the Contralesional Hand Can Reduce Cross-modal Extinction of Touch on that Hand,” *Neurocase*, vol. 8, no. 6, pp. 411–416, Dec. 2002, doi: 10.1076/neur.8.5.411.16177.
31. F. Anelli, M. Candini, M. Cappelletti, M. Oliveri, and F. Frassinetti, “The Remapping of Time by Active Tool-Use,” *PLOS ONE*, vol. 10, no. 12, p. e0146175, Dec. 2015, doi: 10.1371/journal.pone.0146175.
32. C. Brozzoli, L. Cardinali, F. Pavani, and A. Farnè, “Action-specific remapping of peripersonal space,” *Neuropsychologia*, vol. 48, no. 3, pp. 796–802, Feb. 2010, doi: 10.1016/j.neuropsychologia.2009.10.009.
33. M. Biggio, A. Bisio, P. Ruggeri, and M. Bove, “Defensive peripersonal space is modified by a learnt protective posture,” *Sci Rep*, vol. 9, no. 1, Art. no. 1, May 2019, doi: 10.1038/s41598-019-43258-8.
34. C. F. Sambo, M. Liang, G. Cruccu, and G. D. Iannetti, “Defensive peripersonal space: the blink reflex evoked by hand stimulation is increased when the hand is near the face,” *Journal of Neurophysiology*, vol. 107, no. 3, pp. 880–889, Feb. 2012, doi: 10.1152/jn.00731.2011.
35. E. Childs and H. de Wit, “Subjective, behavioral, and physiological effects of acute caffeine in light, nondependent caffeine users,” *Psychopharmacology (Berl)*, vol. 185, no. 4, pp. 514–523, May 2006, doi: 10.1007/s00213-006-0341-3.
36. B. Efron and R. J. Tibshirani, *An introduction to the bootstrap*. CRC press, 1994.

