FISEVIER

Contents lists available at ScienceDirect

Consciousness and Cognition

journal homepage: www.elsevier.com/locate/concog



Dissociating contributions of head and torso to spatial reference frames: The misalignment paradigm



Adrian J.T. Alsmith^{a,*}, Elisa R. Ferrè^b, Matthew R. Longo^{c,*}

- ^a Center for Subjectivity Research, University of Copenhagen, Denmark
- ^b Department of Psychology, Royal Holloway, University of London, UK
- ^c Department of Psychological Sciences, Birkbeck, University of London, UK

ABSTRACT

When we represent someone's view of a scene as egocentrically structured, where do we represent the origin of the reference frame? By analysing responses in a spatial perspective-taking task as a function of spatial location with respect to both head and torso, we isolated the respective contribution of each part to spatial judgments. Both the head and the torso contributed to judgements, though with greater contributions from the torso. A second experiment manipulating visual contrast of the torso showed that this does not reflect low-level differences in visual salience between body parts. Our results demonstrate that spatial perspective-taking relies on a weighted combination of reference frames centred on different parts of the body.

1. Introduction

In egocentric frames of reference, coordinate axes are locked to one's body and move along with it. Facing east looking at the Duomo in Milan, the Museo del Novecento is to your right and the Galleria is to your left; facing west from the steps of the Duomo, the opposite is true (Bisiach & Luzzatti, 1978). Egocentric representations are perspectival in this sense. They capture a way the world is experienced from an individual's location, in a manner sensitive to how the individual's body is disposed. Hence, what you see as 'to the left' would be seen as 'to the right' for someone facing you. Consequently, egocentric representations are thought to be essential to the self-specifying nature of spatial perception, presenting the world in relation to oneself (Bermúdez, 1998, 2002; Cassam, 1997; Evans, 1982). Moreover, recent research on self-consciousness is dominated by the idea that the experienced first-person perspective should be identified with the point of origin of an egocentric frame of reference (Blanke & Metzinger, 2009; Foley, Whitwell, & Goodale, 2015; Vogeley & Fink, 2003).

This, however, raises a difficulty: human bodies are not points. Rather, they are composed of articulated parts, which can move independently. Accordingly, changes in relative orientation can dissociate frames of reference anchored to different parts. This might affect the way things appear, as Peacocke describes:

Looking straight ahead at Buckingham Palace is one experience. It is another to look at the palace with one's face still toward it but with one's body turned toward a point on the right. In this second case the palace is experienced as being off to one side from the direction of straight ahead, even if the view remains exactly the same as in the first case.

Peacocke, 1992, p. 62

Fig. 1 shows a schematic depiction of Peacocke's scenario. In the left panel, the observer is facing Buckingham Palace directly,

E-mail addresses: adrian.alsmith@hum.ku.dk (A.J.T. Alsmith), m.longo@bbk.ac.uk (M.R. Longo).

^{*} Corresponding authors.













Fig. 1. A schematic depiction of Peacocke's (1992) Buckingham Palace scenario. With both torso and head in alignment, the Palace is directly in front of the observer in both head and torso anchored reference frames (*left panel*). Peacocke asks us to imagine the torso being turned to the right (*centre panel*), expressing the intuition that the Palace would be experienced by the observer as being to the left. This intuition, however, privileges the torso. To fully explore the scenario, the additional case of the head being turned to the right (*right panel*) must also be considered. Would Buckingham Palace also be experienced as to the left in this latter case?

whereas in the centre panel the observer's torso is turned to the right. The intuition here is that the Palace would then be experienced as to the left. Critically, however, this intuition is torso-centric. To probe Peacocke's conclusion, we might adapt the example as shown in the right panel and consider what would happen if the converse were the case: what if one turned one's face to the right while keeping one's body still toward the palace? Would the palace then be experienced as straight-ahead or off to the side? In short, where is the ego in egocentric representation?

As noted above, much of the interest in studying egocentric representation is to learn something about the structure of first-person experience. There are well known difficulties involved in asking subjects to report upon the structure of their own experience (Schwitzgebel, 2011). However, one interpretation of Peacocke's Buckingham Palace scenario above suggests a slightly oblique approach to the problem. When engaging in the thought experiment we are not asked to judge how the world appears from our own perspective, rather we are asked to predict how the world would be experienced from an imagined perspective. This general ability, known as *perspective-taking*, may involve representing any of a large variety of an agent's internal states and their relations to objects and other individuals in their environment (Moll & Meltzoff, 2011). Spatial perspective-taking tasks, in particular, concern spatial relations between an object and an individual (Salatas & Flavell, 1976).

Spatial perspective taking involves a reference frame of a similar kind to an egocentric reference frame, in that both specify how things are presented to an individual viewing a scene from a particular position. But it is not, strictly speaking, egocentric, in that it does not specify how things are presented to the subject herself. Hence, we shall use the term 'alter-egocentric representation' to describe the form of spatial representation employed here (Grush, 2000, 2007) and thus pursue the corresponding question: where is the ego in alter-egocentric representation?

