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Letter to the Editor

Running Title: Proprioception contributes to perspective-taking

Let's share our perspectives, but only if our body postures match

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Introduction

Knowing where our body is in space depends on the brain's ability to process proprioceptive signals from the muscles, joints and tendons, and to integrate them with information from other sensory modalities. Previous research has shown that conflicting proprioceptive information influences the perception of our own body. For example, altering signals from the muscle spindles by simultaneous vibrations of the biceps and triceps tendons evoked a "telescoping of the arm towards the elbow" (Longo, Kammers, Gomi, Tsakiris, & Haggard, 2009). Similarly, conflicting visuo-proprioceptive signals when viewing a moving hand in a mirror gave the illusion that the other, immobilised, hand was also moving, increasing motor excitability for the motionless hand (Touzalin-Chretien, Ehrler, & Dufour, 2010).

Here we are interested in how the current position of our body in space affects visuo-spatial third-person perspective-taking. When interacting with others, we need to distinguish between our own and others' perspectives. Our position in space might play a key role for this ability. For instance, observers explicitly instructed to judge whether a glass of water is located to someone else's left or right are on average faster to perform this task when they share a same body posture (Kessler & Rutherford, 2010; Kessler & Thomson, 2010; Surtees, Apperly, & Samson, 2013b) or a same body configuration (e.g. arms crossed: Furlanetto, Gallace, Ansuini, & Becchio, 2014) than the distant person. Previous studies classified this mental process as '*level-2 perspective taking',* which relies on embodied mental rotation of the self in order to identify how others see the world from a different perspective (Michelon & Zacks, 2006). Although, level-2 perspective-taking has been traditionally considered a rather deliberate mental simulation grounded on proprioceptive signals (Kessler & Rutherford, 2010; Kessler & Thomson, 2010; Surtees et al., 2013b) recent studies have shown that it is potentially automatic when one person is informed of the form and perspective properties of their partner's task (Elekes, Varga, & Király, 2016). By contrast, *'level-1 perspective taking'* reflects our understanding of what someone else can see and it is generally not considered an embodied process (Kessler & Rutherford, 2010; Michelon & Zacks, 2006; Surtees et al., 2013b). Furthermore, level-1 perspective-taking has been described as an implicit process, which refers to the pre-reflective, automatic and effortless simulation of what someone else sees from their position in space (Nielsen, Slade, Levy, & Holmes, 2015; Pavlidou, Ferre, & Lopez, 2018; Samson, Apperly, Braithwaite, Andrews, & Scott, 2010; for a critical perspective on this issue, however, see Santiesteban, Catmur, Hopkins, Bird, & Heyes, 2014).

A useful measure of implicit level-1 perspective-taking in a laboratory setting is the *dot-counting task* (Samson et al., 2010). Participants are asked to make perceptual judgments about the number of dots visible from *their* egocentric viewpoint in the presence of a task-irrelevant avatar. Response times increase for trials in which the avatar "sees" a number of dots incongruent with the number of dots visible from the participants' viewpoint. This increase in response times reflects the time taken to implicitly adopt the avatar's perspective, referred to as *altercentric intrusion* (Samson et al., 2010). While postural effects were documented in explicit judgments about how someone else sees the environment (left/right judgment) and in explicit judgments of what is visible from someone else's position, this has not been reported for implicit level-1 perspective-taking using the dot-counting task. The present study investigates novel embodiment effects by measuring the contribution of body posture to implicit level-1 perspective-taking. We hypothesize a decrease in altercentric intrusions when participants adopt an incongruent body posture to that of the avatar compared to a congruent body posture.

Methods

Fourty-eight healthy participants completed a modified version of the *dot-counting task* (Samson et al., 2010). A group of 24 participants (mean age ± SD, 24.2 ± 4.04 years) judged whether a number presented at the beginning of each trial matched the number of balls seen in a visual scene that followed (Figure 1A). A task-irrelevant avatar oriented towards the left/right wall was shown seated in the center of a room. Participants' body posture (facing left or right) was manipulated to either match or mismatch that of the avatar's in the visual scene (see Supplementary Material and Figure 1B). This allowed us to investigate whether visuo-proprioceptive information about the body posture in space affects altercentric intrusion. All participants completed both body postures. For each body posture, participants completed two blocks: one block where the participants and the avatar shared the same body posture (Matching Body Posture) and one block where the participant and the avatar had a different body posture (Mismatching Body Posture). The starting body posture and orientation were counterbalanced across participants. Another group of 24 participants (mean age ± SD, 22.3 ± 4.0 years) completed a version of the task in which the avatar was replaced by an arrow (Santiesteban et al., 2014), to exclude non-specific, visuo-spatial and attentional effects on altercentric intrusion (see Supplementary Material for full details).

The Congruency Effect (CE) (Nielsen et al., 2015), i.e. the difference in response times between incongruent and congruent viewpoints for each visual stimulus (avatar/arrow), was estimated for both matching and mismatching body postures. We also calculated the number of errors for each experimental condition.

Results

A mixed-model repeated-measures ANOVA revealed a significant interaction between Visual Stimulus and Body Posture ($F_{1,46} = 12.0$, $p < 0.01$, $\eta^2_p = 0.21$; Figure 1C and Supplementary Figure 2). Post-hoc analysis using Bonferroni tests revealed increased CE, namely stronger altercentric intrusions, when participants shared the posture with the avatar compared to when they were in different postures ($p = 0.01$; Supplementary Figure 2). Altercentric intrusions were significantly stronger for the avatar than for the arrow when body postures matched ($p = 0.02$; Figure 1C and Supplementary Figure 2). Critically, congruency between participants' posture and the arrow's orientation did not modulate CE ($p = 0.45$). No main effect of Visual Stimulus ($F_{1,46} = 1.44$, $p = 0.23$, η^2_p = 0.03) or Body Posture ($F_{1,46} = 0.81$, $p = 0.37$, $\eta^2_p = 0.02$) was observed.

