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RESEARCH ARTICLE

Visuo-Proprioceptive Matching Errors Are Consistent with Biases in Distance Judgments

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ABSTRACT. People make systematic errors when matching the location of an unseen index finger with that of a visual target. These errors are consistent over time, but idiosyncratic and surprisingly task-specific. The errors that are made when moving the unseen index finger to a visual target are not consistent with the errors when moving a visual target to the unseen index finger. To test whether such inconsistencies arise because a large part of the matching errors originate during movement execution, we compared errors in moving the unseen finger to a target with biases in deciding which of two visual targets was closer to the index finger before the movement. We found that the judgment as to which is the closest target was consistent with the matching errors. This means that inconsistencies in visuo-proprioceptive matching errors are not caused by systematic errors in movement execution, but are likely to be related to biases in sensory transformations.

Keywords: proprioception, perceptual judgments, proprioceptive position sense, sensory matching

INTRODUCTION

In their daily interaction with objects, people do not encounter problems in bringing their hand to the objects or deciding which object is closest. However, if they cannot see their hand, they make substantial idiosyncratic visuo-proprioceptive matching errors (Kuling, Brenner, & Smeets, 2013; Kuling, Brenner, & Smeets, 2016; Rincon-Gonzalez, Buneo, & Helms Tillery, 2011; Smeets, van den Dobbelsteen, de Grave, van Beers, & Brenner, 2006; Sousa, Brenner, & Smeets, 2010). These matching errors are typically a few centimetres, and they have been shown to be consistent over time (Kuling et al., 2016; Smeets et al., 2006).

Although they are consistent within a single task, the matching errors differ between tasks (Kuling, van der Graaff, Brenner, & Smeets, 2014; Kuling, van der Graaff, Brenner, & Smeets, 2017; Simani, McGuire, & Sabes, 2007). For example, moving the unseen hand to a visual target does not lead to the same matching error as moving a visual cursor to the unseen hand (by using a computer mouse; Kuling et al., 2017). As the cursor in the latter task was identical to the target in the former task, the sensory matching problem is identical: the task for the participants is to match the position of the unseen hand to that of a visual location. One can conclude from these results that the matching errors do not just reflect a mismatch between sensory representations. If the systematic errors in moving an unseen hand to visual targets are not only due to a mismatch between sensory representations, an alternative explanation that considers some additional factor is needed.

A possible explanation is that the matching errors partially arise from the sensory transformations that are needed for the task, and therefore depend on whether a hand or the cursor is moved (Kuling et al., 2017; Tagliabue & McIntyre, 2011). When moving a cursor towards one's index finger, one must transform the proprioceptive information from the arm into a desired position for the cursor (in visual coordinates). When moving one's unseen finger towards a visual target, one must transform the visual location into a desired arm configuration (in proprioceptive coordinates).

An alternative explanation for the inconsistent task-dependent matching errors is that the matching errors arise from the movements themselves rather than from the sensory transformations underlying such movements. When people make goal-directed movements they obviously make motor errors, some of which may not be corrected. If such errors are systematic they might introduce a bias in visuo-proprioceptive matching (Brown, Rosenbaum, & Sainburg, 2003a, 2003b).

To distinguish between the two possible explanations, we compared biases in a task in which participants had to make judgments about their unseen finger's distances to two visual targets before moving the finger, with biases in the subsequent movement to one of the targets. If matching errors are related to the required sensory transformations, the judgment will presumably be related to the movements that are made when trying to reach each target, and the precision of performance should be comparable for judgments and movements. On the other hand, if the matching errors are largely of motor origin,

