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Shared contributions of the head and torso to spatial reference frames across spatial judgments

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ABSTRACT

Egocentric frames of reference take the body as the point of origin of a spatial coordinate system. Bodies, however, are not points, but extended objects, with distinct parts that can move independently of one another. We recently developed a novel paradigm to probe the use of different body parts in simple spatial judgments, what we called the *misalignment paradigm*. In this study, we applied the misalignment paradigm in a perspective-taking task to investigate whether the weightings given to different body parts are shared across different spatial judgments involving different spatial axes. Participants saw birds-eye images of a person with their head rotated 45° relative to the torso. On each trial, a ball appeared and participants made judgments either of whether the ball was to the person's left or right, or whether the ball was in front of the person or behind them. By analysing the pattern of responses with respect to both head and torso, we quantified the contribution of each body part to the reference frames underlying each judgment. For both judgment types we found clear contributions of both head and torso, with more weight being given on average to the torso. Individual differences in the use of the two body parts were correlated across judgment types indicating the use of a shared set of weightings used across spatial axes and judgments. Moreover, retesting of participants several months later showed high stability of these weightings, suggesting that they are stable characteristics of people.

1. Introduction

Egocentric frames of reference take the body as the point of origin of a spatial coordinate system (Klatzky, 1998). Recent work on self-consciousness has identified our first-person perspective with the point of origin of such an egocentric reference frame (Blanke & Metzinger, 2009; Foley, Whitwell, & Goodale, 2015; Vogeley & Fink, 2003). This raises a problem, however, since bodies are not points, but rather extended objects with multiple articulated parts which can move independently of each other. Changes in body posture therefore dissociate potential reference frames anchored to different body parts. It is therefore critical to understand the way in which different parts of the body contribute to judgments about the perceived spatial locations of objects.

The role of individual body parts in shaping judgments of visuospatial location is highlighted by Peacocke's (1992) Buckingham Palace thought experiment (pg. 62):

> "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."

This example nicely captures the intuition that changes of body posture can dissociate the relative spatial relations of objects to different body parts, highlighting the problem of which body part – if any – serves as the origin of body-centred reference frames. Interestingly, Peacocke's own intuition seems to be *torso-centric*. The judgment that the palace is "experienced as being off to one side" links a change in the visuospatial location of the palace with a change in torso orientation. One could, however, pose the analogous question of where the palace would seem to be if one's torso remained oriented facing the palace but one's head was turned to the right.

It is also important to note that while it is natural to perform Peacocke's thought experiment by imagining *oneself* in front of Buckingham Palace, exactly the same issues arise if we make judgments about another person. This capacity for reasoning about another's visuospatial perception has been described as perspective-taking

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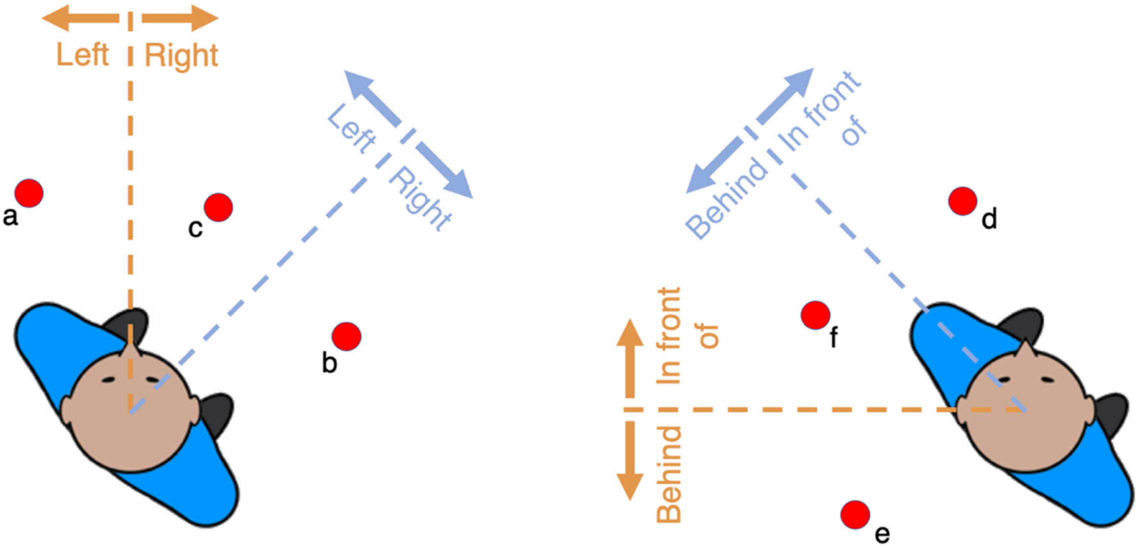

Fig. 1. Logic of the *misalignment paradigm*. *Left panel*: The *left/right* judgment task. The locations of balls *a* and *c* are unambiguously to the person's left and to their right, respectively. The more interesting case is locations such as that of ball *c*: because of the misalignment of the head and torso, ball *c* is to the person's right if the head is taken to be the origin of the reference frame, but to their left if the torso is taken to be the origin. *Right panel*: The *in front of/behind* judgment task. The locations of balls *d* and *e* are unambiguously in front of and behind the person, respectively. The key question is about locations such as that of ball *f*, which is in a situation analogous to that of ball *c* for *left/right* judgments. The dashed blue lines and blue arrows show an axis locked to the torso, while the orange lines and arrows show an axis locked to the head. These lines and arrows were not shown to participants. In this figure, the torso is in the 'Northeast' (NE) orientation and the head is rotated 45° to the left. Across blocks, the body was presented in a range of orientations (as shown in Fig. 2, below) to ensure that participants were responding based on a reference frame centred on the person depicted, rather than on their own body or on the monitor. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Michelon & Zacks, 2006; Salatas & Flavell, 1976). In taking another's perspective, we may employ a body-centred frame of reference, in so far as we take (a part of) that person's body as the origin of the relevant spatial frame of reference. For instance, taking the *Queen's* perspective, as her procession approaches Buckingham Palace moving East along The Mall, our answer to the question "Is the palace to left or right?" may be sensitive to whether her torso is orientated toward St James's Park (roughly to the South) or St James's Square (roughly to the North), even as her gaze remains fixed on the palace ahead. The issue about which body parts shape spatial reference frames is therefore not specific to judgments in which one determines an object's location in relation to oneself. Rather, it applies more generally to judgments in which one determines an object's location in relation to any particular person.

