

Multisensory Research 26 (2013) 3-18



Segmented Space: Measuring Tactile Localisation in Body Coordinates

Vanessa Harrar^{1,*}, Lisa M. Pritchett² and Laurence R. Harris²

¹ Department of Experimental Psychology, University of Oxford, South Parks Road, Oxford, OX1 3UD, UK

² Department of Psychology, Centre for Vision Research, York University, Toronto, Ontario, M3J 1P3, Canada

Received 1 March 2012; accepted 10 August 2012

Abstract

Previous research showing systematic localisation errors in touch perception related to eye and head position has suggested that touch is at least partially localised in a visual reference frame. However, many previous studies had participants report the location of tactile stimuli relative to a visual probe, which may force coding into a visual reference. Also, the visual probe could itself be subject to an effect of eye or head position. Thus, it is necessary to assess the perceived position of a tactile stimulus using a within-modality measure in order to make definitive conclusions about the coordinate system in which touch might be coded. Here, we present a novel method for measuring the perceived location of a touch in body coordinates: the Segmented Space Method (SSM). In the SSM participants imagine the region within which the stimulus could be presented divided into several equally spaced, and numbered, segments. Participants then simply report the number corresponding to the segment in which they perceived the stimulus. The SSM represents a simple and novel method that can be easily extended to other modalities by dividing any response space into numbered segments centred on some appropriate reference point (e.g. the head, the torso, the hand, or some point in space off the body). Here we apply SSM to the forearm during eccentric viewing and report localisation errors for touch similar to those previously reported using a crossmodal comparison. The data collected with the SSM strengthen the theory that tactile spatial localisation is generally coded in a visual reference frame even when visual coding is not required by the task.

Keywords

Multisensory coding, localisation, somatosensory, touch, passive touch, tactile, reference frames, reference cues, segmented space method, coordinate system, visual imagery

^{*} To whom correspondence should be addressed. E-mail: vanessa.harrar@psy.ox.ac.uk

[©] Koninklijke Brill NV, Leiden, 2012

1. Introduction

The location of an object or event must be coded relative to some reference. When localising an object, errors related to eye position are expected only if the position of the eyes is needed for reference frame transformations. Systematic errors in touch localisation related to gaze position are, therefore, evidence that the representation of touch is coded in an gaze-centered reference frame. If, on the other hand, touch were only ever coded in a body-centred reference frame, eye position would not be needed and no eye position related errors should be found. When interacting with an object, both the object and the effector need to be represented in the same reference frame making it necessary to convert sensory information across reference frames. Indeed, the perceived location of stimuli from many modalities are often found to vary with gaze (Boussaoud and Bremmer, 1999) suggesting that the perceived position of tactile, auditory, and proprioceptive stimuli may all be at least partially represented in retinal coordinates (Andersen, 1997; Andersen and Mountcastle, 1983; Batista et al., 1999; Röder et al., 2008). That space might be coded in a visually based reference frame might also partially explain correlated visual and auditory spatial deficits in neglect patients (Pavani et al., 2004) making the system maladaptive in some cases.

There is some neurophysiological evidence for how reference frame conversions may be handled by the brain. The human parietal cortex appears to be involved in representing space in multiple reference frames simultaneously (Cohen and Andersen, 2002). Representing space in several reference frames allows the most appropriate representation of a stimulus to be accessed for a given task (see Fig. 6, p. 559 in Cohen and Andersen, 2002). Thus, a visual target might have its location simultaneously coded in both eye and head reference frames to guide a gaze movement, or relative to a limb when used as a target for reaching and grasping. By measuring perceptual localisation errors when multiple potential reference frames are misaligned, we can obtain behavioural evidence identifying which reference systems are used to represent sensory space. However, some previous studies have used measurements which could force visual coding making interpretation more difficult.