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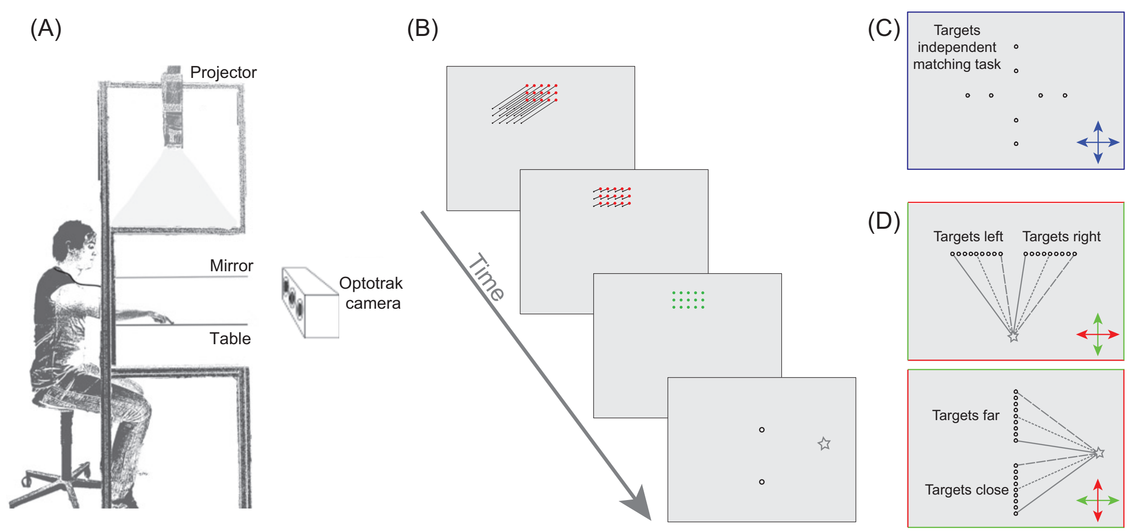

FIGURE 1. Experimental set-up and stimuli. (A) Targets were projected onto a screen located above a half-silver mirror, so that the targets appeared to be on the table. (B) Procedure for visually guiding the hand towards the starting position in the second block. Fifteen red dots were presented when the hand was not at the starting position. Lines from those dots indicate the direction and distance (scaled by a factor 10) from the hand to the target. When moving in the right direction the lines become smaller. When the starting position is reached the dots turn green and a target pair appears. The star indicates the position of the index finger at the (invisible) starting position. (C) The eight target positions of the first block (independent matching task). (D) The 18 target pairs for the second block (judgment trials), plotted separately for the two judgment directions. The red arrows indicate the judgment direction (upper panel: left-right; lower panel: far-close), while the green arrows indicate the non-judgment direction.

the judgments should be less biased than the movements, and not even necessarily biased in the same direction. The judgments should than also be more precise than the movement endpoints.

METHODS

Participants

Fifteen participants (all right-handed, 9 men, 22–30 years) volunteered to take part in the experiment, including one of the authors (WB). Except for the author, participants were naive about the purpose of the experiment. All gave their written informed consent for participation. The experiment is part of an ongoing research program that has been approved by the ethics committee of the Faculty of Behavioural and Movement Sciences of Vrije Universiteit Amsterdam.

Experimental Set-up and Tasks

Participants were seated in a chair in front of a mirror set-up, in which visual information was projected onto a horizontal surface (as in Kuling et al. (2016), Figure 1A). The semi-transparent mirror prevented participants from seeing their arms when the lights under the mirror were off. During the whole experiment, position data of the index finger were recorded at 200 Hz with an Optotrak 3020 system (Northern Digital, Waterloo, Canada) for which an infrared emitting marker was placed on the nail of the index finger.