A substantial literature on the use of reference frames for visuomotor control of action has revealed evidence for a range of different reference frames. One influential view has linked the dorsal and ventral visual pathways to egocentric and allocentric reference frames, respectively (Foley et al., 2015; Goodale & Haffenden, 1998; Milner & Goodale, 2006). Single-unit neurophysiological studies in monkeys have demonstrated the existence of neurons with receptive fields coding the visual location of objects in references frames anchored to specific body parts, including the eyes (e.g., Andersen, Essick, & Siegel, 1985), head (e.g., Duhamel, Bremmer, BenHamed, & Graf, 1997), and hands (e.g., Graziano, Yap, & Gross, 1994). There is also evidence for neurons coding hybrid combinations of body parts (Carrozzo & Lacquaniti, 1994; Chang, Papadimitriou, & Snyder, 2009; Pesaran, Nelson, & Andersen, 2006; Piserchia et al., 2017), and modulation of responses coded in an eye-centred frame of reference by the position of other body parts (Chang et al., 2009; Zipser & Andersen, 1988) as well as idiosyncratic reference frames presumably related to transformation between different reference frames (Chang & Snyder, 2010; Gazzaniga, LeDoux, & Wilson, 1977), which has been found to involve a process of vector subtraction of the location of one body part relative to another (Batista, Buneo, Snyder, & Andersen, 1999; Buneo, Jarvis, Batista, & Andersen, 2002).

Studies in humans using both neuroimaging (Bernier & Grafton, 2010; Mcguire & Sabes, 2009; Sober & Sabes, 2005) and behavioural reaching paradigms (Beurze et al., 2006; Heuer & Sangals, 1998; Lemay & Stelmach, 2005; McIntyre, Stratta, & Lacquaniti, 1998) have shown that multiple reference frames centred on different body parts can be simultaneously activated and flexibly weighted based on the availability of different types of sensory information and task goals. Other studies have reported similar weighting of egocentric and allocentric representations (Byrne & Crawford, 2010; Chen et al., 2014). A gradient has been proposed between the posterior parietal and premotor cortices, with the former coding location more strongly in eye-centred and the latter in hand-centred reference frames (Pesaran et al., 2006). Nevertheless, introspection suggests that perceptual experience is unified to form a single first-person perspective (Bayne, 2010; Bermúdez, 1998), indicating that reference frames centred on different body parts may become integrated into a single ultimate reference frame underlying subjective perceptual experience. Various empirical and theoretical considerations have been advanced for why either the head (Avillac, Denève, Olivier, Pouget, & Duhamel, 2005; Sherrington, 1907), the eyes (Cohen & Andersen, 2002), or the torso (Alsmith & Longo, 2014; Blanke, 2012; Grubb & Reed, 2002; Grush, 2000; Karnath, Schenkel, & Fischer, 1991; Serino et al., 2015) might have such a privileged role. Sherrington (1907), for example, notes the wide range of sensory apparatus in the head, emphasising in particular the vestibular system's role in providing the overall posture of the whole body relative to gravity, a perspective also emphasised by recent research (Abekawa, Ferrè, Gallagher, Gomi, & Haggard, 2018; Pavlidou, Ferrè, & Lopez, 2018). Other researchers have emphasised the torso's position as a stable anchor for the limbs and head (Blanke, 2012; Grush, 2000), as "the great continent of the body" (Alsmith & Longo, 2014, pg. 74).

We recently developed a novel approach to quantifying the contribution of different body parts to 3rd-person spatial judgments, what we call the *misalignment paradigm* (Alsmith, Ferrè, & Longo, 2017). This paradigm is essentially an experimentalization of Peacocke's (1992) Buckingham Palace thought experiment, described above. Participants saw a top-down view of a person with their head rotated 45° to either the left or right of the torso, as shown in Fig. 1. On each trial, a red ball appeared, and participants judged whether the ball was to the person's left or to their right. Because the head and torso are misaligned, there are locations in which the ball is to the left with respect to one body part, but to the right with respect to the other. By presenting balls at different locations, we quantified the relative weighting given to the head and to the torso for *left/right* spatial judgments. We found that both the head and the torso were used, with greater weight on average being given to the torso. However, a wide range of patterns was observed across participants, with some people relying almost entirely on the torso, others relying almost entirely on the head, and others using a combination of both body parts. These results indicate that left/right spatial judgments rely, at least in some people, on a combination of frames of reference centred on the torso and on the head, and may do so with unequal weighting that may differ across people.

It remains unclear whether these results reflect the weighting of the torso and head specifically for judgments of right and left, or if they reflect a more general feature of spatial cognition. There is evidence that the *Left/Right* dimension may be uniquely confusable (Farrell, 1979; Nicoletti & Umiltà, 1984), which may relate the it being the axis in which vertebrate bodies are bilaterally-symmetric (Corballis & Beale, 1970). There are well-established functional connections between tactile representations of homologous locations on the left and right sides of the body (e.g., Iwamura, 2000; Tamè et al., 2012; Tamè, Farnè, & Pavani, 2011), as well as evidence that the *Left/Right* dimension can be selectively impaired as in conditions such as the Gerstmann syndrome (e.g., Benton, 1959; Kinsbourne & Warrington, 1963). It is therefore possible that the weighted use of the head and torso we described in our previous study (Alsmith et al., 2017) may be specific to the left/right axis rather than being a more general feature of spatial cognition. Alternatively, given that egocentric frames of reference can be used to identify locations in full 3-D space, and not only in the left/right axis, if these body-parts weightings are a more generalizable aspect of spatial cognition they may be used across very different types of spatial judgments. It is therefore important to show that the use of both torso and head we which reported previously (Alsmith et al., 2017) generalises across multiple spatial tasks, and is not specific to the left/right axis.

