

The effects of immediate vision on implicit hand maps

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Abstract Perceiving the external spatial location of the limbs using position sense requires that immediate proprioceptive afferent signals be combined with a stored body model specifying the size and shape of the body. Longo and Haggard (Proc Natl Acad Sci USA 107:11727–11732, 2010) developed a method to isolate and measure this body model in the case of the hand in which participants judge the perceived location in external space of several landmarks on their occluded hand. The spatial layout of judgments of different landmarks is used to construct implicit hand maps, which can then be compared with actual hand shape. Studies using this paradigm have revealed that the body model of the hand is massively distorted, in a highly stereotyped way across individuals, with large underestimation of finger length and overestimation of hand width. Previous studies using this paradigm have allowed participants to see the locations of their judgments on the occluding board. Several previous studies have demonstrated that immediate vision, even when wholly non-informative, can alter processing of somatosensory signals and alter the reference frame in which they are localised. The present study therefore investigated whether immediate vision contributes to the distortions of implicit hand maps described previously. Participants judged the external spatial location of the tips and knuckles of their occluded left hand either while being able to see where they were pointing (as in previous studies) or while blindfolded. The characteristic distortions of implicit hand maps reported previously were clearly apparent in both conditions, demonstrating that the distortions are not an artefact of immediate

vision. However, there were significant differences in the magnitude of distortions in the two conditions, suggesting that vision may modulate representations of body size and shape, even when entirely non-informative.

Keywords Body representation · Body schema · Position sense · Vision

Introduction

Several classes of afferent signals from the periphery provide information about the location of the limbs, including receptors in joints signalling flexion or extension, from the skin signalling stretch and from muscle spindles signalling contraction or lengthening (Proske and Gandevia 2012). Each of these signals provides information *body posture*, that is, about the relative flexion or extension of each joint. In order to use these proprioceptive signals for position sense to localise the absolute spatial location of part of the body in external space, such information about joint angles must be combined with information about the size and shape of the body segments between joint. Critically, however, no afferent signals directly specify body size or shape, indicating that this information must come from a stored *body model* (Longo et al. 2010).

In a series of recent studies, my colleagues and I have investigated this body model using a novel ‘psychomorphometric’ method in which participants judge the perceived location of several landmarks on their occluded hand, and the pattern of responses is used to construct implicit perceptual maps of hand size and shape (Longo and Haggard 2010, 2012a, b; Longo et al. 2012). In these studies, we have found that the body model of the hand is massively distorted, in a highly stereotyped way across people. Specifically, there

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were three clear patterns of distortions: (1) overestimation of hand width, quantified as the distance between pairs of knuckles; (2) overall underestimation of finger length, quantified as the distance between the knuckle and tip of each finger and (3) a radio-ulnar gradient, with underestimation of finger length increasing systematically from the thumb to the little finger. In contrast, explicit estimates of hand shape were approximately veridical (Longo and Haggard 2010), suggesting that the body model is implicit, and outside of conscious bodily awareness.

The current paper focuses on one aspect of the procedure used in previous studies investigating implicit hand maps (e.g. Longo and Haggard 2010, 2012a, b; Longo et al. 2012), namely the fact that participants have been able to see where they were pointing on each trial. Vision in this context is uninformative about the location of individual landmarks (except for a very broad sense in which seeing the boundaries of the occluding board imposes extreme limits on landmark location). Vision was allowed in these studies to ensure that participants' responses were as precise as possible, but was not considered to be an important contributing factor to the distortions observed. It is important to consider, however, whether immediate vision might be driving aspects of the results. Two recent studies investigating the effects of vestibular stimulation on body representation did have participants respond while blindfolded (Ferrè et al. 2013; Lopez et al. 2012). Ferrè and colleagues reported distortions similar to those reported by Longo and Haggard (2010). Lopez and colleagues did not report statistical comparisons of represented and actual hand size (focusing instead on vestibular stimulation vs. sham), but the pattern of their results appears qualitatively consistent with distortions reported in other studies. In both these studies, participants were blindfolded in all conditions, making the potential effects of immediate vision impossible to estimate.