When studying perceived location, the selection of response measure is crucial. This is because a reference frame conversion may be performed for the sole purpose of responding. Thus, if the response is relative to a visual scale, the perceived location of a stimulus must be converted to visual coordinates to make the comparison, but this may not represent a usual coding system for that stimulus. Another potential confound resulting from the choice of a particular response method is that the response itself may be vulnerable to reference frame misalignment. For example, if pointing is used to measure the effect of eye position on perceived location, the data obtained may show a combination of the effect of eye position on the location perception and also on pointing (see Dessing et al., 2012). Crossmodal methods for measuring localisation, and especially those using a visual reference point, are therefore subject to alternative interpretations.

Crossmodal methods for assessing perceived touch location have included reporting the position of a touch relative to a visual scale, a visual reference point, or a remembered visual target (Harrar and Harris, 2009, 2010; Ho and Spence, 2007; Pritchett and Harris, 2011). Such methods may force a transformation of the location of the touch into a visual reference frame. Similarly, experiments that have involved judgments relative to the body such as pointing to a stimulus or comparing its position relative to the head or nose may *necessitate* a transform into an egocentric body based reference frame that might otherwise not occur. The potential confounding effects of the response measure must be considered before the conclusion that sensory information is coded in a particular reference frame can be made.

The finding that perceived location of visual objects appears to shift in the opposite direction to eye position may be connected to an underestimated representation of the gaze signal (Harris and Smith, 2008; Hill, 1972; Morgan, 1978; Yamaguchi, 2007). Reports of tactile localisation errors related to eccentric fixation are much more recent. Ho and Spence (2007) first reported tactile localisation errors when the head was rotated and gaze was held eccentrically. Their measurements of tactile localisation varying with head and eye position were, however, collected relative to a visual scale. Participants were touched on their abdomen and had to place a cursor on a computer monitor to indicate the position of the touch (the leftmost part of the screen corresponded to leftmost part of the abdomen). They performed the same task while looking straight ahead, to the left, and to the right, and found a systematic shift in the perceived touch location relative to gaze. This was a very novel experiment since it was not yet known that perceived touch location shifted with gaze position and provided the first hint that touch on the skin's surface might be coded in visual coordinates (for touch in space, including limb position, remapped into a visually defined reference frame see Röder et al., 2004). However, Ho's response measure was visual and, therefore, may have necessitated a transfer of the location of the touches into visual space in order to complete the task. In addition, the visual scale on the screen may have been perceived as skewed because of the eccentric gaze during responding. This necessitated transfer, in addition to the potentially skewed response scale, may have contributed to the results.

Similarly, Harrar and Harris (2009) reported that the perceived location of touch was mislocalized on the body when the head was held straight but the eyes were eccentric. Their participants reported the perceived position of touches by calling out the number on a ruler (which was placed adjacent to the arm) that was perceived as being at the same location as the touch. Since significant shifts in the perceived location of the touch were found to depend on eye position, the authors suggested that touch was partially coded in a visual reference frame. However, here again the use of a visual reference when responding may have forced a transform from a body based reference frame into a visual one in order to complete the task. Thus, the question still remains as to whether touch is coded in a visual reference frame naturally — irrespective of whether the response is in a visually defined space.

Harrar and Harris (2010) attempted to avoid this confound by asking participants to make a goal-directed movement to the perceived location of a touch. Participants were touched on their arm while their eyes were held eccentrically. In order to report the perceived position of the touch, they were asked to move their other hand as if to touch the location that had been stimulated. Directly above the stimulated arm was a touch screen positioned so that participants did not actually touch their arm (therefore did not receive tactile feedback). Since the mechanoreceptors in the skin and the signals required to move the arm are also, at some stage, both in body coordinates, this task might not necessarily require an intermediate visual reference frame. However, pointing has its own issues. Eccentric viewing can affect the perceived position of the arm (Henriques et al., 1998) suggesting that arm position may also be coded in a visual reference frame at a very early stage. Thus pointing errors varying with eye position may have been due to errors in pointing — as opposed to the stimulus (touch on the arm) actually being mislocalized (Dessing et al., 2012). Participants were, however, instructed to fixate the pointing hand which should have minimized errors associated with the response (though it might encourage visual coding), whereas if they were instructed to continue to fixate eccentrically there would surely be a bias in the response (cf. Pritchett and Harris, 2011, where a centrally viewed visual scale was used to minimize errors in the response). In order to make strong claims about reference frames for touch, a 'non-visual' response measure should be used: a response measure that does not depend on where people are looking, or whether they are looking at all.