Figures

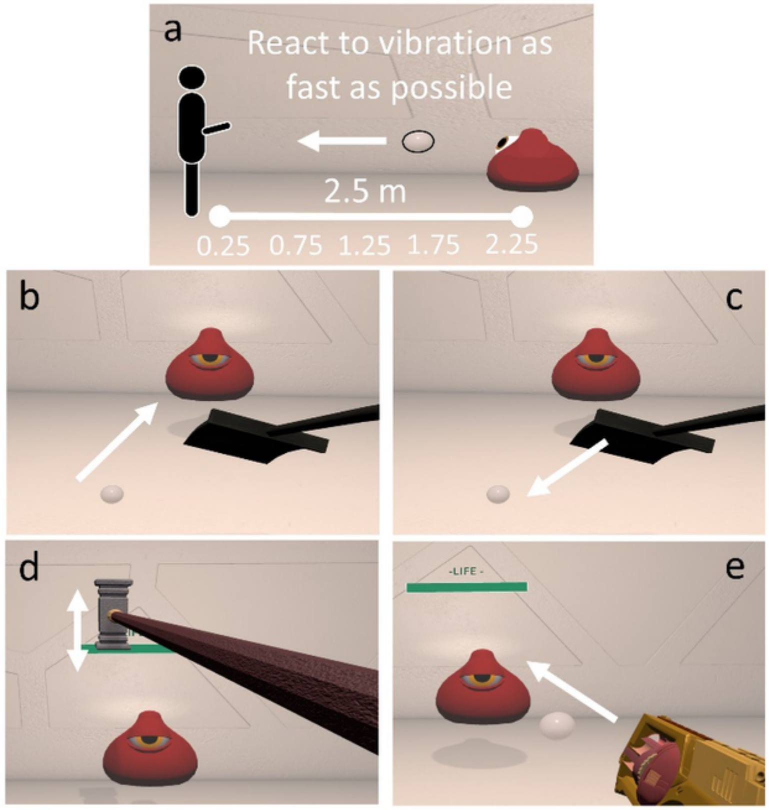

Figure 1

Experimental Paradigm

a. Measuring of PPS. Participants were instructed to react to a vibration delivered through the controller as fast as possible, while ignoring an approaching visual stimulus. **b. Push Training:**participants used the shovel tool to push the marble towards the avatar. **c. Pull Training:** participants used the same shovel tool was used to pull the marble towards their feet. **d. Hammer Training:** participants used a hammer to hit the avatar using an up-and-down vertical motion. A Green Life Bar decreased at each successful hit. **e. Toy-gun Training.** Participants used a gun to shoot the avatar, the same Life Bar used in the Hammer Training was used to signal the progression of the task.

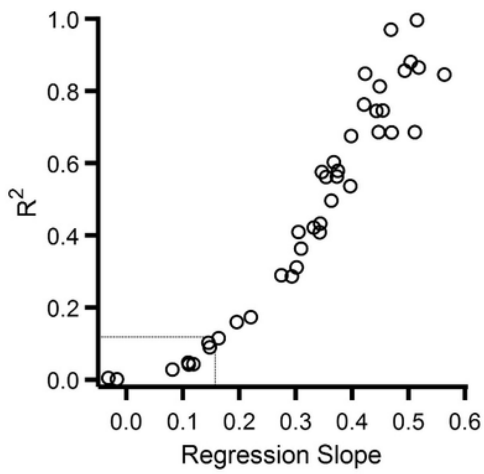

Figure 2

Correlation between R^2 and the slope of the linear fit for each participant's RTs in the baseline condition of Experiment 1.

Individual average RTs as a function of visual stimulus distance were fit with a linear regression model. The goodness of fit and the slope predicted by the model for each participant were then correlated with each other. Participants with both the lowest goodness of fit and flattest slope (shown within the dotted rectangle at the bottom left of the graph) were excluded from further analyses.