Participants each performed two tasks in the horizontal plane. Each task was performed in a separate block of trials. In the first block, they performed a quick visuo-proprioceptive matching task by moving their unseen index finger from visual target to visual target. In the second block, the index finger was guided to an invisible starting position by displaying a field of arrows (Figure 1B; details in next subsection). From there participants had to move it to one of two visible targets: the one that they judged to be closest. We used the same order of blocks for all participants. In our previous studies with a randomized order of blocks, we did not find an influence of a matching task on performance in subsequent blocks (e.g. Kuling et al., 2013; Kuling, Brenner, & Smeets, 2015; Kuling et al., 2016). However, we cannot be sure that performing the judgment task does not influence performance in subsequent visuo-proprioceptive matching, especially since the matches are made to the same targets as one has made judgments about. To be sure to also obtain matching data that cannot be influenced by the judgment task we always first presented the quick matching task, only introducing the judgment task in the second block.

Stimuli

All targets were white disks with a diameter of 1 cm. In the first block, we used eight target positions (Figure 1C). In the second block, we used 18 target pairs. The distance between the targets within a pair was always 18 cm (Figure 1D). The positions of eight of the targets in the second block (four of the target pairs) coincided with the eight positions of the first block. The target pairs for the left-right judgment were 35 cm in front of the participant's trunk (Figure 1D, upper panel), and the target pairs for the far-close judgment were aligned with the body midline (Figure 1D, lower panel). There was a 1 cm step between adjacent target pairs.

In the first block, the endpoint of the previous movement served as the starting position for the next movement. In the second block, the participant's hand was visually guided to one of two starting positions using 15 identical arrows (Figure 1B), representing the vector from the unseen index finger to the invisible starting position (Cheng & Sabes, 2007; Kuling et al., 2016, 2017; Sober & Sabes, 2005), scaled by a factor 10. The starting position for the left-right judgment was in front of the body midline, approximately 20 cm in front of the participant's trunk. The starting position for the far-close judgment was 15 cm to the right and 35 cm from the participant's trunk. Once the index finger was at the unseen starting position, one of the visual target pairs appeared.

Procedure

The set-up was calibrated by asking participants to move with their hand to five positions with full visual feedback of the hand. Then the light under the mirror was switched off, the participant moved his or her hand to a target that appeared at the centre of the screen, and the first block started.

In the first block, participants had to reach with the index finger of their dominant hand to eight different target positions. For each target, the endpoint of the reaching movement was defined as the last of eight successive frames for which the marker was moving slower than 3.5 cm/s after having reached a velocity of at least 50 cm/s. When the endpoint was reached, the target disappeared and the next target was shown. In this block, the endpoint of one trial is thus the starting point of the next trial. The participants performed 80 trials, presented as 10 semi-random sequences of all targets, with the first target of a sequence obviously never being identical to the last target of the previous sequence.

In the second block, judgment trials were presented. Once the hand had been guided towards one of the two starting positions, two visual targets appeared, separated by 18 cm. The participants were asked to decide which of the two targets was closest to their index finger, and move towards that target. When the endpoint was reached (same criterion as in the first block), the targets disappeared and the hand was guided towards the next starting position. The 18 target pairs (with guidance to the associated starting position) were presented in 10 semi-random sequences of all pairs, resulting in 180 experimental trials. The total experiment (two blocks) took about 20 minutes to complete.

Analysis

For all trials of both blocks, we first determined the differences between the target positions and the endpoints of the movements towards those positions. We then calculated the mean over all trials to the same target. The standard deviation of the endpoints was taken as a measure of precision. This was done separately for the left-right and far-close directions.

For the second block we additionally analysed the judgments. For each target pair, the judgment was expressed as the fraction of choices for the right target (left-right judgment) or for the furthest target (far-close judgment). A cumulative normal distribution was fitted to these data. The shift of the mean of the fitted distributions with respect to the initial position of the finger corresponds to the judgment bias; the standard deviation of the fitted distribution is our measure of the precision of the judgment.