We therefore propose and demonstrate the Segmented Space Method (SSM) in which participants report the perceived position of a touch in body coordinates. Subjects imagine a body part (in this case their forearm) divided into numbered segments and report the segment in which they were touched.

2. Material and Methods

2.1. Participants

The first group contained 30 undergraduate participants with a median age of 21 years, and the second group contained 15 undergraduate participants

with a median age of 21 years. Participants received course credit for their participation. Each participant completed a written informed consent form. All experiments conformed to the ethical guidelines of York University and the Declaration of Helsinki.

2.2. Tactors

Touch stimulators (tactors) were made from four small solenoids mounted on a plate 5.3 cm apart with the pins facing upwards. When the solenoid was powered the pin was pushed out about 2 mm. Solenoids were controlled by amplified 5-volt signals from a CED1401 (Cambridge, England) controlled by a PC (see Harrar and Harris, 2005, for additional tactor details). All touches were 50 ms in duration. Participants laid their arm (group 1 — left arm, group 2 — right arm) over the tactile plate with their wrists in line with a marker (exact positioning was not required as all analysis was within subjects and we only ever compared perceived touch locations to other conditions within a given subject's run). A sheet of paper initially covered the tactors so that their locations could not be seen by the participant. The paper was removed only when the participant's arm obscured the tactors from view. Participants wore headphones to reduce auditory cues from the tactors, and a chinrest was used to maintain head position (eyes were thus held 38 cm away from the tactors).

2.3. Measuring the Location of Perceived Touch Using the SSM

Participants were told to imagine their forearm divided into ten equal numbered sections where section 0 was closest to their elbow and section 9 contained their wrist (see inserts in Fig. 1). Participants verbally reported the section of their arm in which they perceived the touch. Pilot experiments were performed (on a different sample of participants) in which actual lines were drawn on the participants' arms to indicate the intervals, providing a more concrete understanding of the segments. Similar results in the pilot experiment and the one presented here demonstrates that imagined divisions were comparable to physically drawn divisions.

2.4. Procedure

The left or right forearm (group 1 and 2 respectively) was held in front of the torso on a horizontal plane with the elbow bent at approximately 90° (see insert in Figs 1A and 1B for left and right arm respectively). The visual angle of the four touches was $\pm 11.8^{\circ}$ and $\pm 4.0^{\circ}$ relative to the straight ahead. Participants rested their arm on the tactile plate containing the four solenoids and their arm was covered with a cloth.

Eye position was manipulated by means of fixation crosses. To start each trial, one of the four fixation crosses, chosen in a pseudorandom order, was illuminated and participants were instructed to fixate it. Fixation crosses were

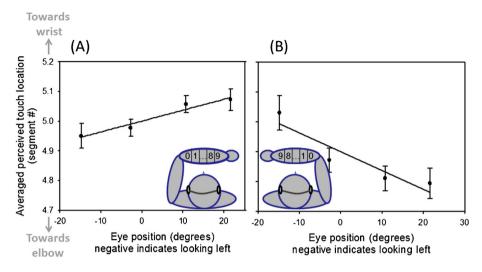


Figure 1. The averaged perceived position of touch measured with the segmented space method varies with eye position. Participants imagined their forearm divided into 10 equal sections (zero always being on the elbow, and 9 on the wrist) and reported in which segment a touch was perceived. The segment numbers (or the perceived position of the touches) were averaged across all touch locations and plotted as a function of eye position. Linear regression lines were fitted as shown. Error bars show standard errors within participants (Cousineau, 2005). (A) data from group 1 (tested on the left arm: see top view schematic diagram of body arrangement) (B) data from group 2 (tested on the right arm: see opposite schematic diagram).