A sense of the range of plausible answers to this question can be gained by considering the complexity of the processes involved in egocentric representation and their connection with the structure of experience. Sensory systems are known to process information in frames of reference anchored to specific body-parts (e.g., Graziano, Yap, & Gross, 1994), as well as hybrid frames involving combinations of these (e.g., Carrozzo & Lacquaniti, 1994), and idiosyncratic frames for transformation between body-part anchored frames (e.g., Chang & Snyder, 2010; Gazzaniga, Ledoux, & Wilson, 1977). Though frames of reference of this kind are often called 'egocentric', some are keen to distinguish this range of body-part anchored coding from the 'egocentric' structure of perceptual experience (Brewer & Pears, 1993; Foley et al., 2015; Levinson, 1996). Indeed, first-person reflection suggests that perceptual experience is unified according to a single perspective (Bayne, 2010; Bermúdez, 1998; Husserl, 1952). To the extent that the perspectival character of experience is due to body-part anchored spatial representation, this would suggest the general hypothesis that information in distinct frames of reference is translated into a single, ultimate frame of reference.

From this general hypothesis, we may draw distinct hypotheses concerning which body-part would anchor an ultimate frame. Research on spatial representation suggests independent motivation for such an ultimate frame being anchored to the head (e.g., Avillac, Denève, Olivier, Pouget, & Duhamel, 2005) or to the torso (e.g., Grubb & Reed, 2002; Karnath, Schenkel, & Fischer, 1991). A key motivation for a head-centric hypothesis is the number and significance of the sensory organs found in the head: the eyes, ears, and the vestibular labyrinth. As Sherrington noted, the latter is a particularly significant source of self-specific information, in that the vestibular system "maintains not merely a limb in flexion or extension, but a posture of the whole animal in regard to gravitation" (Sherrington, 1907, p. 480). But considering morphological structure, the torso is, effectively, the great continent of the body, relative to which other parts are mere peninsulas (Alsmith & Longo, 2014). Accordingly, a key motivation for a torso-centric hypothesis is that the torso is the most stable anchor for the construction of a consistent egocentric representation (Blanke, 2012; Grush, 2000).

8010525741680Both of these hypotheses face a common difficulty, which is that there is a lack of any strong theoretical basis for thinking that there must be such an ultimate frame anchored to a single body part. Correspondingly, there is as yet little exploration

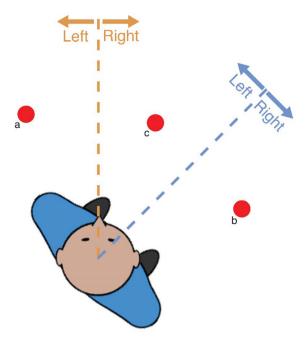


Fig. 2. The *Misalignment Paradigm*. The locations of balls a (to the person's left) and b (to their right) are clear. The critical trials are those like ball c: is it to the person's right or to their left? If the torso is the origin of the egocentric reference frame, ball c is to the person's left; if the head is the origin, it is to their right. The dashed orange line and arrows show an axis locked to the head; the blue line shows an axis locked to the torso. These lines are illustrative and were not shown to participants. On this trial, the torso is in the 'Northeast' orientation with the head turned 45° to the left. The three balls are shown at the 'Mid' distance. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of the alternative general hypothesis that the complex structure of egocentric representation is reflected in experience, such that both the head and the torso contribute to the determination of egocentric perspective (Alsmith & Longo, 2014; Smith, 2010). This would accommodate the fact that the head and torso are each functionally significant in the ways outlined above. But it would violate the largely introspective intuition that egocentric spatial perception involves a single, ultimate egocentric frame of reference.

The Misalignment Paradigm, the logic of which is shown in Fig. 2, provides a means of testing these general hypotheses. By rotating the head relative to the torso one can dissociate frames of reference centred upon the two body parts. Thus, a single object may be 'to the right' with respect to the head, yet 'to the left' with respect to the torso. By measuring how responses change as a function of spatial relation to head and torso, one can isolate the respective contributions of each body part to egocentric representation.

We investigated the structure of alter-egocentric representation through a third-person implementation of the Misalignment Paradigm – essentially, a psychophysical version of the Buckingham Palace thought-experiment. We showed participants a bird's eye view of an avatar whose head and torso were misaligned and asked them to judge whether objects were "to the person's left" or "to the person's right". By measuring how these judgments change as a function of the position of the ball relative to the head and torso, we were able to determine the respective contributions of each body part to alter-egocentric spatial judgments of this kind. In *Experiment 1*, we show that both head and torso contribute to alter-egocentric judgments, though the weight given to the torso is greater. In *Experiment 2*, we show that the greater weight given to the torso is not an artefact of greater visual salience.

2. Experiment 1: dissociating head- and torso-centred contributions

2.1. Methods

2.1.1. Participants

Twenty participants (nine female) between 18 and 60 years of age participated. All but two were right-handed as assessed by the Edinburgh Inventory (Oldfield, 1971; M: 72.8, range: -90.9 to 100). Procedures were approved by the local ethics committee.

2.1.2. Procedures

Sample stimuli are shown in Fig. 1. Stimuli were displayed on a monitor (approximately 40 cm from the participant) controlled by a custom MATLAB (Mathworks, Natick, MA) script. On each block of trials the torso (200 pixels in width, 10.63° visual angle) was centred on the monitor, oriented toward one of five compass directions (E, NE, N, NW, W), with the head rotated 45° to either the right or left, resulting in ten different positions. Each of the ten positions was presented once in random order. Rotating the body across blocks forced participants to respond based on the location of the ball with respect to the person, rather than using cues such as whether the ball appeared on the right or left side of the screen. The S, SE, and SW orientations were not used because pilot testing revealed that they imposed a high cognitive load in trying to rotate one's own perspective to match the person's, consistent with

previous results showing that perspective-taking tasks of this kind are more difficult when there is a rotation of the avatar and the participant (Kessler & Rutherford, 2010; Surtees, Apperly, & Samson, 2013b).