To see whether we could predict the judgment bias from the visuo-proprioceptive matching errors, three comparisons were made for both the left-right and the far-close directions. The first relates the judgment bias to the visuo-proprioceptive matching errors made in the judgment direction in the same block, i.e. the left-right matching errors in the far-closet judgment task and the far-close matching errors in the far-close judgment task (red arrows in Figure 1D). The second comparison relates the judgment bias to the visuo-proprioceptive matching errors in the non-judgment direction in the same block, i.e. the left-right matching errors in the far-close judgment task and vice versa (green arrows in Figure 1D). Note that the trials of the left-right judgment are in the judgment direction for the left-right direction, and the non-judgment direction for the far-close judgment and vice versa. The second comparison therefore relates errors on unrelated trials. The third comparison relates the judgment bias to the matching in an independent matching task, i.e. in the first block (blue arrows in Figure 1C). The third comparison therefore relates judgment errors to matching errors made before any judgments were made.

The predictions for the comparisons mentioned in the previous paragraph follow from the reasoning that reaching to the left of a visual target implies that participants would perceive their hand to be to the right of the visual target if it was aligned with the target (Figure 2). In that case, when choosing between two visual targets, the one on the right

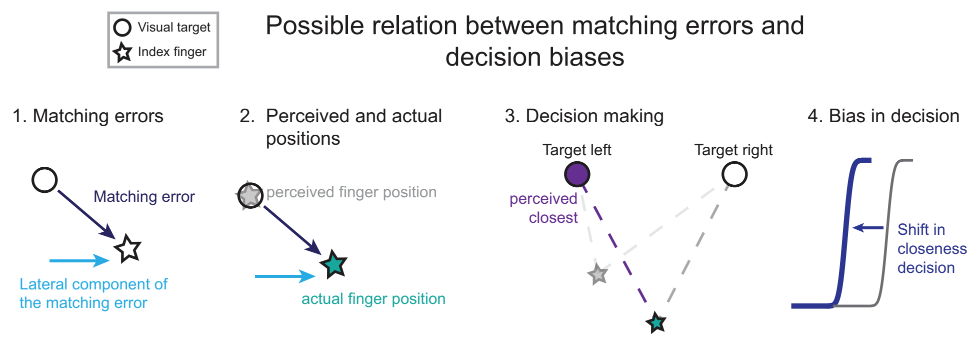

FIGURE 2. Graphic explanation of the assumed relation between matching error and judgment bias. A matching error for reaching with the hand towards a visual target to the right will lead to a bias towards choosing the left target (i.e. a leftward shift in the psychometric curve) and vice versa.

will be perceived to be closer to the hand than it actually is. Therefore, a matching error to the left is consistent with a judgment bias to the right (see Figure 3 for data of an example participant). To see whether this reasoning is reflected in our data we plotted the individual matching errors against the corresponding judgment biases (Figure 4). If the errors are related, the data will cluster along a line with an angle of –45°. To test whether our data are in line with this prediction, we calculated the angle of the major axis of the 95% confidence ellipse of the distribution. We did this 20,000 times in a bootstrapping paradigm using the 15 data point combinations (with repetitions) from our data. The mean and standard deviation of the angle of the major axis of the 95% confidence ellipse of the data can be compared with the predicted angle of –45°.

As outlined in the introduction, one might expect judgments to be more precise than matching. We tested whether the precision in block 2 differed between matching and judgments by comparing the standard deviations in the judgments with those of the reaches in the judgment direction for the left-right and far-close directions with a 2×2 RM ANOVA. As the main task in block 2 was to make the distance judgment, it might be that the participants underperformed in the matching that they used to indicate their judgment. We therefore also checked whether the precision in the judgments in block 2 differed from that of the reaches in the judgment direction in block 1 with a 2×2 RM ANOVA on the standard deviations.

RESULTS

The matching errors were similar in both blocks. Their magnitudes varied considerably across participants (range 0.5–9.1 cm), which is in line with previous findings with a similar task in the same set-up (Kuling et al., 2016, 2017).

The psychometric curves for the example participant in Figure 3 show that this participant has a judgment bias to the left (Figure 3A) and a slight judgment bias in the far direction (Figure 3B). The raw position data show a bias to the right and close, which is (as expected) in the opposite direction than the judgment bias.