presented on a computer monitor 34.5 cm away from, and directly in front of, the participant. Four possible fixation crosses were positioned at: -14.8° , -2.7° , 10.8° and 21.6° relative to the straight ahead (negative indicates left). The luminance of the fixation crosses was 4.8 cd/m^2 . After 1-1.5 s the fixation cross was turned off and participants were instructed to maintain fixation during the presentation of the tactile stimulus. After another 100-450 ms one of the four tactors was activated, chosen in a pseudorandom order. Following the touch, participants reported the section of their arm in which it was felt (0–9). The experimenter recorded the number in a file which also contained the trial details and then initiated the next trial. Participants were allowed to report that they were unsure of the position of the touch in which case that trial was skipped and repeated later. Each combination of fixation and touch was repeated ten times ($4 \times 4 \times 10$) for a total of 160 presentations which took about 15 min to complete.

3. Results

Responses were averaged for the 10 trials in each experimental condition and the average response for each condition (necessarily between zero and nine) was the dependent variable used for the analysis. The results from the participants in group 1 (stimulated on their left arm) were analysed with a repeated measures ANOVA (Greenhouse–Geisser correction for sphericity) with two repeated measures variables (touch location– $4 \times$ fixation position–4).

Trend analysis revealed a significant linear effect of fixation ($F_{3,29} = 4.36$, p = 0.046, $\eta_p^2 = 0.131$) indicating that the perceived position of the touches varied linearly with fixation (see Fig. 1A). The effect of eye position was 0.01 cm/deg of eye position, calculated by taking the average slope of the solid line in Fig. 1A (in arm segments per degrees of eye position) and converting it into cm/deg assuming a typical forearm length of 25 cm. A positive slope indicates that as participants fixated to the right, they reported a *larger number* indicating that the touch appeared shifted towards the right (a more wristwardly location for the touch).

In addition to the effect of fixation, there was a significant main effect of touch location ($F_{3,87} = 490.38$, p < 0.001, $\eta_p^2 = 0.944$) indicating that participants were able to distinguish between the four different touches (see filled circles in Fig. 2). Further, there was also a significant interaction (touch location × fixation: $F_{9,261} = 2.05$, p = 0.034, $\eta_p^2 = 0.066$) suggesting that the effect of fixation was different for the different touch locations. This interaction further suggests that the effects of eye position cannot solely be due to a response bias (since in that case there should be the same bias across all tactor locations).

A concern was that, since number lines are generally arranged with smaller numbers on the left and larger numbers on the right (Fisher *et al.*, 2003; Loetscher *et al.*, 2008), participants might have a bias towards reporting larger

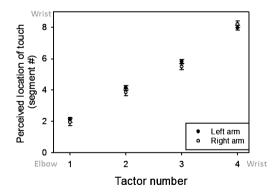


Figure 2. Tactor locations perceived as distinct. The perceived position of touch reported using the segmented space method (segments 0–9) is plotted as a function of tactor number. The four touches were reported in different segments on the arm. Perceived location (in segment numbers) was the same regardless of the whether the left arm (solid symbols) or right arm (open circles) were tested. Error bars show standard errors within subjects (Cousineau, 2005).

numbers when fixating to the right — confounding these results. In order to rule out the potential confound of a spatial number line, we repeated the experiment on a second group of participants using the same methodology but this time stimulating them on the right arm. Since 'zero' corresponded to the region of the arm closest to the elbow, and 'nine' to the region containing the wrist, the number line was reversed spatially for the second group compared to the first group. If the effect of fixation genuinely causes touches to be perceived shifted in the same direction as fixation, then fixating to the right should result in *smaller number* responses for group 2 (the opposite response from group 1). On the other hand, if the effect were due to a spatially arranged number line, then the same response pattern should be observed for both groups tested on either the left or right arm.