The present study used the misalignment paradigm to investigate whether comparable weighting is given to the head and torso for different forms of spatial judgment. Like in our previous study, participants saw a top-down view of a person with the head and torso misaligned (Fig. 1). In the *Left/Right judgment task*, participants judged whether each ball was to the person's left or to their right, as in our previous study. In the *In front of/Behind judgment task*, participants judged whether each ball was in front of the person or behind them. By comparing conditions in which the head was rotated either clockwise or anti-clockwise relative to the torso, we quantified the weighting given to both the head and to the torso for each type of judgment. If the weightings given to the head and torso that we have previously reported result from a general mechanism for determining locations in relation to particular body parts, then similar weightings should be found in the two judgment types, which should be correlated across participants. In contrast, if the weightings we found previously are specific to the left/right axis, then no such correspondence across judgments should be found.

In addition, in order the investigate the stability of these individual differences, we brought a subset of participants back into the lab several months after initial testing to examine whether the weightings they used were similar to that they used in the initial session. In our previous study (Alsmith et al., 2017), there were strong correlations ($r > 0.9$) between the weightings used by participants in different conditions. It is possible, however, that these correlations reflect transient differences between people in terms of their mood or other state-level characteristics. If these weightings reflect stable and enduring characteristics of people, they should be correlated across different sessions separated in time.

2. Methods

2.1. Participants

Thirty people (19 women) between 17 and 50 years of age (*M*: 27.7 years, *SD*: 9.7) participated for payment. All but 3 were right-handed as assessed by the Edinburgh Inventory (Oldfield, 1971), *M*: 65.7, *range*: −91.3–100. Participants gave written informed consent before participating. Procedures were approved by the Department of Psychological Sciences Research Ethics Committee at Birkbeck, and were consistent with the Principles of the Declaration of Helsinki.

Twenty-one of the participants were re-tested on the same paradigm on another day. A minimum of four months separated each testing session (*M*: 160 days; range: 139–184 days). The procedure of the re-test session was identical to the original session except that the Edinburgh Inventory was not given. One of these participants was excluded from analyses based on poor model-fit (i.e., R^2 substantially below 0.5 in both tasks), leaving a final sample of 20 participants for our test-retest analysis.

In our previous study (Alsmith et al., 2017), we tested participants making left/right judgments in different conditions (i.e., three different ball distances in Experiment 1 and three different torso colours in Experiment 2). The correlations between the weightings for these conditions were high, the smallest pairwise correlation in Experiment 1 being 0.968 and in Experiment 2 being 0.936. This demonstrates that there are strong and highly reliable individual differences between people in the weightings they give to each body part. The two judgment types in the present experiment differ more substantially than the different conditions in our previous study, so we did not expect such high correlations between the judgment types here. Nevertheless, if the judgments rely on a common set of weightings, we should expect a robust correlation between them. Our sample size of 30 participants gives us greater than 0.8 power to detect a correlation of 0.5 (assuming alpha of 0.05 and a two-tailed test). Similarly, our sample size of 20 participants for the re-test analysis gives us greater than 0.8 power to detect a correlation of 0.6 (again for a two-tailed test with alpha of 0.05), substantially smaller than the test-retest correlations we have found within-session.

2.2. Procedure

Stimuli were similar to our previous study (Alsmith et al., 2017) and are shown in Fig. 1. Stimuli were presented on a 24-in. monitor located approximately 40 cm in front of the participant under control of a custom MATLAB (Mathworks, Natick, MA) using the Psychophysics Toolbox 3 (Brainard, 1997; Pelli, 1997). On each block, the position of the body was held constant with the torso (200 pixels in width, 7.7° visual angle) oriented toward one of five compass directions (E, NE, N, NW, W) and with the head rotated 45° clockwise or anti-clockwise, as shown in Fig. 2. As in our previous study, we did not use the S, SE, and SW orientations because pilot testing suggested that they imposed substantial cognitive load related to rotating one's own perspective to match the shown person's, consistent with other results (Kessler & Rutherford, 2010; Surtees, Apperly, & Samson, 2013a). The motivation for presenting the body in different orientations was to ensure that participants were basing their judgments on a reference frame centred on the person depicted, rather than on their own body, visual field, or on the monitor. If a participant were to respond based on the location of the ball with respect to themselves, this would produce an essentially flat psychometric function when averaged across the different rotations of the person depicted. That we find clear psychometric functions with high goodness-of-fit (see below), which span the full range from 0 to 1, provides direct evidence that participants were in fact basing their responses on the location of the ball relative to the person depicted. On each trial, a red ball (21 pixels in diameter, 0.8°) appeared 250 pixels (9.6°) from the centre of the person and participants were asked to

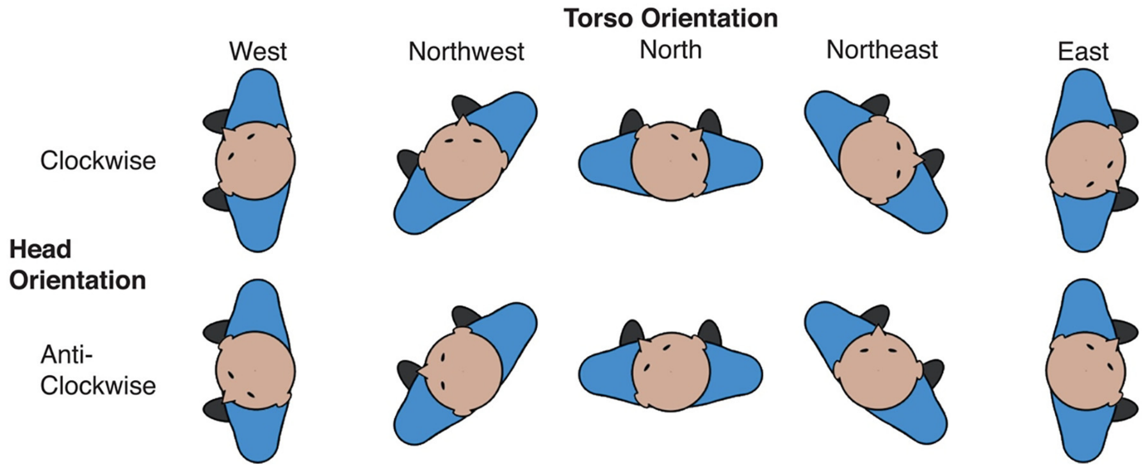

Fig. 2. The different orientations of the head and torso used in different blocks. By presenting the body in different orientations, we ensured that judgments were made based on a frame of reference centred on the person depicted, rather than one centred on the participants (e.g., on their retina or body) or on the monitor.

make simple spatial judgments about the location of the ball with respect to the person.