When comparing the matching errors and the judgment biases for all participants, the two measures are related in the way we anticipated (Figure 4). For 5 of the 6 comparisons the predicted angle of –45° is within two standard deviations of the main axis of the 95% confidence ellipse (as determined by bootstrapping). This shows that for these comparisons the judgment biases are consistent with the corresponding visuo-proprioceptive matching errors. The matching errors in the left-right direction for the non-judgment direction were larger than one would expect on the basis of the corresponding biases in judgments (95% confidence interval does not include –45°).

Finding the anticipated relationship means that the biases do not mainly arise from systematic motor errors, because such errors would not influence the distance judgments. However, systematic motor errors presumably contribute to the deviations from the anticipated relationship. To evaluate the extent of such a contribution we tested whether judgments are more precise than matching, as one would expect if matching errors partly arise from the movements themselves. We compared the variability in judgments with that of matching (Figure 5A). Within block 2, the variability is larger in the matching than in the judgments, and larger in the far-close direction than in the left-right direction. The 2x2 RM ANOVA on the standard deviations in the judgments and in the matching in the judgment direction showed that these effects were significant (task: $F_{1,14} = 10.98$, $p = .005$; direction: $F_{1,14} = 9.98$, $p = .007$). There was no significant interaction between task and direction ($F_{1,14} = 4.22$, $p = .059$).

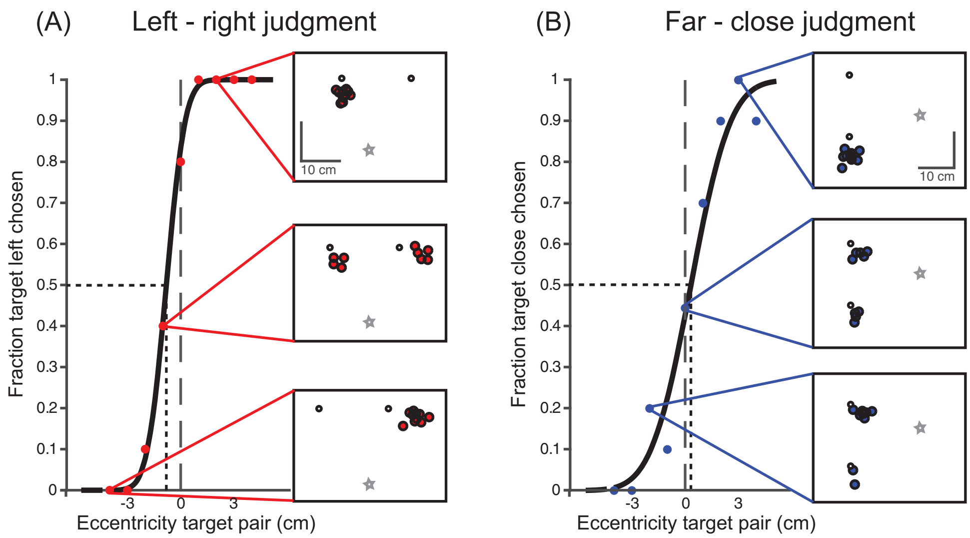

FIGURE 3. Data of an example participant in the second block. (A) Psychometric curve for the left-right target choice. The grey dashed line indicates the true midline, which is where we would expect the curve to reach 50% far choices if there were no bias. The black dotted lines indicates the actual position at which the curve crosses 50%; i.e. the actual judgment bias. The insets show the raw movement endpoints for this participant for three indicated target pairs. The open squares indicate the two target positions, and the dashed line indicates the actual position of the finger in the relevant direction. (B) Psychometric curve and raw data for the far-close judgment; details as in (A).