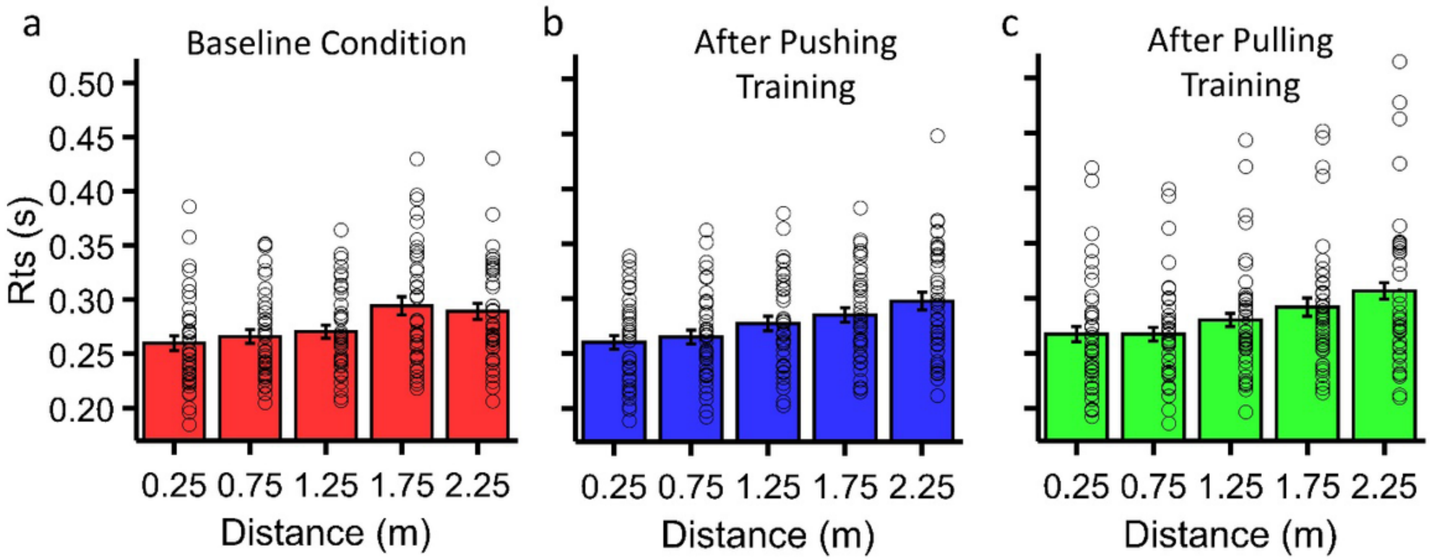

Figure 3

Average RTs as a function of visual stimulus distance in the three conditions.

Hollow circles represent individual reaction times, vertical bars depict average reaction times ±S.E.M. In all three conditions there is an evident increase in RTs as the distance of the visual stimulus from the participant increases when the tactile vibration is delivered.

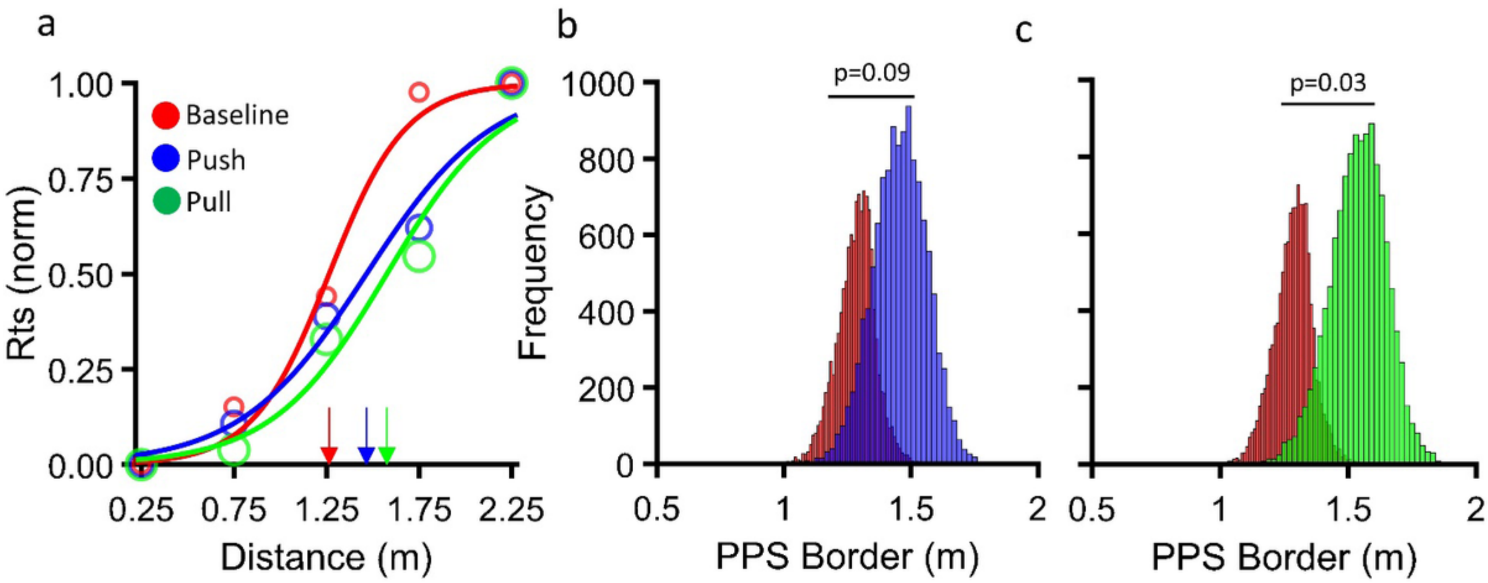

Figure 4

Reaction times sigmoid fit and bootstrapping.

a. Average reaction times (normalized in a 0-1 range) are plotted against visual stimulus distance and fit with a sigmoid function. The point of maximum slope of the fit (x0) is considered the border between the PPS/EPS. **b.** Bootstrap distributions for the Baseline and Push conditions. Each column represents how many times a certain value was obtained out of 12 000 iterations. The difference between the 2 distributions is then tested with a bootstrap t-test. **c.** Bootstrap distributions for the Baseline and Pull conditions. In this case the difference between the two distributions is statistically significant.