In different blocks of trials, participants were asked to make two different types of spatial judgment. The *Left/Right judgment task* was identical to that used in our previous study (Alsmith et al., 2017); the participant had to judge "whether the ball is to the person's LEFT or to their RIGHT". If the ball appeared to be to the person's left, the participant pressed the 'Q' key on the keyboard with their left index finger, and if it appeared to be to the person's right, they pressed the 'P' key with their right index finger. In the *In front of/Behind judgment* task the participant had to judge "whether the ball is IN FRONT OF the person or BEHIND them". If the ball appeared to be in front of the person, the participant pressed the 'Q' key with their left index finger, and if it appeared to be behind the person they pressed the 'P' key with their right index finger. Labels showing the response options for the present block and associated keys remained on the bottom left and bottom right corners of the screen throughout the block. Responses were un-speeded and participants were instructed to be careful in their responses, but not to spend a lot of time thinking about each individual trial. After each response the ball disappeared and the next ball appeared after a random inter-trial interval of between 200 and 500 ms. The person remained on the screen during the inter-trial interval.

There were 20 experimental blocks, each consisting of 32 trials. The entire experiment took around 30 min. The blocks were formed by the combination of the 5 torso orientations, 2 orientations of the head relative to the torso, and 2 tasks. The blocks were presented in random sequence. At the beginning of each block, the participant was instructed which of the two spatial judgments they would make during the upcoming block. In the Left/Right judgment task, the ball appeared at one of 13 angles between -90° and $+90^\circ$, where 0° was defined as the angle midway between the orientations of the head and torso. To maximize the number of trials that were maximally informative, the three central angles (0°, $\pm 15^\circ$) were each presented four times in each block, while the more extreme angles ($\pm 30^\circ$, $\pm 45^\circ$, $\pm 60^\circ$, $\pm 75^\circ$, $\pm 90^\circ$) were each presented twice. This procedure is similar to our previous study, but the exact distribution across the different angles was changed slightly to balance the In front of/Behind task and control the overall duration of the experiment.

In the In front of/Behind judgment task, the ball locations were divided into two sets, one centred on the person's left side (i.e., clockwise from 0° to 180°) and the other centred on the person's right side (i.e., anti-clockwise from 0° to 180°). The distribution of trials across locations was the same as in the Left/Right judgment task except that half the trials were on the left side and half on the right side.

2.3. Analysis

The analysis of data from the Left/Right judgment task was similar to that we used in our previous paper (Alsmith et al., 2017). We analysed the results in two ways to isolate the contributions of the head and the torso to judgments. To investigate the contributions of the head, we analysed responses as a function of angular deviation from the torso, comparing the conditions in which the head was rotated 45° to the left or to the right. If the head makes no contribution to judgments, then these two conditions should produce identical results since they only differ in terms of the orientation of the head. Analogously, to investigate the contributions of the torso, we analysed responses as a function of angular deviation from the head, comparing the conditions in which the torso is rotated 45° to the left or right relative to the head. If the torso makes no contribution to judgments, then these two conditions should produce identical results since they only differ in terms of the orientation of the torso.

The logic of the analysis for the In front of/Behind judgment task was analogous. To investigate contributions of the head, we analysed responses as a function of angular deviation from the torso, and vice versa to investigate contributions of the torso. The one difference from the left/right judgment task was that separate analyses were conducted on data from the left and right sides.

Psychometric functions were fit to data from each condition using the Palamedes toolbox (Prins & Kingdom, 2009) for MATLAB. Best-fitting cumulative Gaussian functions were fit with maximum-likelihood estimation for each participant in each condition. For each curve, the point of subjective equality (PSE) was calculated, that is the angular location at which the participant was equally likely to judge the ball as being to the person's left vs. right, or in front of vs. behind them. The contribution of the head and torso was quantified by calculating the *PSE Shift* for each body part. The PSE Shift is the difference in PSE between the conditions in which that body part was rotated to the left vs. to the right. If a body part does not contribute to judgments, the psychometric functions should overlap and on average the PSE Shift should equal 0. Because the two rotations involved in each comparison differ by a total of 90° (i.e., 45° in each direction), the PSE Shift for the head and the torso by definition sum to 90°. By comparing the PSE Shifts for the two parts, we can therefore estimate the contribution of each to spatial judgments.

Raw data from both sessions are available in supplemental materials.