Several previous results suggest that vision, even when non-informative, affects several aspects of somatosensory processing. For example, in the *visual enhancement of touch* (Kennett et al. 2001; Cardini et al. 2011) and *visual analgesia* (Longo et al. 2009; Mancini et al. 2011) effects, vision of the stimulated body part enhances the spatial acuity of touch and reduces the perceived intensity of acute pain, respectively, even when completely non-informative about the stimulation. Those studies are importantly different from the proprioceptive localisation situation in that they involve vision of the body itself, rather than just in the direction of the body's location, but nevertheless show that non-informative vision can clearly affect somatosensation. Perhaps more directly relevant, Forster and Eimer (2005) found that looking in the direction of an unseen body part altered tactile attention on that body part. These results clearly show that even when vision provides no actual

task-relevant information, it may nevertheless be modulating somatosensory processing.

Further, numerous studies have suggested that vision can determine the reference frame for somatosensory perception. For example, Harris and colleagues have argued in a number of recent papers that tactile information is localised using a gaze-centred frame of reference (Harrar and Harris 2009, 2010; Pritchett and Harris 2011). Other results have suggested that when vision is present, kinaesthetic information may be automatically transformed into a visual reference frame (Darling and Miller 1993). Indeed, recent studies have shown effects of gaze direction on proprioceptive localisation judgments (Fiehler et al. 2010; Jones and Henriques 2010). Collectively, these results suggest profound interactions between vision and both somatosensation generally, and proprioception specifically. Thus, it cannot be assumed that the presence of immediate vision in previous studies of implicit hand maps has not contributed to the distortions observed.

The present study therefore compared implicit hand maps obtained using the method of Longo and Haggard (2010) in conditions in which participants could see where they were pointing on the occluding board (as in previous studies) and while blindfolded. To the extent that distortions observed in previous studies reflect transformation of proprioceptive information into a gaze-centred reference frame, they should not appear when participants respond while blindfolded. In contrast, to the extent that the distortions reflect characteristics of stable body representations underlying position sense, they should not be dependent on the presence of immediate vision.

Methods

Participants

Twelve individuals (eight female) between 19 and 34 years of age from the University of London community participated for payment. All but one were right handed as assessed by the Edinburgh Inventory (M : 74.88; range: -100 to $+100$). Procedures were approved by the local ethics committee.

Procedures

Procedures were similar to those I have used in previous studies with this paradigm (e.g. Longo and Haggard 2010, 2012a, b; Longo et al. 2012). Participants sat with their left hand lying palm-down on a table, approximately aligned with their body midline. Participants were asked to sit upright, with their torso up against the edge of the table. The hand rested flat on the table, with fingers straight. An occluding board (40×40 cm) rested on four pillars (6 cm in

height) and covered the hand. A webcam (Creative Live Cam Voice) suspended approximately 27 cm above the table captured still photographs ($1,280 \times 960$ pixels) under control of a custom MATLAB (Mathworks, Natick, MA) script.

In the *Sighted* condition, participants responded as in my previous studies using this paradigm, with full vision of the occluding board and the stick they were pointing with. In the *Blindfolded* condition, in contrast, participants wore a blindfold so that the task had to be completed using only haptic feedback.

Participants used a short wooden stick (11.4 cm in length) to indicate the perceived location of landmarks on their left hand. In my previous studies using this paradigm, participants used a long (35 cm) baton to point to different landmarks on their hand. Because participants in this study had to point without visual guidance, a shorter stick was used, so that participants could more easily feel where the tip was pointing. The tip of the stick tapered gradually to a point. Participants made judgments about ten different landmarks: the tip (i.e. the most distal point) and the knuckle (i.e. centre of the knuckle at the base of each finger) of each finger. Participants were given verbal instructions on each trial about which landmark to judge. At the beginning of the experiment, they were instructed that they should be precise in their responses, avoid ballistic pointing and avoid strategies such as tracing the outline of the hand. To ensure that responses on each trial were independent, participants were asked to move the stick to tap a metal post that rested to the side of the board, within easy reach of their right hand. The post was used in place of the blue dot used in previous studies since it could be found even when participants were blindfolded. A photograph of each response was taken when the participant indicated that they were happy with their response.