Within each block, the ball appeared at one of thirteen angles between -90° and $+90^{\circ}$ degrees calculated from their deviation from the line midway between the orientation of the head and torso. For each angle, there were three distances of the ball from the person, *Near* (120 pixels, 6.39°, from the centre of her head), *Mid* (240 pixels, 12.78°), and *Far* (360 pixels, 19.17°). It has long been established that perceptual processes partition space surrounding an observer according to increased distance from the body (Cutting & Vishton, 1995; Previc, 1998). One particularly salient (though gradual) transition is between the peripersonal region immediately surrounding the body and the region beyond (Longo & Lourenco, 2006; Lourenco & Longo, 2007). Recent work on peripersonal spatial representation (PPS) has demonstrated that its extent is not uniform across the body. Rather, "the size of PPS" varies "according to the stimulated body part, being progressively bigger for the hand, then face, and largest for the trunk" (Serino et al., 2015, p. 1). Accordingly, for the near distance the ball was well within the person's arm reach, in the mid condition it was at about the limit of arm's reach, and in the far condition was well outside of arm's reach. This allowed us to investigate the spatial gradient of the respective influences of head and torso.

In order to maximize the number of most informative judgments, within each distance the three centre angles $(0^{\circ}, 15^{\circ}, -15^{\circ})$ were each presented three times, the next three most extreme on each side $(30^{\circ}, 45^{\circ}, 60^{\circ}, -30^{\circ}, -45^{\circ}, -60^{\circ})$ were each presented twice, and the most extreme angles $(75^{\circ}, 90^{\circ}, -75^{\circ}, -90^{\circ})$ were each presented once. Thus, there were a total of 75 trials on each block and 750 overall.

Participants were instructed to "judge whether the ball is to the person's left or to their right". They made unspeeded responses by pressing the 'q' key on the keyboard with the left index finger if they judged the ball as being to the person's left and the 'p' key with their right index finger if they judged it as being to the person's right. After each response the ball disappeared and there was a random inter-trial interval between 200 and 500 ms. The person remained on the screen during the interval. Participants were asked to be careful with their responses, but to not spend a lot of time thinking about individual responses and to use whichever response seemed intuitive to them.

2.2. Analysis

The data were analysed in two different ways to isolate contributions of the head and of the torso to judgments. First, to isolate contributions of the head, we analysed responses as a function of angular deviation of the ball from an axis aligned with the torso, comparing the conditions in which the head was rotated to the right vs. to the left. If judgments were based entirely on the torso, with no contribution from the head, these conditions should not differ from each other, since they are identical aside from the orientation of the head. Analogously, to isolate contributions of the torso, we analysed responses as a function of angular deviation of the ball from an axis aligned with the head, comparing the conditions in which the torso was rotated to the right vs. to the left. If judgments were based entirely on the head, with no contribution from the torso, these conditions should not differ from each other, since they are identical aside from the orientation of the torso.

In each case, psychometric functions were fit to the data using the Palamedes toolbox for MATLAB (Prins & Kingdon, 2009). Best-fitting cumulative Gaussian functions were fit using maximum-likelihood estimation for each participant in each condition. For each psychometric function, the point of subjective equality (PSE) was calculated as the angular deviation at which participants were equally likely to judge the ball as being to the person's left or to their right. We quantified the contribution of the head and of the torso by calculating the *PSE Shift* for each part, defined as the difference in PSE between the conditions in which the relevant part was rotated to the left and to the right. If a part makes no contribution to judgments, PSE Shifts for that part should be clustered around zero, whereas if it does make a contribution, PSE Shifts should be greater than 0. By definition, the PSE Shifts for the head and for the torso must sum to 90° for each distance. Thus, by comparing the PSE Shifts for the two parts, we can estimate the contribution of each to judgments of alter-egocentric location.

2.3. Results and discussion

The results are shown in Fig. 3. Overall, the psychometric functions showed excellent fit to the data, with an average R^2 of 0.957 (range: 0.764–1). The top panel shows data locked to the torso, meaning that the two conditions differ only in terms of the rotation of the head. A clear contribution of the head to judgments was apparent at all distances (i.e., the blue curves are shifted relative to the orange ones). The bottom panel shows the same data locked to the head, meaning that the two conditions differ only in terms of the rotation of the torso. A clear contribution of the torso was also apparent at all distances, and was of larger magnitude than that of the head.

The contribution of each body part was quantified by calculating the PSE Shift. These PSE shifts are shown in the left panel of Fig. 4. PSE shifts for both body parts were clearly greater than 0 at all distances (torso: t(19) = 8.18, 8.41, 8.81, for the three distances, respectively, all p's < 0.0001, Cohen's d = 1.89, 1.88, 1.97; head: t(19) = 4.36, 4.03, 3.78, all p's < 0.002, Cohen's d = 0.97, 0.90, 0.84).