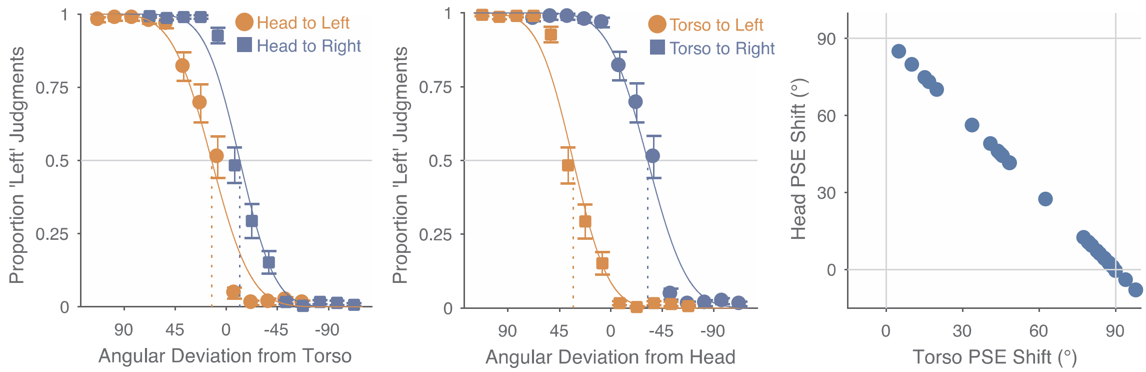

Fig. 3. Results from the *left/right* judgment task. *Left panel*: The data locked to the torso. If the head had no influence on judgments, the blue and orange curves should lie directly on top of each other. The clear separation between the two curves (i.e., the PSE Shift) demonstrates a contribution of the head to judgments. *Centre panel*: The same data locked to the head. If the torso had no influence on judgments, the blue and orange curves should lie directly on top of each other. The separation of the two curves therefore demonstrates a contribution of the torso to judgments. Comparison of the PSE Shift in the two panels shows that the contribution of the torso is, on average, larger than that of the head. *Right panel*: Scatterplot showing PSE Shifts for the torso (x-axis) and head (y-axis). Because the PSE Shifts for the two body parts necessarily sum to 90°, the correlation between them is by definition −1. The notable point about the scatterplot is the range of weightings used by different participants, with some people relying almost exclusively on the head (i.e., at the top-left), others relying almost exclusively on the torso (i.e., at bottom-right), and some using a mixture of the two (i.e., in the centre). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Left/Right judgments

The results from the Left/Right judgment task are shown in Fig. 3. The psychometric functions showed excellent fit to the data, with a mean R^2 of 0.970 (range: 0.784–1). The left panel shows data locked to the torso, such that the two conditions differ only in terms of the rotation of the head. The PSE Shift showed a clear contribution of the head to judgments, $t(29) = 4.78$, $p < .0001$, $d = 0.874$. The centre panel shows data locked to the head, such that the two conditions differ only in terms of the rotation of the torso. The PSE Shift showed a clear contribution of the torso to judgments, $t(29) = 11.87$, $p < .0001$, $d = 2.168$.

A comparison of the magnitude of PSE Shifts for the head and torso indicated that on average significantly more weight was given to the torso, $t(29) = 3.54$, $p < .002$, $d_z = 0.650$. Nevertheless, as can be seen in the scatterplot in the right panel of Fig. 3, there was a wide range of performance across participants, with some participants basing responses almost entirely on the torso, others almost entirely on the head, and others using a combination of the two. Together, these results provide a clear replication of the main findings of our previous study (Alsmith et al., 2017).

3.2. In front of/Behind judgments

The results from the In front of/Behind judgment task are shown in Fig. 4. The psychometric functions showed excellent fit to the data, with a mean R^2 of 0.931 (range: 0.781–1) in the left side analysis and 0.937 (range: 0.771–1) in the right side analysis. No differences were apparent for the left side and right side analyses, which were therefore collapsed for subsequent analyses. The top left and top centre panels of Fig. 3 show data locked to the torso, meaning that the two conditions differ only in terms of the rotation of the head. The PSE Shift (*M*: 27.3°, *SD*: 30.8°) showed a clear contribution of the head to judgments, $t(29) = 4.86$, $p < .0001$, $d = 0.888$. The bottom left and bottom centre panels of Fig. 3 show data locked to the head, meaning that the two conditions differ only in terms of the rotation of the torso. The PSE Shift (*M*: 62.7°, *SD*: 30.8°) showed a clear contribution of the torso to judgments, $t(29) = 11.14$, $p < .0001$, $d = 2.03$. The top right panel of Fig. 4 showed a scatterplot of the torso PSE Shifts for the left side and right side analyses, which were strongly correlated, $r(28) = 0.944$, $p < .0001$. (Note that because the PSE Shifts for the torso and head by definition sum to 90°, exactly the same correlation is found between the head PSE Shifts in the two conditions.)

Direct comparison of the PSE Shifts for the head and torso showed that on average the torso received significantly more weight than did the head, $t(29) = 3.14$, $p < .005$, $d_z = 0.573$. As can be seen in the scatterplot in the bottom right panel of Fig. 4, there was a range of weightings, with some participants basing judgments almost entirely on the torso and others relying almost entirely on the head, as well as intermediate patterns. Thus, the overall pattern of results for the In front of/Behind judgment task is extremely similar to that found for the Left/Right judgment task.

3.3. Comparison of spatial judgments

We next directly compared the use of head-centred and torso-centred frames of reference for the two types of spatial judgment. The left panel of Fig. 5 shows PSE Shifts for the head and torso in the two tasks. There was no difference in the weighting of the torso in the two tasks, $t(29) = 0.36$, $p = .723$, $dz = 0.065$. (Note that because the PSE Shifts for the torso and head sum to 90°, a *t*-test comparing PSE Shifts on the head would produce an equivalent test.) To determine whether this non-significant result provides support for the null hypothesis of no difference between judgments, we conducted a Bayesian paired t-test using JASP 0.8.1.1 (JASP Team, 2017), using the default parameters (Cauchy prior width = 0.707). There was moderate evidence in favour of the null hypothesis, $BF_{01} = 4.85$.

The right panel of Fig. 5 shows a scatterplot of the torso PSE Shift for the two judgments. There was a clear correlation between judgments in the weighting given to the different body parts, $r(28) = 0.736$, $p < .0001$. That is, participants who were torso-centric for the *Left/Right* judgment task were also torso-centric for the *In front of/Behind* judgment task.

3.4. Stability of weightings across time

To assess the stability of the individual differences we report across time, we re-tested participants on the same paradigm several (> 4) months after the original test. Twenty participants provided usable data. The overall pattern of results from the re-test sessions was nearly identical to that from the main experiment. The results from the left/right judgment task are shown in Supplemental Fig. 1 and from the in