Finding more variability in matching than in judging supports a sizeable contribution of systematic motor errors. However, we argued in the subsection *Analysis* that we might find a larger variability in matching than in judgments in block 2 because the main task in this block was to make judgments. We therefore also compared the precision in judgments (block 2) with that of the matching in block 1 (Figure 5B). The 2x2 RM ANOVA on the standard deviations of the matching in block 1 and the judgment in block 2 showed an effect of block (i.e. of judgment versus matching; $F_{1,14} = 17.45$, $p = .001$), a main effect of direction ($F_{1,14} = 11.46$, $p = .004$), and an interaction between block and direction ($F_{1,14} = 16.90$, $p = .001$). All these effects appear to be the result of poor judgments being made in the far-close direction. As anticipated, the participants were much more precise in their reaches when they tapped a target to indicate its position (block 1, blue bars in Figure 5B) than when they moved to indicate their selection (block 2, red bars in Figure 5A). Taking this into account, we conclude that judgments of the distance of one's unseen hand relative to a visual target are not more precise than matching the position of one's unseen hand to a visual target. Thus, systematic motor errors cannot have a very large contribution to the matching errors under these circumstances.

DISCUSSION

In this study, we investigated whether visuo-proprioceptive matching errors can predict biases in distance judgments. This was tested in an experiment that consisted of a task in which two different judgment and movement directions were used, as well as a task in which participants had to move from target to target. Our results show that in general the individual matching errors can predict the judgments that one makes when asked to reach towards the closest of two targets (Figure 4). Furthermore, the variability in matching was not always larger than the variability in the judgments (Figure 5). Both findings are very unlikely if matching errors would originate in motor errors in the goal-directed movements but are compatible with matching errors that originate in sensory transformations.

Some aspects of our results deserve some discussion. The first aspect is that the precision of the matching clearly differed between the two blocks (compare red bars in Figure 5A with blue ones in Figure 5B). In contrast with the idea of a possible accumulation of motor errors (Brown et al., 2003a, 2003b), the variability was smaller in block 1, in which such accumulation could occur. A likely explanation for this difference is that participants put less effort in their matches in block 2 than block 1, because they mainly considered the matching to be a way to indicate which target was closest. In block 1, indicating the location was the task. We therefore consider block 1 to provide the correct comparison for the precision in judgment. Although the judgments were more precise than matching after the judgment in block 2, they were not more precise than matching in block 1. We therefore conclude that judgments are not more precise than matching.