A mixed model ANOVA was conducted to compare the results collected on the left and right arms (Greenhouse–Geisser correction for sphericity) with two repeated measures variables (touch location–4 × fixation position–4) and one between groups variable (arm tested–2, left or right). Trend analysis revealed a significant linear interaction effect between arm tested and fixation $(F_{3,129} = 8.50, p = 0.006, \eta_p^2 = 0.165)$ showing that the effect of fixation was different for the two groups tested on opposite arms (see Fig. 1). This significant difference indicates that touches were perceived as shifted to the left when fixating a left fixation point and to the right when a right fixation point was used, irrespective of the increasing or decreasing number line-to-space relationship. The effect of eye position for those tested with the right arm was -0.017 cm/deg of eye position (calculated as described above for the left arm, see slope in Fig. 1B) (see Note 1).

Additionally, there was a significant main effect of tactor position ($F_{3,129} =$ 783.4, p < 0.001, $\eta_p^2 = 0.948$) but no interaction effect between arm tested and touch location ($F_{3,129} = 1.91$, p = 0.154, see Fig. 2). Together, these observations suggest that the four tactors were reliably localised, participants perceived the touches as distinct, and that the SSM enables participants to reliably report the location of the touches on the arm. On average, across fixation positions, participants perceived and reported the touches to be in the same segments whether tested on the left or right arm. There was also a significant interaction of touch location by fixation ($F_{9,387} = 3.231$, p = 0.001, $\eta_p^2 = 0.070$) as reported above for the left arm analysis. Importantly, there was no 3-way interaction of touch location \times fixation \times arm (F < 1) suggesting that the difference in fixation effects across the four tactor positions did not depend on the arrangement of the number line in space (which was reversed on the left and right arm). Finally, the mean perceived position of touches on the left arm (M = 5.02, SE = 0.114) and right arm (M = 4.88, SE = 0.162), were not significantly different (no significant between-subjects/between-arm effects F < 1).

4. Discussion

We have introduced the Segmented Space Method (SSM) for reporting perceived touch location in a body based reference frame. This method does not require vision, or previous experience with vision, and we would therefore expect the same pattern of responses whether participant's eyes were open or closed. This body based method was used to verify that coding the location of tactile stimuli requires eye position to convert from an original body based coding of a touch on the skin most likely to a gaze based system. The results presented here, in combination with the previous report of effects of gaze position on localization, strongly reinforce the claim that localising passive touches is at least partially coded in a visual coordinate system, even when a transformation into visual coordinates is not necessitated by the response measure.

If stimuli are coded relative to gaze, then any systematic error in coding the position of gaze shifts the perceived location of stimuli. As was discussed in the introduction, several authors have concluded that gaze direction is underestimated (Harris and Smith, 2008; Hill, 1972; Morgan, 1978). If an underestimated gaze eccentricity is used to make the transformation into a gaze-centred coding system, then the perceived locations of objects in that coordinate system would be shifted in the same direction as gaze. Take the case of a touch delivered 5° to the right of the body midline while the eyes are displaced 15° to the right. In gaze coordinates, the touch would be 10° left. However, if the neural signal indicated that the gaze was only at 10° , then, in gaze coordinates, the touch would be estimated to be 5° further to the right than it actually was, and its location would be perceived as shifted in the same direction as eccentric eye position.

Auditory localisation errors dependent on eccentric eye and head position have also been found. In 1971, Weerts and Thurlow reported that auditory stimuli appeared shifted when the eyes were held eccentrically. They measured the perceived location of auditory stimuli by pointing a flashlight at the perceived source of the sound. However, this method requires the position of both the arm and the light to be accurately known — but both are known to be mislocalized during eccentric fixation (see Lewald and Ehrenstein, 2000, for arm position, and Rossetti *et al.*, 1994 for point of light). Thus, this experiment cannot yield a precise estimate of how much auditory stimuli are mislocalized as a result of eccentric eye position.