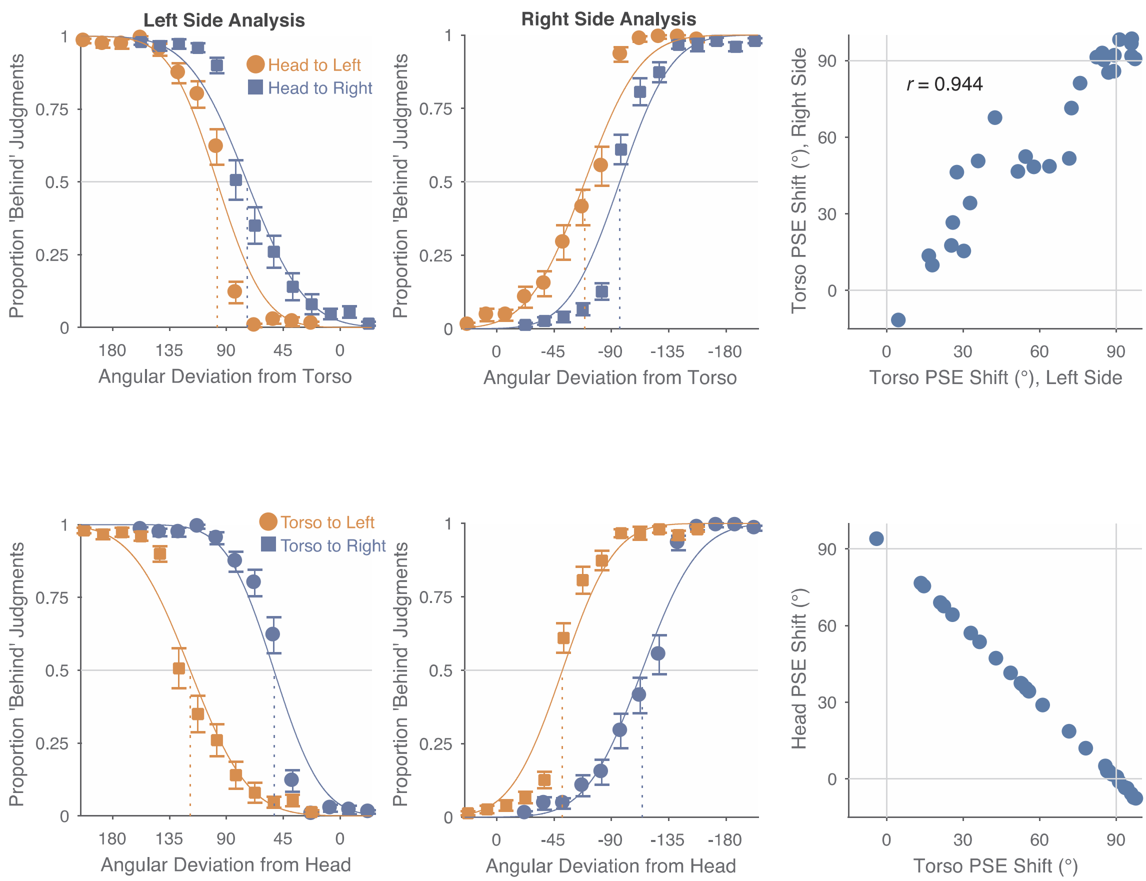

Fig. 4. Results from the *In front of/Behind* judgment task. *Top left and centre panels*: The data locked to the torso for the left side and right side analyses, respectively. If the head had no influence on judgments, the blue and orange curves should lie directly on top of each other. The clear separation between the two curves (the PSE Shift) demonstrates that the head contributes to judgments. *Bottom left and centre panels*: The same data locked to the head. If the torso had no influence on judgments, the two curves should lie on top of each other. The clear separation between the curves thus demonstrates a contribution of the torso to judgments. Comparison of the PSE Shifts for the torso and head shows that on average greater weighting is given to the torso than to the head. *Top left panel*: Scatterplot showing PSE Shifts for the torso for left side (x-axis) and right side (y-axis) analyses, showing highly similar responses in the two cases. *Bottom left panel*: Scatterplot showing PSE Shifts for the torso (x-axis) and head (y-axis). Because the two PSE Shifts sum to 1, the correlation between them is by definition −1. Across participants, there was a wide range of weightings given to the two body parts, with some participants relying largely on the head (top left) and other relying largely on the torso (bottom right), as well as mixed patterns. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

front of/behind judgment task in Supplemental Fig. 2. The psychometric functions showed excellent fit to the data, both for the *left/right* task (mean R^2: 0.960, range: 0.801–1) and the *in front of/behind* task for the left side analysis (mean R^2: 0.981, range: 0.687–1) and the right side analysis (mean R^2: 0.901, range: 0.608–1).

For the *left/right* task, PSE shifts showed clear contributions of both the head (M: 31.1°, SD: 31.6°), $t(19) = 4.40$, $p < .0005$, $d = 0.984$, and the torso (M: 58.9°, SD: 31.6°), $t(19) = 8.33$, $p < .0001$, $d = 1.862$, to judgments, with marginally stronger weighting on average for the torso, $t(19) = 1.96$, $p = .065$, $d_z = 0.439$. As in the main experiment, there were no apparent differences between the left side and right side analyses for the *in front of/behind* task, which were therefore collapsed. PSE shifts showed a clear contribution of both the head (M: 28.1°, SD: 31.1°), $t(19) = 4.05$, $p < .001$, $d = 0.906$, and the torso (M: 61.9°, SD: 31.2°), $t(19) = 8.89$, $p < .0001$, $d = 1.988$, to judgments, with significantly stronger weighting given on average to the torso, $t(19) = 2.43$, $p < .05$, $d_z = 0.543$.

A comparison of the two spatial tasks is shown in Supplemental Fig. 3. We found no difference in the weighting given to the torso in the two tasks, $t(19) = 0.77$, $p = .45$, $d_z = 0.172$. A Bayesian t-test again gave moderate evidence in favour of the null hypothesis, $BF_{01} = 3.31$. Also as in the main experiment there was a strong correlation between the weighting given to the different body parts, $r(18) = 0.838$, $p < .0001$.

Having shown that the overall pattern of results in the re-test session was similar to that in the initial session, the key question concerns the individual differences in the weightings given to the head and torso across sessions. As shown in Fig. 6, there were strong correlations between the two sessions, both for the *left/right* task (left panel), $r(18) = 0.906$, $p < .0001$, and the *in front of/behind* task (right panel), $r(18) = 0.731$, $p < .0005$. This shows that the individual differences we find between people in their use of the head and torso are stable across time.