There were four blocks of thirty trials each. Sighted and blindfolded blocks were counterbalanced in an ABBA fashion, with the first condition counterbalanced across participants. Each block consisted of three mini-blocks of ten trials each, including one of each of the ten landmarks in random order. At the beginning and end of each block, an image was taken without the occluding board, which allowed measurement of the true proportions of the participant's hand, and confirmation that the hand had not moved during the block. To facilitate coding, a black dot was made on each of the knuckles with a black pen. A ruler (10 cm in length) was affixed to the table and appeared in the pictures without the occluding board, allowing conversion between distances in pixels and cm.

Analysis

The camera used a wide-angle ('fisheye') lens, which induced some spatial distortion. This fisheye distortion was

corrected using the Panotools plug-in (<http://www.panotools.com/>) for Adobe Photoshop CS2. The x–y pixel coordinates of each landmark on the photographs of the hands and of the corresponding judged locations were coded using ImageJ software (Abramoff et al. 2004). The length of different parts of the hand was then calculated. The length of each finger was calculated as the distance between the knuckle and tip of each finger. Hand width was similarly quantified as the distance between pairs of knuckles, with the distance between the knuckles of the index and little fingers being used as an overall measure of hand width. For each distance, percent overestimation was calculated as $100 \times (\text{Judged Length} - \text{Actual Length}) / \text{Actual Length}$.

Maps of both actual and judged locations were put into Procrustes alignment using the CoordGen software, part of the Integrated Morphometric Program (IMP; David Sheets, Canisius College, <http://www.canisius.edu/~sheets/morphsoft.html>). Procrustes superimposition removes differences in location, rotation and overall size to isolate differences in shape between configurations of homologous landmarks (Rholf and Slice 1990; Bookstein 1991).

Because the fingers are articulated and can move independently, we rotated the fingertips of each map to be in a constant posture, as in our previous study (Longo and Haggard 2010). First, we calculated the average angle of each finger relative to the hand in the photos of each participant's actual hands, defined as the angle between a line running through the knuckles of the index and little fingers and another line running through the knuckle and tip of each finger. These angles were 39.6° , 64.4° , 76.5° , 87.1° and 108.8° , for the thumb through little fingers, respectively. Then for each experimental block and for each participant, the fingertip of each finger was rotated so that the fingers were at those angles (i.e. hand posture was matched across blocks and across participants).

As there were two experimental blocks for each task, maps from each participant were first put into Procrustes alignment so that an average map could be calculated for each participant for both actual location and judgments in each of the two tasks. Then a second-level generalised Procrustes analysis was conducted putting actual and judged maps from all participants into simultaneous alignment, separately for the two tasks.

Results

All three of the patterns of distortion I have reported in my previous studies using this paradigm (Longo and Haggard 2010, 2012a, b) were investigated here. The left panel of Fig. 1 shows overestimation of finger length. The values are negative, indicating overall underestimation. Averaging across the five fingers, there was clear underestimation of

Fig. 1 *Left panel* Percent overestimation (i.e. $100 \times (\text{Judged Length} - \text{Actual Length}) / \text{Actual Length}$) for each of the five fingers in the two conditions. *Right panel* Percent overestimation for the distance between pairs of knuckles. The distance between the index and little fingers is taken as an overall measure of hand width. Error bars are one S.E.M