To compare PSE shifts across distances and body parts we conducted a repeated-measures Analysis of Variance (ANOVA) with factors 'body part' (torso, head) and 'distance' (near, mid, far). As is clear in Fig. 4, there was a significant main effect of body part, F (1, 19) = 4.97, p < 0.05, η_p^2 = 0.207, with significantly larger coefficients for the torso than the head. There was no main effect of distance, F(1.50, 28.51) = 0.72, p < 0.05, η_p^2 = 0.036, but there was a significant interaction, F(1.47, 27.88) = 4.06, p < 0.05, q_p^2 = 0.176. The interaction reflects an increase in the contribution of the torso, and a corresponding decrease in the contribution of

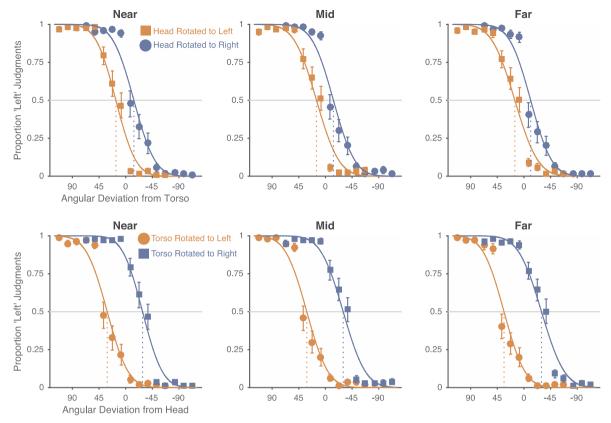


Fig. 3. Results from Experiment 1. The top panel shows data locked to the torso for each of the three ball distances. If the head were irrelevant to judgments, then the blue and orange curves should lie directly on top of each other. The observed separation between these curves (i.e., the PSE Shift) reflects the contribution of the head to judgments. The bottom panel shows the same data locked to the head. If the torso were irrelevant to judgments, the blue and orange curves should overlap. The observed separation between the curves thus reflects the contribution of the torso to judgments, which is clearly larger than that of the head. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the head, with increasing ball distance.

The right panel of Fig. 4 shows a scatterplot of PSE Shifts for the head and for the torso, averaged across the three distances. By definition, the correlation between these variables is -1, since they must sum to 90° . The range of inter-subject variability is striking. For example, the three participants at the top-left relied almost exclusively on the head, whereas the larger group at the bottom-right relied almost exclusively on the torso. Finally, another group of participants in the centre of the plot relied on both head and torso.

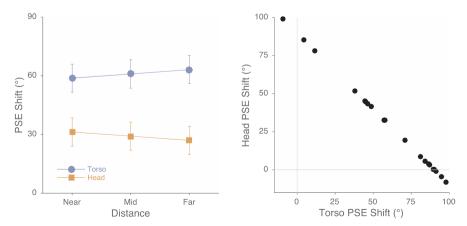


Fig. 4. *Left panel:* Mean PSE Shifts for the torso and head at each of the three distances in Experiment 1. PSE Shifts were clearly greater than 0 for both body parts at all distances, suggesting contributions of both head and torso to alter-egocentric judgments. The overall contribution from the torso, however, was clearly greater than that of the head. Error bars are standard errors. *Right panel:* Scatterplot of PSE Shifts for the torso and head, averaged across the three distances. Because the PSE Shifts for torso and head add to 90° , their correlation is -1 by definition. The interest in the scatterplot is in the range of inter-subject variability in judgments, with some participants relying exclusively on the head (at top-left), others on the torso (at bottom-right), and others still using a weighted combination of the two.

Thus, the pattern seen in the left panel of Fig. 4 masks considerable individual differences.

Both the head and the torso contribute to judgments of alter-egocentric spatial location. This calls into question the idea that any single body part constitutes the unique 'origin' of the alter-egocentric reference frame. However, the torso's overall contribution to judgments was substantially stronger than that of the head. Further, people appear to divide into three distinct groups: 'torso' people, 'head' people, and 'both' people. The overall stronger weighting for the torso comes about because there are simply more 'torso' than 'head' people. This still leaves open the question of why overall the torso is preferred. We investigated one potential interpretation of this result in a second experiment.

3. Experiment 2: weights do not reflect differences in visual salience

One potential interpretation of the overall greater weight given to the torso than the head could be the greater salience of the torso. This idea could play out in different ways. In one sense, the torso is more visually salient simply in the sense that it's substantially larger than the head is. This isn't a confound in the design of Experiment 1 so much as a basic fact about the structure of human bodies. It could very well be the case that the torso is weighted heavily exactly because it constitutes the major bulk of the physical body. But it could also be that differences in the visual salience of the torso and head *in our stimuli specifically* might have affected performance. To investigate this possibility, the second experiment manipulated the contrast between the colour of the torso and the screen background. If the visual salience of a body part affects the extent to which participants base their judgments on that part, then the contribution given to the torso should increase systematically with the contrast between it and the background. We chose to manipulate visual contrast, rather than the size of the torso because we were concerned that using unrealistic proportions between different body parts could make the figure less human, and therefore reduce the extent to which participants were able to adopt the avatar's perspective.

3.1. Methods

3.1.1. Participants

An additional twenty participants (nine female) between 18 and 58 years participated. All but one were right-handed as assessed by the Edinburgh Inventory (M: 71.9, range: -83.3 to 100).