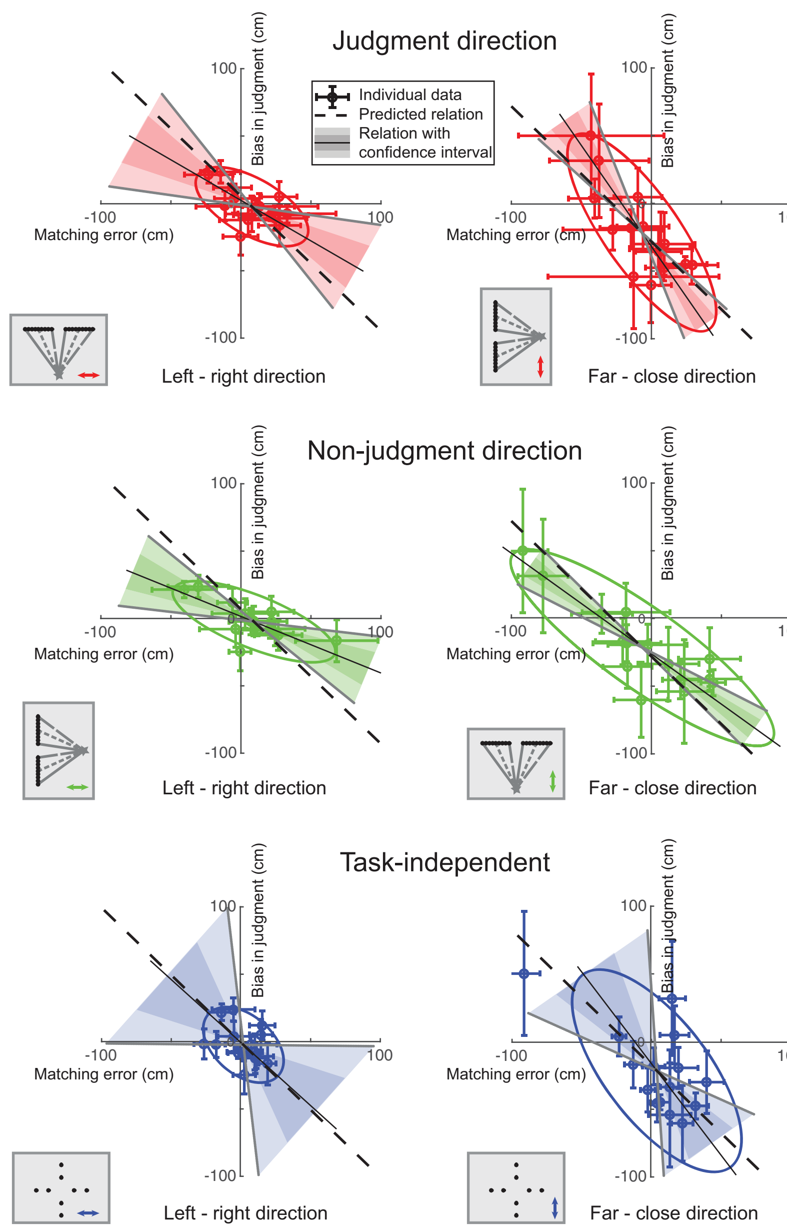

FIGURE 4. Relationship between the bias in judgments of closeness (block 2) and matching errors in the judgment direction of block 2 (upper row), non-judgment direction of block 2 (middle row), and task-independent block 1 (lower row). Each dot shows the mean value for one participant, with error bars indicating its precision (standard deviation). The –45° orientation of the predicted relation (dashed line) lies within in the 95% confidence interval (shaded areas indicate one and two standard deviations of the bootstrap results) of the mean axis of the ellipses (thin lines) for all panels, except for the non-judgment direction in the left-right direction. Note that the range of the 95% confidence interval of the angle of the main axis of the ellipse is larger in the task-independent results, indicating less consistency across the measures.

The second aspect of the results that deserves some discussion is that, although quite similar, the matching errors were not completely the same as the biases in the distance judgments (i.e. there is much variability in the relation between both measures, see Figure 4). Furthermore, although the task-independent matching was more precise (Figure 5), the deviations from the prediction (i.e. the 95% confidence area of the ellipse orientation) were much larger (poorer prediction) than within a task (Figure 4). This suggests that there are differences between the two tasks in how matching is performed. If this difference would involve the use of different sensory

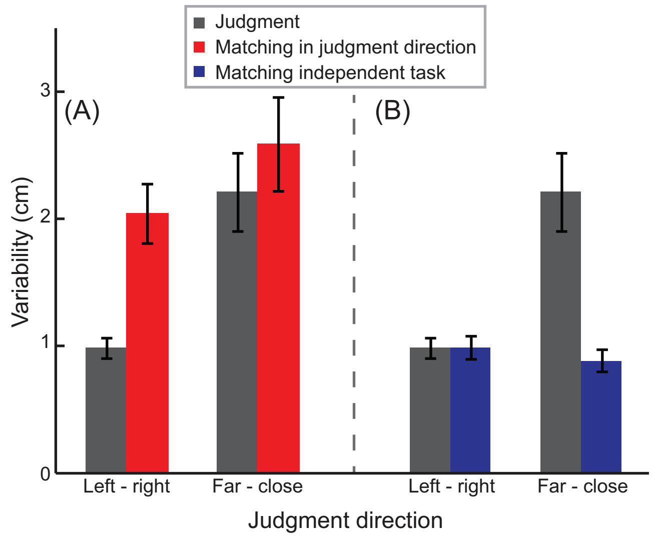

FIGURE 5. Variability. (A) The standard deviations in the distance judgments in block 2 (grey) compared to the standard deviations in the matching errors in the same trials (red) for the two directions. (B) The standard deviations in the distance judgments in block 2 (grey, same as in panel A) compared to the standard deviations in matching in the independent matching task in block 1 (blue). Error bars show the SEM.