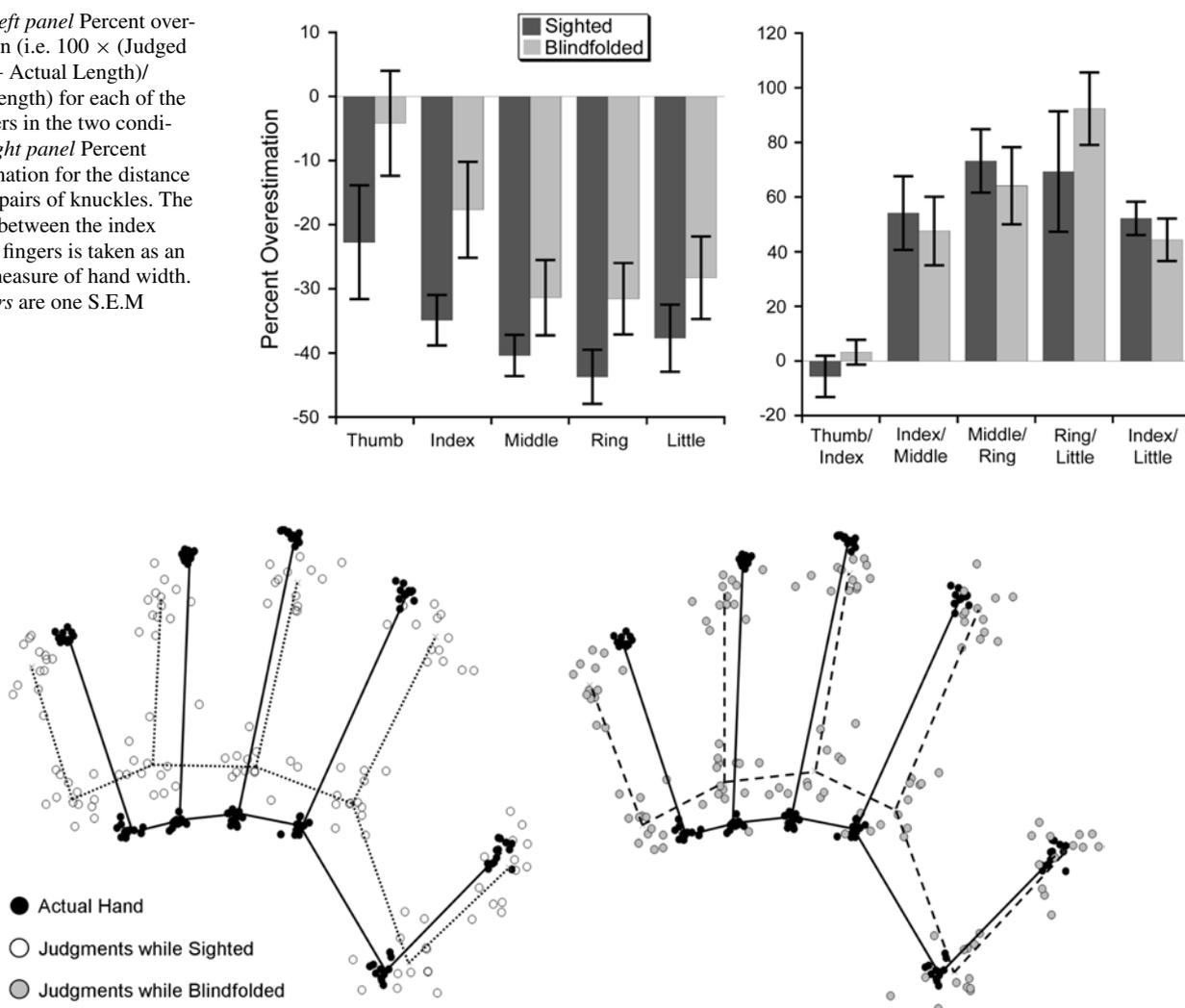


Fig. 2 Hand maps in the two conditions placed in generalised Procrustes superimposition (GPS) alignment with maps of each participant's actual hand

finger length in both the sighted (-35.9% underestimation), $t(11) = -7.73$, $p < .0001$, and blindfolded (-22.6% underestimation), $t(11) = -3.85$, $p < .005$, conditions. Nevertheless, there was a significant reduction in the magnitude of underestimation in the blindfolded condition, $t(11) = 2.24$, $p < .05$. There was a modest (but non-significant) positive correlation between the magnitude of underestimation in the two conditions, $r(10) = 0.381$, *n.s.*