3.1.2 Procedures

Procedures were identical to Experiment 1 with two exceptions. First, and most critically, the torso was of three different colours across blocks to manipulate the visual salience of the torso against the background (see Fig. 5). The three torso colours were all shades of grey. The middle contrast was set to have the same difference in colour from the background as the head, where difference was defined as the Euclidean distance of the two colours in RGB space. The low contrast torso had half the Euclidean distance to the background, while the high contrast torso has 150% of the distance. Second, all balls appeared at the middle distance.

3.2. Results and discussion

Results from Experiment 2 are shown in Fig. 6. The psychometric functions showed excellent fit to the data, with an average R^2 of 0.945 (range: 0.709–1). As in the first experiment, there were clear effects of both the head and the torso, which were apparent for all three levels of contrast. In every case, the contribution of the torso was of larger magnitude than of the head.

PSE Shifts are shown in Fig. 7. These were significantly greater than 0 for both torso and head at all three contrasts (torso: t(19) = 10.01, 10.07, 10.12, for the three contrasts, respectively, all p's < 0.0001, Cohen's d = 2.24, 2.25, 2.26; head: t(19) = 3.29, 3.46, 4.05, all p's < 0.005, Cohen's d = 0.74, 0.77, 0.91).

An ANOVA on PSE Shifts revealed a significant main effect of body part, F(1, 19) = 10.88, p < 0.0005, $\eta_p^2 = 0.364$, with larger shifts for the torso than for the head. Critically, however, there was no main effect of contrast level, F(2, 38) = 1.05, n.s., $\eta_p^2 = 0.053$, nor an interaction of body part and contrast, F(2, 38) = 1.43, P(2, 38) = 0.052, P(2, 38) = 0.053.

These results replicate the key effects from Experiment 1. Critically, they also show that the difference between the contribution of

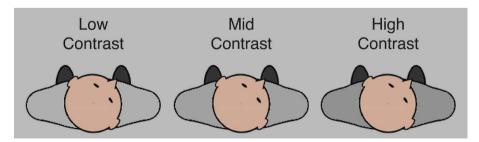


Fig. 5. Examples of stimuli used in Experiment 2. Across blocks, the torso was displayed in three different colours to manipulate its visual salience against the background. In the mid contrast condition, the colour difference between the torso and background was set to equal the difference between the head and background. In the low contrast condition, this difference was halved, while in the high contrast condition it was increased by 50%.

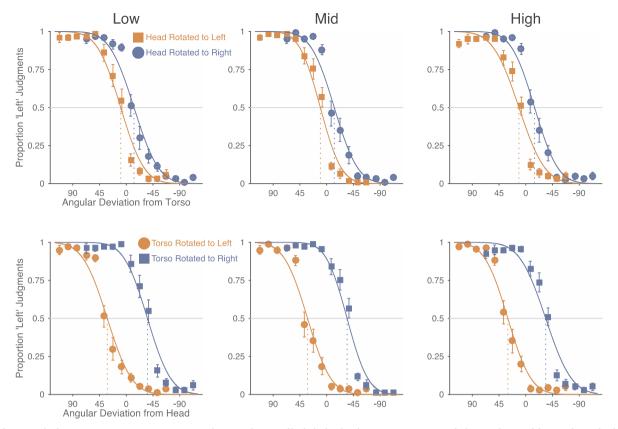


Fig. 6. Results from Experiment 2. As in Experiment 1, clear contributions of both the head and torso were apparent, with the contribution of the torso being clearly larger. The same pattern was apparent across all levels of contrast.

the head and the torso is unlikely to reflect greater visual salience of the torso.

4. General discussion

Our results are consistent with the general hypothesis that both the head and the torso contribute to the determination of alter-egocentric perspective. Our task involves third-person, alter-egocentric judgements, but it raises the question of what misalignment might tell us about the structure of first-person experience. There is certainly evidence that spatial structures involved in first-person experience are also used in imagined experience of objects from elsewhere (Creem, Wraga, & Proffitt, 2001; Wraga, Creem, & Proffitt,

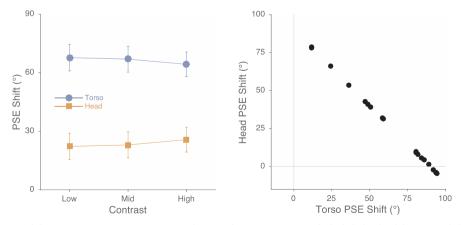


Fig. 7. Left panel: Mean PSE Shifts in Experiment 2. As in Experiment 1, clear contributions were apparent for both the head and the torso, with the torso's contribution being larger than the head's. Critically, this effect was not affected by the contrast of the torso against the background, suggesting that the difference between the body parts is unlikely to reflect a difference in visual salience. *Right panel*: Also as in Experiment 1, there was a large range of individual differences in the weights given to the head and torso.

2000). Moreover, it has been shown that 'left'/'right' judgements are affected by the angular disparity between the 'avatar' (the referent of the perspective-taking judgement) and the subject making the judgement (Michelon & Zacks, 2006). Subsequent studies have also demonstrated that reaction times increase when a subject's posture is incongruent with that of the avatar (Kessler & Rutherford, 2010; Surtees et al., 2013b). This suggests that subjects perform tasks of this kind by transforming their own perspective accordingly. They imagine rotating their own body until it aligns with that of the avatar, in order to judge the relative position of the object (Kessler & Thomson, 2010). Nothing in our study demonstrates that subjects do in fact perform the task in this way, but this possibility warrants a comparison between egocentric judgements in the first-person case and in the third-person case.