Much earlier reports of auditory localisation shifting during eccentric head and eye fixation seem to have used methodology that is not confounded by using a visual measure. Pierce, in 1901, allowed participants to adjust the location of a sound source until it was perceived at 0 or 180 degrees, straight ahead or behind the anterior-posterior axis. His results indicated that the subjective axis shifted in the same direction as head turn but in the direction opposite to the eyes. It is important to note that the direction of shift of the subjective axis will be opposite to the shift of the perceived location of sounds (shifting the central axis to the left will shift perception to the right). This measure, although somewhat crude as it employed the method of adjustment, was clean in that it did not ask the subjects to relate the position of the stimulus to a visual reference. Perhaps dividing up auditory space into segments and using a force choice methodology might confirm these results.

4.1. Number Line Validity

A potential source of error in the SSM comes from known properties of 'number space'. Humans have an internal representation of numbers in space with smallest digits typically on the left side of space and larger digits on the right side of space (Fisher et al., 2003). Loetscher et al. (2008) showed that leftward and rightward eye displacement could nearly perfectly predict the types of errors people made when trying to determine the number halfway between two numbers. When people looked left, they tended to report a number that was less than halfway, and when they looked right they tended to report a number that was more than halfway. Can 'number space' explain the findings reported here and previously? When people looked left and reported the position of a touch on a numbered scale perhaps they reported smaller numbers, irrespective of the tactile stimulus, because of reference to an internal number line? Indeed, our first group (stimulated on the left arm) were more likely to choose lower numbers when they were looking to their left. But, when the experiment was repeated with a second group (stimulated on the right arm, where smaller numbers still corresponded to the elbow now on the right side of space), fixations to the left now caused subjects to report larger numbers (towards the wrist) and fixations to the right were now associated with smaller numbers (towards the elbow). Figure 1 also shows the opposite slopes for data collected on the left and right arms which negates the possibility that people were shifting their responses simply because they were looking at an internal ascending or descending number line. Gaze-dependent influences on numerical estimation do not seem to have had any significant effect on the results reported here. The SSM is thus validated and can henceforth be adapted to measure localisation in a wide variety of modalities. For example, the SSM could easily be modified to report the perceived location of a sound in head coordinates by imagining a clock face seen from above radiating out from the middle of the head.

4.2. Comparing Eye-Position Dependent Effects Measured by Different Methods

With caution, we can compare the effect of eye position recorded with the SSM to previous reports from Harrar and Harris (2009) where location was measured relative to a visual stimulus (a ruler). Comparisons can be made using the partial eta^2 values. The partial eta^2 value is an unbiased estimate of effect size (ANOVA equivalent to r^2 for correlations — the larger the value, the larger the effect of eye position on the perceived location of a touch). Using the SSM, we report an effect size of 13% while Harrar and Harris reported an effect size of 68%. Similarly, we can tentatively compare the actual amount of shift. Comparing the effects reported here using the SSM we found touches to shift by 0.01-0.02 cm/deg of eye position while Harrar and Harris report shifts between 0.02 and 0.1 cm/deg, up to 10 times the present effect. This comparison therefore suggests that the effect of eye position on tactile localisation reported by Harrar and Harris might have been inflated because the methodology required subjects to report the position of the touch relative to a visual stimulus. Interpreting past results requires careful consideration of the methodology used and whether the response measure itself may have been influenced by eye position. Future experimenters looking into the reference frames used for coding various modalities should choose their methodology carefully to match response and stimulus modalities (see Note 2).

A similar conclusion about the importance of selecting response measures was reached by Jones *et al.* (2010). They compared visual and non-visual references for measuring perceived body position when the arm was placed actively and passively. They report eye-position-dependent errors in localizing the limb in all conditions and, like Harrar and Harris (2010), suggest that perceptual errors may carry over to conditions in which actions are required. As an additional comparison, future experiments could compare errors for arm position measured using the SSM.