4. Discussion

These results show that similar weightings of body parts are used for different types of spatial judgment. We replicated our recent finding that *Left/Right* judgments involve a reference frames centred both on the head and torso, with differences between people in the use of these body parts and use of a weighted combination of both parts in at least some people (Alsmith et al., 2017). We further show that highly similar weightings are used for a different type of spatial judgment (*In front of/Behind*). Moreover, we showed that individual differences between people are shared between these two judgments. These findings show that these weightings are a generalisable aspect of spatial cognition and not an idiosyncrasy of any specific task or judgment. In addition, we show that these weightings show a high degree of stability across

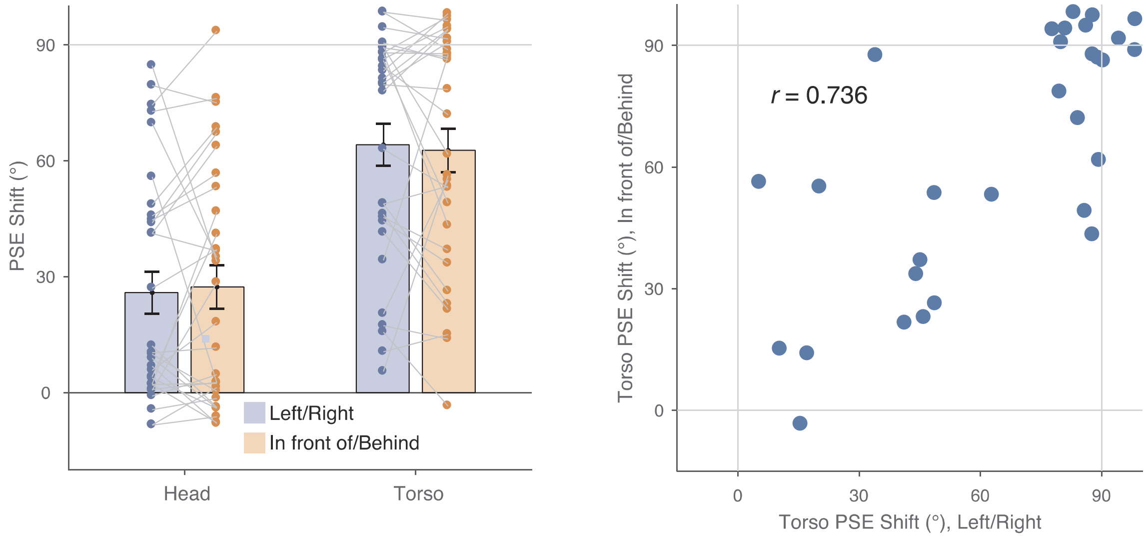

Fig. 5. Comparison of the *Left/Right* and *In front of/Behind* judgment tasks. *Left panel*: PSE Shifts for the head and torso for the two types of judgment. Bars indicate the mean across participants and error bars indicate the standard error. Blue and orange circles show individual participant responses with grey lines connecting the same participant's data for the two judgments. The horizontal grey line at 90° indicates the PSE Shift expected on average if a body part received 100% weighting. On average, highly similar weighting was given to the head and to the torso for the two types of judgment. *Right panel*: Scatterplot showing torso PSE Shifts for the two judgment types. There was a clear correlation between judgment types in the weighting given to each body part. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

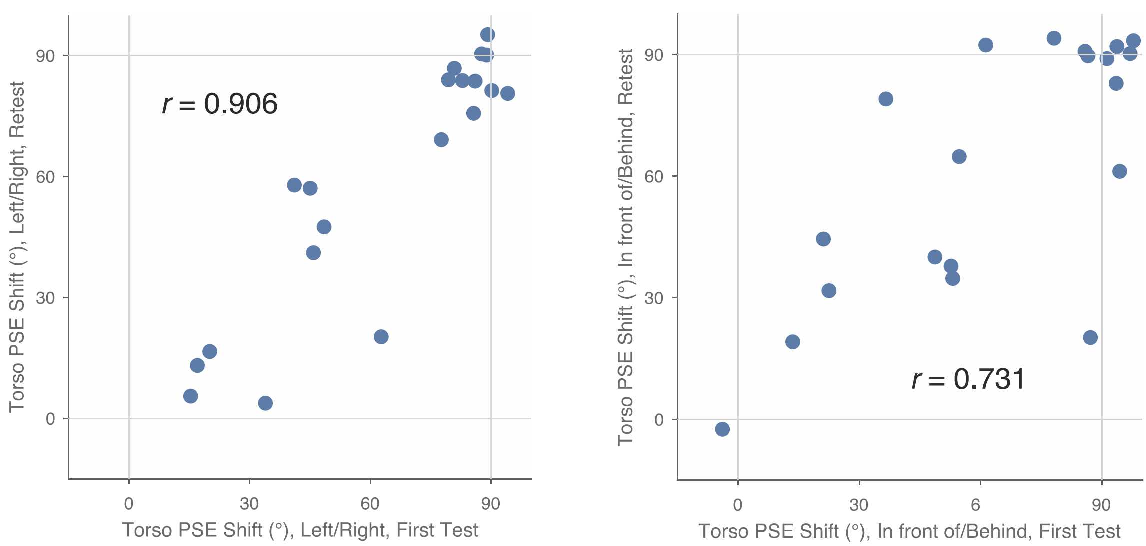

Fig. 6. Comparison of weightings for the first test session (x-axis) and the re-test session (y-axis) several months later. For both *left/right* judgments (left panel) and *in front of/behind* judgments, there were strong correlations between the weightings in the two sessions. This suggests that these weightings reflect stable individual differences between people.

testing sessions separated by several months. This suggests that these individual differences reflect enduring differences between people, rather than momentary fluctuations.

Previous work has indicated that perspective-taking judgments on the *Left/Right* dimension are qualitatively different from judgments on the *In front of/Behind* dimension. Hintzman, O'Dell, and Arndt (1981) found that pointing to targets in front of or behind a position in an imagined environment was significantly faster than for other horizontal directions. Similarly, Franklin and Tversky (1990) found that identification of objects by their locations on the *Left/Right* dimension was significantly faster than *In front of/Behind*. It is plausible that these dimensions are hierarchically related: the *Left/Right* dimension is itself a consequence of the front-back asymmetry of the body; asymmetry can provide cues for accurate reference, cues which are unavailable on the *Left/Right* dimension (Coventry & Garrod, 2004); and, indeed, competence in use of the prepositions “left of” and “right of” emerges well after “in front of” and “behind” (Harris, 1972). Our results suggest that if participants' conception of the *Left/Right* dimension is, in some respect, derived from the *In front of/Behind* dimension, they are able to make use of cues provided by the asymmetry of both the head and the torso.