To our knowledge, no existing study of spatial perception has implemented the misalignment paradigm *per se*, i.e., independently manipulating the orientation of both head and torso to create a critical region with opposite laterality in relation to different body parts. Some studies have employed rotation of the torso in order to demonstrate its contribution to spatial attention, with mixed results. Rorden, Karnath, and Driver (2001) found that inducing illusions of torso rotation did not produce concomitant effects in attentional orientation. However, Grubb and Reed (2002) were able to induce pseudoneglect in a covert attention task by leftward rotation of the torso. Hasselbach-Heitzeg and Reuter-Lorenz (2002) also found that rightward rotation reduced response times for targets on the right. Using a similar paradigm (adapted to enable treadmill walking) Grubb, Reed, Bate, Garza, and Roberts (2008) show that torso orientation facilitates target detection only when subjects are under increased motor load.

The misalignment paradigm, here employed in an alter-egocentric task, allows the determination of the relative contributions of body parts to spatial judgements. We found that both the head and the torso contributed to judgements, with slightly greater reliance on the torso, despite the fact that motor load remained constant. Future research should address whether a fully egocentric implementation of the task would find similar results.

Considering the contributions of multiple body parts to spatial perspective highlights an often unconsidered complexity inherent in the concept of an egocentric frame of reference. In the simplest case, the axes of an egocentric frame of reference are all anchored to a single body part and the origin of that frame is embedded within that body part. But this need not be the case (cf. Bisiach, 1996; Howard, 1982). Consider, for instance, Peacocke's example of viewing an object when one's torso is twisted to the right. Even if the object is seen as off to the side due to the orientation of the torso, it might still be the case that the origin is embedded within the head. Hence, what is seen may be seen from the head, but in a manner determined by the orientation of the torso; or even vice versa.

Closely related to the idea that there is a single, ultimate egocentric frame of reference is the idea that a particular part of the body fixes a subject's ultimate location. Recent studies have explored this latter idea, with varying methods and somewhat mixed results. Starmans and Bloom (2012) found that pre-school children and adults deemed an object to be closest to a subject when it is in front of the subject's eyes, suggesting that "children and adults intuitively think of the self as occupying a physical location within the body, close to the eyes" (Starmans & Bloom, 2012, p. 317). By contrast, Limanowski and Hecht (2011) found that participants asked to mark the location of the self within an outline of a human body provided responses clustered around both the head and torso. Similarly, Alsmith and Longo (2014) found that perceptually based self-location judgements distribute between particular regions of the head and torso.

These mixed results are difficult to reconcile with the idea of an ultimate egocentric frame, but are wholly consistent with the hypothesis that both the head and torso play a key role in determining the position of objects relative to an individual. Indeed, if egocentric representations involved in first-person experience of a surrounding world do not have a single anchor, it may be that egocentric representations do not have a single or determinate origin: when one sees something relative to oneself, one may see it relative to various parts of one's body, even simultaneously. By using an alter-egocentric task in which head and torso orientations could be systematically misaligned, we are able to demonstrate the feasibility of these otherwise perhaps counter-intuitive ideas as fruitful areas of research on egocentric representation.

Our study also advances the spatial perspective-taking literature's increasing concern with subjects' sensitivity to the bodily disposition of the avatar. Early studies in this area used unarticulated dolls as avatars, focusing principally on manipulations of the relative position of the avatar and the target object (Michelon & Zacks, 2006; Salatas & Flavell, 1976). More recent studies have investigated the extent to which such mental transformations are 'embodied' by manipulating proprioceptive input through changes in posture, specifically hand position relative to torso (Furlanetto, Gallace, Ansuini, & Becchio, 2014) and torso orientation (Kessler & Rutherford, 2010; Kessler & Thomson, 2010; Surtees et al., 2013b). The present study demonstrates that if subjects perform such tasks by means of imagined alignment with the body of the avatar, they could do so by either imaginatively aligning their head or their torso with that of the avatar.

In Experiment 1 there was a significant interaction between distance and body part, with the weight given to the head decreasing with the distance of the ball from the avatar, though this effect was quite small in comparison to the overall difference between the head and torso. Indeed, the role of distance in perspective-taking studies is somewhat unclear. Michelon and Zacks (2006) found longer response times at greater distance in a left-right task, but they were able to determine that this was likely due to a conflation of linear distance and angular distance from the avatar's midline. More recently, Surtees, Apperly, and Samson (2013a) did a comparison of four different kinds of perspective-taking task (including a left-right task) and found a main effect of distance, but no interaction between distance and the type of task. But in another study, Surtees et al. (2013b) found no effect of distance in a left-right spatial perspective-taking task. A compelling hypothesis here is that distance effects could be due to demands on spatial attention, i.e., that "this difference in difficulty is really more due to the distance across which we must sustain our visual attention to connect the Other and the Object" (see also Carlson & Van Deman, 2008; Surtees et al., 2013a, p. 436).