Similarly, Lewald (1997) compared perceived shifts of auditory stimuli in experimental conditions in which localisation errors were measured with both visual and non-visual references. Four experiments were conducted: a force choice and an adjustment task, each with and without a visual reference (in the latter case the head/nose was used as the reference point). In the two experiments in which auditory stimuli were localized relative to a visual reference, reliable shifts of auditory localization related to gaze position were found. However, in the two experiments when non-visual body based references were used (straight ahead, extension of the nose, etc.) inconsistent results were found. These inconsistencies may be due to the non-visual references sometimes being body based (head and nose) and sometimes being, arguably, amodal (straight ahead). The SSM could be modified to measure auditory or proprioceptive localisation for both passive arm movements (moving a participant's arm and having them report the perceived segment of space) and active arm movements (telling participants to move to a particular segment of space).

4.3. Visual Imagery of the Arm

In order to perform the SSM, subjects had to imagine their arm divided into segments. Spatial tasks might normally be put into a visuo-spatial reference frame (at least for sighted people) but it seems that with explicit instructions participants can use non-visual body centred spatial references or an external reference frame. For example, the Müller-Lyer illusion (both the visual and the tactile versions) almost completely disappear if observers are instructed to use body centred references (Millar and Al-Attar, 2002). Similarly, when Millar and Al-Attar (2004) gave blindfolded participants explicit instructions to use a square frame in order to tactually localise objects on a table, their localisation errors decreased in comparison to when no such 'external frame' instructions were given. Since instructions to use particular references can have significant effects, we feel that the SSM (in which participants are told to relate the touches to body centred cues, relative to their elbow or wrist) is adequate to encourage a non-visual body centred decision. It is, of course, still possible that some people may have used visual imagery when doing this task.

As we did not specifically test for effects of visual imagery, we do not know if participants employed visual imagery for a task. We can only report, based on our results, that touch is coded relative to a visuo-spatial reference. If participants had imagined their arm and the touch location 'correctly' then there would not have been any errors relative to the eye position. Thus, although we have no direct evidence of visual imagery, we can only say that if participants did use visual imagery then any visual imagery that they did employ appears to itself be coded relative to a visuo-spatial reference.

The fact that visual imagery is used for most non-visual spatial tasks (and that most readers will feel that they must imagine their arm in order to perform the SSM) is even greater reason for concluding that space (even tactile space) is generally visually coded — at least for sighted individual (Millar, 2008). Katz (1925) suggested that touch is nearly always projected into external space where tactile impressions are visualised in order to identify objects. Indeed, people seem to use visual imagery when they have to perform haptic tasks while blindfolded (e.g. matching the left hand to an unseen right hand in Lederman *et al.*, 1990). Taking this to the extreme, Titchener (1909, as cited in Millar, 2008) concluded that visual imagery is needed in order to have any kind of mental representation of an object or even meaning. Thus, for Tichener it would seem impossible to imagine the smell of coffee, the feeling of

pain, or the sound of a car without visualising the objects that generated these sensations. From this extreme view, it would seem that all psychophysics experiments in which stimuli are presented without explicitly defined objects, rely (or elicit) visual imagery.

Even still, if visual imagery were used by some of our subjects, experiments have shown that visual imagery is not the same as sensory vision. Visual imagery does not update spatially for rotations (Klatsky *et al.*, 1998) and relies on working memory (Baddeley and Andrade, 2000) making it highly degraded compared to sensory vision. Thus, we conclude that if visual imagery were being used it would still be acceptable to regard the SSM as a task which effectively does not have a visual probe.

5. Conclusions

Here we introduce the Segmented Space Method (SSM) for measuring localisation. In SSM a particular area of space is divided into equal sections and the participant is asked to report in which section a stimulus occurred. When the SSM was applied for touches on the arm, the technique confirmed that gaze affects tactile localisation, i.e. touch location is at least partially coded in a visual reference frame even when such a coding scheme is not necessitated by a particular task. Previous studies (based on measurements using a visual reference) found larger gaze-dependent shifts, probably due to combined effects on the perceived location of the stimuli and the measurement probe used. The response method should, therefore, be carefully considered when interpreting data of this kind, keeping in mind that any effects observed may result from a combination of errors in both perception and response.