A similar analysis applied to the number of errors revealed no significant effects of Visual Stimulus, Body Posture or interaction between factors (all $F < 3.8$ and $p > 0.05$; Supplementary Figure 1). The overall number of errors was very small and not informative to detect significant differences.

Discussion

Proprioception has been considered an *intrinsically somatic* signal, which senses the body posture and movement in space (Proske & Gandevia, 2012). Critically, proprioceptive signals are constantly integrated with visual information to build up a coherent representation of the bodily self. Here, we demonstrate that incongruent visuo-proprioceptive signals between one's own body posture and someone else's decreases the likelihood of adopting their visuo-spatial perspective. This postural effect is in line with electrophysiological studies in primate studies, which showed area 5 neurons did not respond to a fake arm placed in unrealistic postures. However, neurons in area 5 responded to the position of the monkey's arm, even if the arm was hidden from view, or if it was replaced by a fake arm located in realistic positions (Graziano, Cooke, & Taylor, 2000). Similarly, in our study adopting congruent body postures significantly strengthened the shared perspective between self and others. In addition, human neuroimaging revealed larger hemodynamic response in the posterior parietal cortex for congruent bimodal visuo-proprioceptive information about the position of the hand in space (Limanowski & Blankenburg, 2016). Critically, the posterior parietal cortex is also involved in determining the spatial relations between the body and objects in its surroundings, which might have been also relevant in estimating the relation between body posture and the avatar's line of sight in our task.

Our task focuses on level-1 perspective-taking and shows that current sensory information about the position of the body in space influences our understanding of what someone else can see on an implicit level. This is in strong contrast to previous studies which manipulated the body posture of participants while explicitly asking them to make level-1 perspective-taking judgments as to whether or not a target is to the front or the back of someone (i.e. Kessler & Rutherford, 2010). This observation however, is in line with the recent finding that low-intensity galvanic vestibular stimulation applied during the dot-counting task decreases altercentric intrusion, making participants more "egocentric" (Pavlidou et al., 2018). Altogether, these results suggest that level-1 perspective-taking may be a more embodied process than previously thought (Kessler & Rutherford, 2010; Surtees, Apperly, & Samson, 2013a; Surtees et al., 2013b).

The dot-counting task has recently been criticized that it does not provide evidence of implicit perspective-taking, as both avatars and arrows have been shown to redirect visuo-spatial attention to one side of the visual scene (Santiesteban et al., 2014; reviewed in Heyes 2014). While Santiesteban et al. (2014) reported significant altercentric intrusions for arrow stimuli, conflicting evidence suggests that altercentric intrusion arises from attributing mental states to the avatar (Furlanetto et al., 2016). Importantly in our study, adopting the visuo-spatial perspective of another was only observed for the avatar and not for the arrow. Thus, sharing visuo-proprioceptive information may help in sharing perspectives only when the “other” is human-like and does not extend to biologically irrelevant objects.

One might think that sharing cultural and ethnic backgrounds shapes how we share the view of the world, however our results indicate that even low-level pre-conscious bodily signals, such as posture, might drive whether we take another person’s perspective. Hence, visuo-proprioceptive signals are not only essential for how we perceive our own body, but also play an important role in influencing basic aspects of social cognition.

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Figure 1. Experimental setup and results. (A) Each trial started with a fixation cross (750 ms), followed by a number (1000 ms) and then a visual scene showing a 3D room (maximum time 2000 ms) containing from zero to three balls dispatched on one or two opposite walls. At the centre of the 3D room a gender-matched avatar (for 24 participants), or an arrow (for 24 other participants), was presented with a viewpoint congruent (18 trials per block) or incongruent (18 trials per block) to that of the participants. Participants had to indicate with a button press whether the number of blue balls observed from their viewpoint matched or mismatched the number presented at the start of the trial. **(B)** The experimental design is factorial combining viewpoint (congruent and incongruent) and body posture (matching and mismatching). Participants were seated on a chair that was oriented to face either the left or right side of the room. Participants' head was turned to face a computer screen where an avatar was also seated facing either the left or right side of a virtual room. For each chair orientation (facing the left or right side of the room) participants either had the same body posture with the avatar or a different one. A matching body posture with a congruent viewpoint and a mismatching body posture with an incongruent viewpoint of the participant facing the left side of the room with respect to the avatar is shown. **(C)** Box-and-whisker plots comparing congruency effect, calculated as the difference in reaction times between trials with incongruent and congruent viewpoints, when the participant and visual stimulus (avatar/arrow) had the same body posture (red box) or a different body posture (blue box). The upper and lower bound of each box represent the 75th and 25th percentiles of the distribution, and the median is represented by the thick horizontal line inside the box. The top and bottom ends of the whisker represent the 95th and 5th percentiles of the distribution, respectively. The white dot represents the mean and the black dots represent outliers.

***Credit Author Statement**

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A.P, C.L and E.R.F designed the study and experimental setup. A.P and M.G recruited participants and acquired the data. A.P performed the data analysis. A.P, C.L and E.R.F contributed to writing the manuscript. All authors approved the final version for submission.

Figure
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