5. Conclusion

Egocentric representations present the world in relation to oneself, taking the body as their point of origin. This seemingly simple statement, however, masks a complexity: bodies are not points. Rather, they are composed of articulated, independently mobile parts. This raises the question: Where on the body is the origin of the egocentric reference frame? A corresponding issue arises for judgements of the egocentric location of objects from another person's perspective, involving 'alter-egocentric' representation. When we represent another person's view of a scene as egocentrically structured, where on their body do we represent the origin of the alter-egocentric reference frame? Intuition suggests that frames of reference anchored to particular body parts are translated into an ultimate egocentric frame of reference. Existing research on spatial representation is inconsistent on this point, suggesting independent motivation for both the head and the torso being the anchor for such an ultimate frame. Our results demonstrate that alter-egocentric spatial judgments rely on a weighted combination of reference frames centred on at least two different parts of the body. This calls into question the idea that any single body part constitutes the unique 'origin' of the egocentric reference frame. The Misalignment Paradigm thus opens up otherwise counter-intuitive avenues of research into the role of bodily disposition in perspective-taking and its connection with self-consciousness.

Acknowledgments

This research was supported by a grant from the Volkswagen Stiftung to A.A. and M.R.L. and by a European Research Council grant (ERC-2013-StG-336050) to M.R.L. Thanks to Elizabeth Kuye and Aisha Abdullah for assistance with data collection.

References

Alsmith, A., & Longo, M. (2014). Where exactly am I? Self-location judgements distribute between head and torso. Consciousness and Cognition, 24, 70–74. http://dx.doi.org/10.1016/j.concog.2013.12.005.

Avillac, M., Denève, S., Olivier, E., Pouget, A., & Duhamel, J.-R. (2005). Reference frames for representing visual and tactile locations in parietal cortex. *Nature Neuroscience*, 8, 941–949.

Bayne, T. (2010). The unity of consciousness. Oxford: Oxford University Press.

Bermúdez, J. L. (1998). The paradox of self-consciousness. Cambridge, MA: MIT Press.

Bermúdez, J. L. (2002). The sources of self-consciousness. Proceedings of the Aristotelian Society (Hardback), 102(1), 87–107. http://dx.doi.org/10.1111/j.0066-7372. 2003.00044.x.

Bisiach, E. (1996). Unilateral neglect and the structure of space representation. Current Directions in Psychological Science, 62-65.

Bisiach, E., & Luzzatti, C. (1978). Unilateral neglect of representational space. Cortex, 14(1), 129-133.

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. Nature Reviews Neuroscience, 13(8), 556–571.

Blanke, O., & Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. Trends in Cognitive Sciences, 13, 7–13.

Brewer, B., & Pears, J. (1993). Introduction: Frames of Reference. In N. Eilan, R. A. McCarthy, & B. Brewer (Eds.), Spatial representation: Problems in philosophy and psychology (pp. 25–31). Oxford: Oxford University Press.

Carlson, L. A., & Van Deman, S. R. (2008). Inhibition within a reference frame during the interpretation of spatial language. *Cognition*, 106(1), 384–407. http://dx.doi.org/10.1016/j.cognition.2007.03.009.

Carrozzo, M., & Lacquaniti, F. (1994). A hybrid frame of reference for visuo-manual coordination. NeuroReport, 5(4), 453-456.

Cassam, Q. (1997). Self and world. Oxford: Oxford University Press.

Chang, S. W., & Snyder, L. H. (2010). Idiosyncratic and systematic aspects of spatial representations in the macaque parietal cortex. *Proceedings of the National Academy of Sciences*, 107(17), 7951–7956.

Creen, S. H., Wraga, M., & Proffitt, D. R. (2001). Imagining physically impossible self-rotations: geometry is more important than gravity. *Cognition*, 81(1), 41–64. http://dx.doi.org/10.1016/S0010-0277(01)00118-4.

Cutting, J., & Vishton, P. (1995). Perceiving layout and knowing distances: The integration, relative potency, and contextual use of information about depth. In W. Epstein, & S. Rogers (Eds.), *Perception of space and motion* (pp. 69–117). San Diego, CA: Academic Press.

Evans, G. (1982). The varieties of reference. Oxford: Oxford University Press.

Foley, R. T., Whitwell, R. L., & Goodale, M. A. (2015). The two-visual-systems hypothesis and the perspectival features of visual experience. Consciousness and Cognition, 35, 225–233.

Furlanetto, T., Gallace, A., Ansuini, C., & Becchio, C. (2014). Effects of arm crossing on spatial perspective-taking. *PLoS ONE*, 9(4), e95748. http://dx.doi.org/10.1371/journal.pone.0095748.

Gazzaniga, M. S., Ledoux, J. E., & Wilson, D. H. (1977). Language, praxis, and the right hemisphere. Neurology, 27(12), 1144.

Graziano, M., Yap, G., & Gross, C. (1994). Coding of visual space by premotor neurons. *Science*, 266(5187), 1054–1057. http://dx.doi.org/10.1126/science.7973661. Grubb, J. D., & Reed, C. L. (2002). Trunk orientation induces neglect-like lateral biases in covert attention. *Psychological Science*, 13(6), 553–556.

Grubb, J. D., Reed, C. L., Bate, S., Garza, J., & Roberts, R. J. (2008). Walking reveals trunk orientation bias for visual attention. Attention, Perception, & Psychophysics, 70(4), 688–696.

Grush, R. (2000). Self, world and space: The meaning and mechanisms of ego-and allocentric spatial representation. Brain and Mind, 1, 59-92.

Grush, R. (2007). Agency, emulation, and other minds. Cognitive Semiotics, 49-67.