transformations, this would support the interpretation of matching errors in terms of sensory transformations (Simani et al., 2007) that depend on the movement that needs to be made (Kuling et al., 2017; Tagliabue & McIntyre, 2011).

The most obvious difference in the matching between the two blocks is that in the first block, the matching was the task itself, whereas in the second block, the matching was used to indicate a perceptual judgment of distance. One can code goal-directed movements in two different ways (van den Dobbelsteen, Brenner, & Smeets, 2001; van der Graaff, Brenner, & Smeets, 2017): by the endpoint of the movement (position-coding; Polit & Bizzi, 1979) or by coding the displacement (vector-coding; Vindras & Viviani, 1998). It is known that we generally use a combination of the two ways of coding, and that details of the task determine the balance between the two (de Grave, Brenner, & Smeets, 2004). In the block in which we asked the participants to indicate their judgment about the length of the vectors between the hand and the two targets, we might have biased the participants to rely more on vector coding than when the task was explicitly to match positions. The different coding schemes correspond to different visuomotor transformations, and thus to differences in matching errors (Kuling et al., 2017; Tagliabue & McIntyre, 2011).

We included a separate block of matching trials in which participants did not make judgments to check whether making the judgments influences the matching errors. This additional block of trials was always done first because we wanted to be sure that the judgments did not influence the matching errors in the other block. We know that in situations with multiple starting points and directions of movement, matching performance remains stable across sequential blocks of trials (e.g. Kuling et al., 2013; Kuling et al., 2016), so we used such a design for the first block of the current study. The consequence was that combinations of starting positions and target positions (and thus the detailed arm postures) differed between the blocks. We do not expect this to influence the results because previous research has shown that matching performance varies gradually and only modestly across the workspace (e.g. Kuling et al., 2013; Rincon-Gonzalez et al., 2011). Furthermore, if there were any effect of these differences between the movements in the different blocks, we would expect to see more variability in the first block (due to the larger variation in movement directions and amplitudes), which is the opposite of what we found. Nevertheless, we cannot be certain that the reduced precision in the second block is a consequence of the movements being made to indicate which of the targets was judged to be nearer, rather than to one of the many other differences between the blocks.

We found that the precision of judgments of the distance between hand and target is about one centimetre, in line with matching precision in the present and previous studies on visuo-proprioceptive matching (e.g. Kuling et al., 2016, 2017). This finding raises a question related to a recent paper (Nashed, Crevecoeur, & Scott, 2014). The authors studied how people reach with their unseen hand towards a target while avoiding an obstacle and overcoming a perturbation that leads the hand towards the obstacle. They suggested that the decision whether to pass the obstacle on the left or on the right was based on the judged position of the hand at the moment of the perturbation, which in their study differed across trials by only a few millimetres. The variability that we found in our judgment task makes it unlikely that people can make spatial judgments about the position of their unseen hand with an accuracy of just a few millimetres. It is therefore unlikely that the spatial position was essential for participants' choice about whether to go left or right to overcome a collision with an obstacle after a force perturbation in the experiment of Nashed et al. (2014). The choice was probably determined by some other factor related to the state of the hand at the time of the force perturbation, such as the hand's velocity or muscle contraction levels.

To conclude, this study shows that idiosyncratic visuo-proprioceptive matching errors measured in matching tasks are consistent with biases in a judgment task. This shows that matching errors do not mainly originate in errors in motor execution, indicating that perceptual biases are systematically present when transforming positions between visual and proprioceptive representations.

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DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

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