A crucial contrast amongst perspective-taking tasks is marked by the difference between judging whether something is *visible* from a given perspective (level-1 perspective taking) and judging how something *appears* from a given perspective (level-2 perspective taking, Flavell, Everett, Croft, & Flavell, 1981). *Left/Right* judgments are typically classed as judgments at level-2, as they seem bound up with the ability to “grasp the relativity of notions and ideas”, as Piaget (1928) puts it. Studies using *Left/Right* judgments as a measure of level-2 perspective-taking have demonstrated that it is affected by both angular disparity

(Michelon & Zacks, 2006) and postural incongruence (Surtees et al., 2013a) between the participant and the avatar. This pattern of results is consistent with the hypothesis that level-2 perspective-taking tasks are solved by the participant imagining a reorientation of their body (Kessler & Thomson, 2010). Although our experimental design is not dispositive on this issue, if our participants did employ this strategy, they would likely have done so by employing subtly different simulations of head and torso orientation, which are nevertheless consistent over time.

The prepositions "in front of" and "behind" are similar to "left" and "right" in that their use can involve negotiating a conflict between their application in relation to the speaker or another object or person (Coventry & Garrod, 2004; Levinson, 1996). Accordingly, *In front of/Behind* judgments are sometimes described as at level-2, in so far as they involve understanding appearances as relative to perspectives in the same respect as *Left/Right* judgments (Moll & Meltzoff, 2011; Perner, Brandl, & Garnham, 2003). Of course, where an object lies on the *In front of/Behind* axis of an individual's body can affect its visibility, and indeed this reflects a favoured design choice for tests of implicit level-1 perspective taking (see, e.g., Samson, Apperly, Braithwaite, Andrews, & Bodley Scott, 2010). However, our participants are explicitly being asked to make judgments of spatial position with respect to the avatar, i.e., our task is clearly a *spatial* perspective-taking task which does not require any judgments about visibility (Surtees, Apperly, & Samson, 2013b). Furthermore, if our participants were performing the *In front of/Behind* task as a test of visibility, one would expect that their judgments would be predominantly biased by head orientation, which is not what we found.

The aim of Peacocke's (1992) Buckingham Palace thought experiment was to show how the structure of an egocentric perspective might be anchored to a particular body part. Our method exploits the fact that individuals can employ this kind of structure to assign locations relative to others. And our results show that they do so in a manner that is consistently determined by the orientation of particular body parts. This is consistent with the idea that we conceive of changes in perspective as linked to changes in body-part orientation in a way that is applicable to both ourselves and others (Alsmith, 2017). However, it does raise the question of whether there may be deep commonalities in the spatial structure of first-person perceptual experience and third-person perspective taking.

The present study only measured judgments using a third-person, perspective taking task. It would be interesting in future work to implement a first-person version of the task. Some studies have found effects of torso orientation on various aspects of attentional orienting (Grubb & Reed, 2002; Grubb, Reed, Bate, Garza, & Roberts, 2008; Hasselbach-Heitzig & Reuter-Lorenz, 2002), but to our knowledge no study has implemented a first-person version of the misalignment paradigm or of Peacocke's (1992) Buckingham Palace thought experiment. It is important to note, however, that there is substantial evidence that first-person experience is used in spatial judgments that do not obviously involve first-person judgments (e.g., Creem, Wraga, & Proffitt, 2001; Wraga, Creem, & Proffitt, 2000). In the case of perspective-taking judgments specifically, several studies have found that performance is modulated by the congruence between the postures of two individuals (e.g., Kessler & Rutherford, 2010; Michelon & Zacks, 2006; Pavlidou, Gallagher, Lopez, & Ferrè, 2019; Surtees et al., 2013a).

Our results have interesting links to studies which have investigated whether there is a specific part of the body that serves as a subject's ultimate location. For example, Starmans and Bloom (2012) showed children and adults drawings of objects in different positions relative to a character and asked them to judge in which picture the object was closest to the person (e.g., "in which picture is the bee closest to Sally?"). They found that people judged the object as closest when it was near the person's eyes. In contrast, Limanowski and Hecht (2011) asked participants to mark the location of "the self" in a human body outline, finding that responses clustered around both the head and the torso. Other studies have asked participants to adjust the position of a pointer until it was "pointing directly at you" (Alsmith & Longo, 2014; van der Veer, Alsmith, Longo, Wong, & Mohler, 2018; van der Veer, Longo, Alsmith, Wong, & Mohler, 2019), generally finding a combination of responses to the face and upper torso, with people differing in the weighting they apply to each part.

It is intuitively natural to suppose that the axes of a body-centred reference frame are all anchored to a single specific body part, but this need not necessarily be true (Bisiach, 1996; Howard, 1982). The present results, along with other recent findings, suggest that there may not be any single part of the body which forms the 'origin' of body-centred reference frames. This fits with research investigating the references frames used by the brain in computing reach trajectories, which appear to involve a range of different reference frames, which are flexibly weighted based on sensory and goal-related factors (e.g., Bernier & Grafton, 2010; Sober & Sabes, 2005).

The present results show that highly similar patterns of weighting of the head and torso are applied to different spatial judgments, and that individual differences between people are (at least partially) shared between these. These weightings may, however, be modulated by other aspects of the context in which judgments are made or which features of a situation are most salient. It will be important for future research to probe the ways in which the weightings given to different body parts are fixed or whether they change flexibly depending on task demands. The results from our follow-up testing, however, does show that these individual differences are stable across time, with very similar weightings being applied by participants in sessions more than four months apart.

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CRediT authorship contribution statement

Matthew R. Longo: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Visualization, Supervision, Project administration, Funding acquisition. **Sampath S. Rajapakse**: Investigation, Writing - review & editing. **Adrian J.T. Alsmith**: Conceptualization, Methodology, Writing - review & editing. **Elisa R. Ferrè**: Conceptualization, Methodology, Writing - review & editing.

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