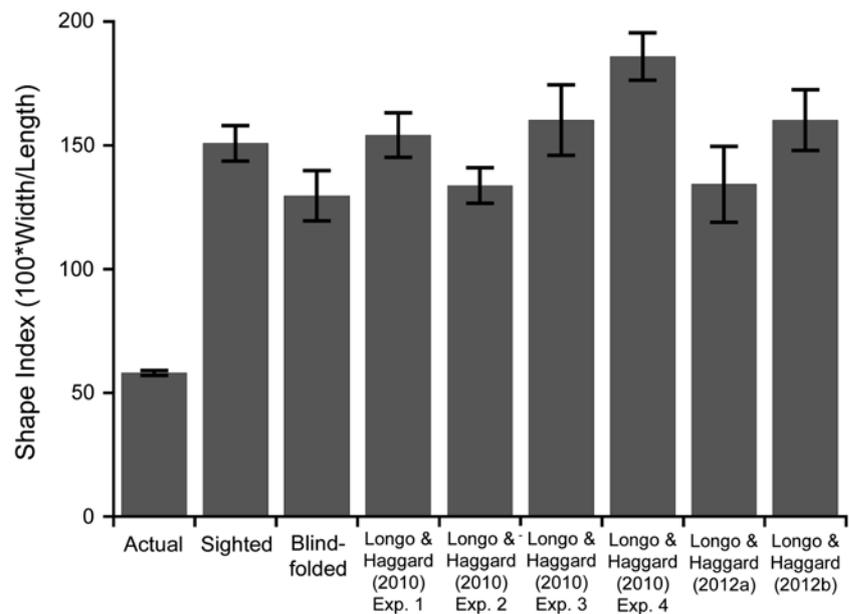
To assess the gradient of underestimation across fingers, least-squares regression was used to estimate the increase in underestimation with a shift of one digit towards the little finger. Consistent with previous findings, there was a clear increase in underestimation from the thumb to little finger in both the sighted (mean $\beta = 3.9\%$ /finger), $t(11) = 2.97$, $p < .02$, and blindfolded (mean $\beta = 6.2\%$ /finger), $t(11) = 4.92$, $p < .001$, conditions. The magnitude of this gradient was marginally larger in the blindfolded

condition, $t(11) = 2.01$, $p = .069$. There was a significant correlation between slopes in the two conditions, $r(10) = 0.594$, $p < .05$.

The right panel of Fig. 1 shows overestimation of the distance between pairs of knuckles. The distance between the knuckles of the index and little fingers was taken as an overall measure of hand width. There was clear overestimation of hand width in both the sighted (52.2% overestimation), $t(11) = 8.54$, $p < .0001$, and blindfolded (44.3% overestimation), $t(11) = 5.70$, $p < .0001$, conditions. The magnitude of overestimation did not differ significantly between the two conditions, $t(11) = 1.11$, *n.s.* There was a marginally significant correlation between the magnitude of overestimation in the two conditions, $r(10) = 0.508$, $p = 0.092$ (two-tailed) (Fig. 2).

The overall aspect ratio of the hand was quantified using Napier's (1980) *shape index*, a ratio of hand width

Fig. 3 The three leftmost bars show shape indices (i.e. $100 \times \text{Width/Length}$) for participants' actual hands and for hand maps in the sighted and blindfolded conditions. Shape indices were clearly larger for the hand maps than for actual hand shape. For comparison, the rightmost six bars present the same values from six previous experiments using the same paradigm with participants responding using a long baton (35 cm). Error bars are one S.E.M



to length. Following my previous studies (Longo and Haggard 2010, 2012b), the distance between the knuckles of the index and little fingers was taken as a measure of hand width, and the length of the middle finger as a measure of hand length. The shape index is calculated as: $SI = 100 \times (\text{width/length})$. Large shape indices indicate a squat, wide hand, while small values indicate a thin, slender hand. The shape index was calculated for each participant for their actual hand, as well as for the hand maps in each condition (shown in the left three bars of Fig. 3). The shape indices for hand maps were significantly greater than for the actual hand in both the sighted (150.8 vs. 58.0), $t(11) = 12.04$, $p < .0001$, and blindfolded (129.6 vs. 58.0), $t(11) = 6.87$, $p < .0001$, conditions. The shape indices for the two experimental conditions did not differ significantly from each other, $t(11) = 1.50$, $n.s.$

One interesting difference between the present study and previous studies using the same paradigm (e.g. Longo and Haggard 2010, 2012a, b) is the use of a much shorter stick for responding in this study (11.4 vs. 35.0 cm). In order to investigate any potential effect of this variable, the right six bars of Fig. 3 show the shape indices from six previous experiments which were similar to the sighted condition of this study except for the length of the stick. These experiments were: (1) Exp. 1 from Longo and Haggard (2010); (2) the 'normal' posture from Exp. 2 from Longo and Haggard (2010); (3) the left hand condition from Exp. 3 from Longo and Haggard (2010); (4) Exp. 4 from Longo and Haggard (2010); (5) the dorsum condition from Longo and Haggard (2012a); (6) the 'localisation' task from Longo and Haggard (2012b). As is clear from Fig. 3, the shape indices in the present study are similar to those found in previous studies using a longer baton, suggesting that the

length of the implement used for responses does not have a major effect on the results.