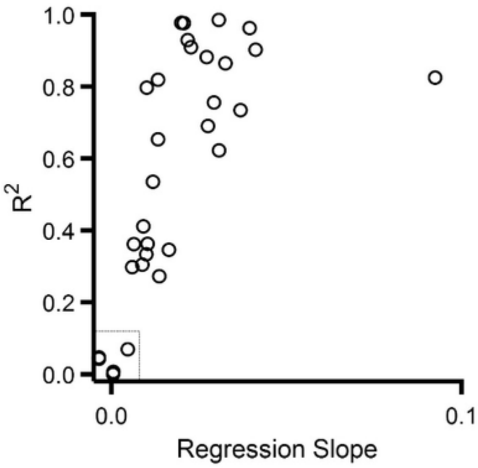

Figure 5

Correlation between R^2 and the slope of the linear fit for participant's RTs in the baseline condition of Experiment 2.

Individual average RTs as a function of visual stimulus distance were fitted with a linear regression model. The goodness of fit and the slope predicted by the model for each participant were then correlated with each other. Participants with both the lowest goodness of fit and flattest slope (dotted rectangle, bottom left) were excluded from further analyses.

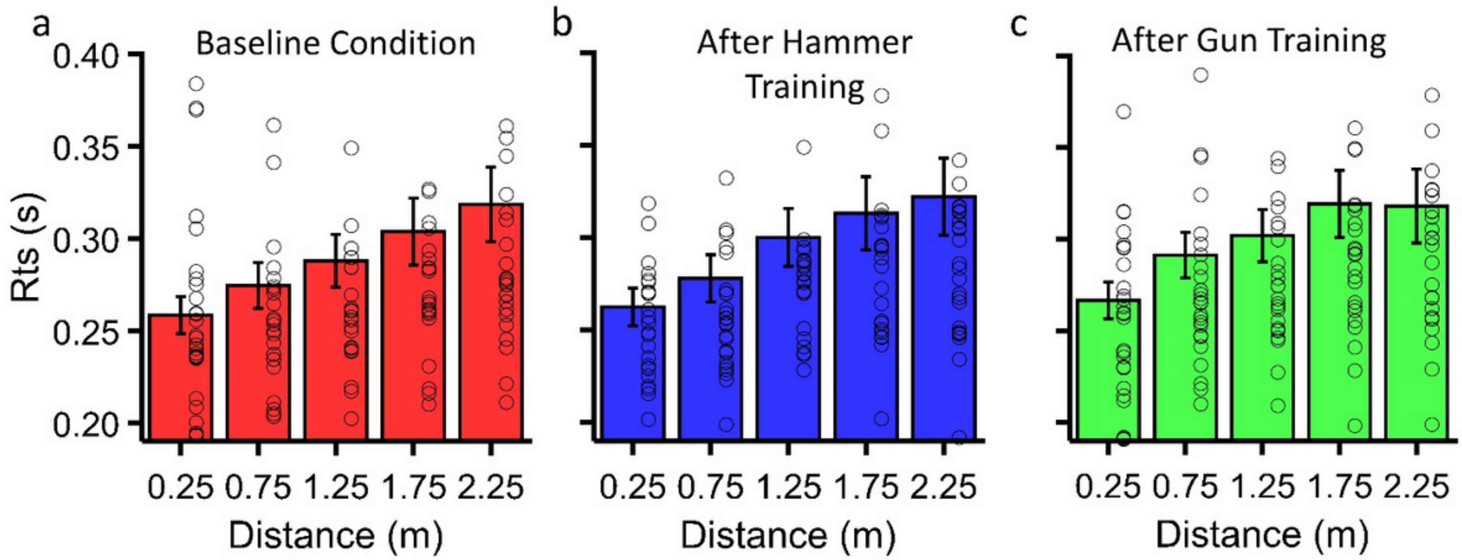

Figure 6

Average RTs as a function of visual stimulus distance in the three conditions.