Hasselbach-Heitzeg, M. M., & Reuter-Lorenz, P. A. (2002). Egocentric body-centered coordinates modulate visuomotor performance. *Neuropsychologia*, 40(11), 1822–1833.

Howard, I. P. (1982). Human visual orientation. London: John Wiley & Sons.

Husserl, E. (1952). Ideen zur einer reinen Phänomenologie und phänomenologischen Philosophie (Zweites Buch): Phänomenologische Untersuchungen zur Konstitution. The Hague: Martinus Nijhoff Publishers.

Karnath, H. O., Schenkel, P., & Fischer, B. (1991). Trunk orientation as the determining factor of the 'contralateral' deficit in the neglect syndrome and as the physical anchor of the internal representation of body orientation in space. *Brain*, 114, 1997–2014.

Kessler, K., & Rutherford, H. (2010). The two forms of visuo-spatial perspective taking are differently embodied and subserve different spatial prepositions. *Frontiers in Psychology*, 1. http://dx.doi.org/10.3389/fpsyg.2010.00213.

Kessler, K., & Thomson, L. A. (2010). The embodied nature of spatial perspective taking: Embodied transformation versus sensorimotor interference. *Cognition*, 114(1), 72–88. http://dx.doi.org/10.1016/j.cognition.2009.08.015.

Levinson, S. C. (1996). Frames of reference and Molyneux's question: Crosslinguistic evidence. In P. Bloom, M. A. Peterson, L. Nadel, & M. Garrett (Eds.), Language and space (pp. 109–169). Cambridge, MA: MIT Press.

Limanowski, J., & Hecht, H. (2011). Where do we stand on locating the self? Psychology, 2(4), 312.

Longo, M. R., & Lourenco, S. F. (2006). On the nature of near space: Effects of tool use and the transition to far space. *Neuropsychologia*, 44(6), 977–981. http://dx.doi.org/10.1016/j.neuropsychologia.2005.09.003.

Lourenco, S. F., & Longo, M. R. (2007). Space perception and body morphology: Extent of near space scales with arm length. *Experimental Brain Research*, 177, 285–290

Michelon, P., & Zacks, J. M. (2006). Two kinds of visual perspective taking. Perception & Psychophysics, 68(2), 327-337.

Moll, H., & Meltzoff, A. N. (2011). Perspective taking and its foundation in joint attention. In N. Eilan, H. Lerman, & J. Roessler (Eds.), *Perception, causation and objectivity* (pp. 286–304). Oxford: Oxford University Press.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia, 9(1), 97-113.

Peacocke, C. (1992). A study of concepts. Cambridge, MA: MIT Press.

Previc, F. H. (1998). The neuropsychology of 3-D space. Psychological Bulletin, 124(2), 123-164.

Prins, N., & Kingdon, F. (2009). Palamedes: Matlab routines for analyzing psychophysical data. Palamedes: Matlab routines for analyzing psychophysical data.

Rorden, C., Karnath, H.-O., & Driver, J. (2001). Do neck-proprioceptive and caloric-vestibular stimulation influence covert visual attention in normals, as they influence visual neglect? *Neuropsychologia*, 39(4), 364–375. http://dx.doi.org/10.1016/S0028-3932(00)00126-3.

Salatas, H., & Flavell, J. H. (1976). Perspective taking: The development of two components of knowledge. Child Development, 103-109.

Schwitzgebel, E. (2011). Perplexities of consciousness. Cambridge, MA: MIT Press.

Serino, A., Noel, J.-P., Galli, G., Canzoneri, E., Marmaroli, P., Lissek, H., & Blanke, O. (2015). Body part-centered and full body-centered peripersonal space representations. *Scientific Reports*, 5, 18603. http://dx.doi.org/10.1038/srep18603 < http://www.nature.com/articles/srep18603#supplementary-information > . Sherrington, C. (1907). On the proprio-ceptive system, especially in its reflex aspect. *Brain: A Journal of Neurology*, 29(4), 467–482. http://dx.doi.org/10.1093/brain/294467

Smith, A. J. T. (2010). Comment: Minimal conditions on the simplest form of self-consciousness. In T. Fuchs, H. Sattel, & P. Henningsen (Eds.), *The embodied self: Dimensions, coherence, disorders* (pp. 35–41). Stuttgart: Schattauer.

Starmans, C., & Bloom, P. (2012). Windows to the soul: Children and adults see the eyes as the location of the self. *Cognition*, 123(2), 313–318. http://dx.doi.org/10. 1016/j.cognition.2012.02.002.

Surtees, A., Apperly, I., & Samson, D. (2013a). Similarities and differences in visual and spatial perspective-taking processes. *Cognition*, 129(2), 426–438. http://dx.doi.org/10.1016/j.cognition.2013.06.008.

Surtees, A., Apperly, I., & Samson, D. (2013b). The use of embodied self-rotation for visual and spatial perspective-taking. Frontiers in Human Neuroscience, 7. http://dx.doi.org/10.3389/fnhum.2013.00698.

Vogeley, K., & Fink, G. R. (2003). Neural correlates of the first-person-perspective. Trends in Cognitive Sciences, 7(1), 38-42.

Wraga, M., Creem, S. H., & Proffitt, D. R. (2000). Updating displays after imagined object and viewer rotations. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, 26(1), 151.