Discussion

Similar patterns of distortion of implicit body representations underlying position sense were found regardless of whether participants had immediate vision while making their responses or not. Three types of distortions of implicit hand maps were apparent in both conditions, replicating recent results (Longo and Haggard 2010, 2012a, b, Longo et al. 2012): (1) overall underestimation of finger length, (2) increasing underestimation of length from thumb to little finger and (3) overall overestimation of hand width. These results demonstrate that the patterns of distortion we have previously reported are not dependent on immediate vision and are unlikely to reflect an artefact of responses being coded in a visual reference frame.

These results have implications for understanding the origins of the distortions we have observed. One critical question concerns whether they reflect distortions representations of the body, per se, or whether they emerge from the manner in which participants are asked to respond. The present results contribute to a growing body of evidence that the distortions we have reported show a high level of generality across different modes of response, reducing the likelihood that they reflect an artefact of any specific mode of response. Similar distorted maps of the hand are apparent when participants have both visual and proprioceptive feedback about the location of their responses (Longo and Haggard 2010; this study), when they have only proprioceptive feedback about their responding hand (this study),

and when they have only visual feedback about their responses (i.e. they verbally guided a naïve experimenter who held the baton, Longo et al. 2012). Further, we found different patterns of distortions for judgments about two sides of a single body part (i.e. the dorsal and palmar hand surfaces, Longo and Haggard 2012a), though the manner in which responses were made was identical in both cases. Together, these results suggest that the measured distortions reflect distorted representations of the body itself, rather than idiosyncratic aspects of the manner in which participants indicate their judgments.

While qualitatively similar patterns of distortion were observed in both the sighted and blindfolded conditions, there was evidence that the magnitude of these distortions differed between them. These results are consistent with the possibility that vision, even though non-informative about the location of the body, might nevertheless alter somatosensory processing (cf. Kennett et al. 2001; Forster and Eimer 2005) or change the reference frame for somatosensory spatial perception (cf. Fiehler et al. 2010; Harrar and Harris 2009). Immediate vision led to a significant reduction in perceived finger length. The direction of this effect is consistent with the recent finding that non-informative vision of the hand leads to a reduction in the perceived tactile distance on the hand (Longo and Sadibolova 2013). The reason for vision producing reductions in represented body part size in both these cases is not fully clear. One possibility is that visually induced reduction may be the converse of the perceived swelling seen following acute deafferentation (Gandevia and Phegan 1999) and in chronic pain (Moseley 2005; Pelz et al. 2011). Both deafferentation (Calford and Tweedale 1991) and chronic pain (Schwenkreis et al. 2003) are known to be associated with disinhibition of sensorimotor cortex. As suggested by Haggard et al. (2013), by increasing such inhibition (Cardini et al. 2011), vision may produce a constellation of effects opposite to those seen in chronic pain, including analgesia (Longo et al. 2009; Mancini et al. 2011), heightened tactile spatial acuity (Kennett et al. 2001; Cardini et al. 2011) and reduced represented body part size (Longo and Sadibolova 2013; this study).

Such an interpretation treats the blindfolded condition as a baseline, reflecting simply the absence of vision. Another possibility, however, is that blindfolding may induce rapid plasticity of somatosensory representations, as has been shown by several previous results (Facchini and Aglioti 2003; Weisser et al. 2005; Wong et al. 2011; Zubek et al. 1964). Indeed, Wong et al. (2011) reported changes in tactile spatial acuity after periods of blindfolding as short as 10 min, similar to the length of time participants in the present study was blindfolded during a single block of trials. Thus, it is also possible to consider the sighted condition as the baseline, and the differences

observed in the blindfolded condition as reflecting short-term plasticity of body representations induced by blindfolding. It is difficult to see what type of condition would be a true baseline in this context to determine whether the differences seen between conditions reflect changes induced by immediate vision or short-term plasticity induced by blindfolding. This is an interesting question for future research.

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