Hollow circles represent individual reaction times, bar depict average reaction times ±S.E.M

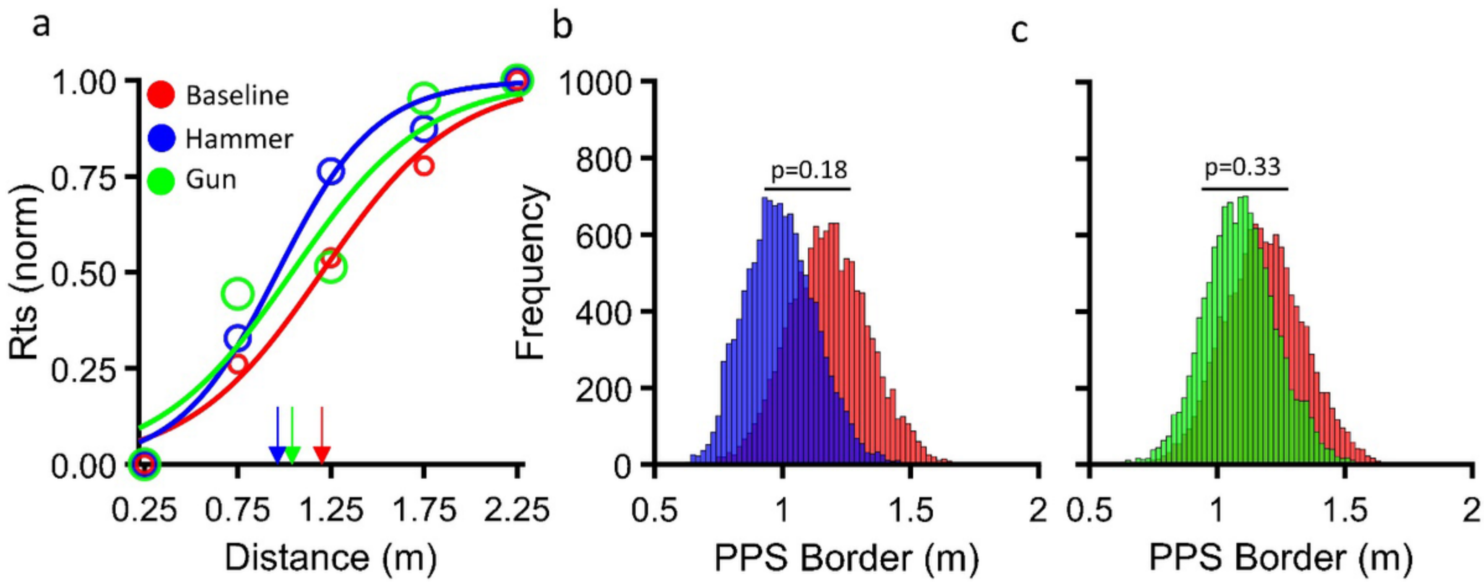

Figure 7

Reaction times sigmoid fit and bootstrapping for Experiment 2.

a. Normalized average RTs are plotted against approaching visual stimulus distance and fit with a sigmoid function. The point of maximum slope of the fit (x0) is defined as the border between the PPS/EPS. **b.** Bootstrap distributions for the Baseline and Hammer conditions. Each column represents how many times a certain value was obtained out of 12 000 iterations. The difference between the 2 distributions is then tested with a bootstrap t-test.

c. Bootstrap distributions comparing the Baseline and Gun conditions.