Acknowledgements

We would like to thank Ryan Dearing for his help in collecting the data. We would also like to acknowledge Susanna Millar for discussions regarding tactile spatial references and the topic of visual imagery. The Natural Sciences and Engineering Research Council (NSERC) of Canada sponsored these experiments. Vanessa Harrar was an NSERC scholar and currently holds the Mary Somerville Junior Research Fellowship of Somerville College, Oxford University.

Notes

1. In order to compare the magnitude of the fixation effect on the two arms (the slopes of the lines in Fig. 1) we 'flipped' the data collected on the right arm along the x-axis. In this way, for both the left and right arm,

looking to the left should cause a smaller response, and looking to the right a larger response. The 3-way ANOVA was repeated (a mixed model with two repeated measures variables (touch location–4 × fixation position–4) and one between groups variable (arm tested–2, left or right)). The linear contrast main effect of fixation was, of course, significant now that both sets of data were no longer cancelling each other out ($F_{1,43} = 8.50$, p =0.006). There was no significant interaction for the linear contrast of the fixation effects by arm (F < 1): that is, the slopes of the fixation effect on the left and the right arms were NOT significantly different. No other interactions of fixation were significant.

2. Additionally, we would suggest that methodology be carefully chosen so as to minimize effects of response bias and attention. We expect that with the SSM, as in Harrar and Harris (2009), roughly 17% of the shifts in the perceived positions of the touch can be accounted for by response bias or attention in the direction of eye position.

References

- Andersen, R. A. (1997). Multimodal integration for the representation of space in the posterior parietal cortex, *Philos. Trans. Royal Soc. Lond. B Biol. Sci.* 352, 1421–1428.
- Andersen, R. A. and Mountcastle, V. B. (1983). The influence of the angle of gaze upon the excitability of the light-sensitive neurons of the posterior parietal cortex, *J. Neurosci.* 3, 532–548.
- Baddeley, A. D. and Andrade, J. (2000). Working memory and the vividness of imagery, J. Exper. Psychol. Gen. 129, 126–145.
- Batista, A. P., Buneo, C. A., Snyder, L. H. and Andersen, R. A. (1999). Reach plans in eyecentered coordinates, *Science* 285, 257–260.
- Boussaoud, D. and Bremmer, F. (1999). Gaze effects in the cerebral cortex: reference frames for space coding and action, *Exper. Brain Res.* 128, 170–180.
- Cohen, Y. E. and Andersen, R. A. (2002). A common reference frame for movement plans in the posterior parietal cortex, *Nat. Rev. Neurosci.* **3**, 553–562.
- Cousineau, D. (2005). Confidence intervals in within-subjects designs: a simpler solution to Loftus and Masson's method, *Tutorials Quant. Meth. Psych.* **1**, 42–45.
- Dessing, J. C., Byrne, P. A., Abadeh, A. and Crawford, J. D. (2012). Hand-related rather than goal-related source of gaze-dependent errors in memory-guided reaching, J. Vision 12, 1–8.
- Fischer, M. H., Castel, A. D., Dodd, M. D. and Pratt, J. (2003). Perceiving numbers causes spatial shifts of attention, *Nat. Neurosci.* 6, 555–556.
- Harrar, V. and Harris, L. R. (2005). Simultaneity constancy: detecting events with touch and vision, *Exper. Brain Res.* 166, 465–473.
- Harrar, V. and Harris, L. R. (2009). Eye position affects the perceived location of touch, *Exper. Brain Res.* 198, 403–410.

- Harrar, V. and Harris, L. R. (2010). Touch used to guide action is partially coded in a visual reference frame, *Exper. Brain Res.* 203, 615–620.
- Harris, L. R. and Smith, A. T. (2008). The coding of perceived eye position, *Exper. Brain Res.* 187, 429–437.
- Henriques, D. Y., Klier, E. M., Smith, M. A., Lowy, D. and Crawford, J. D. (1998). Gazecentered remapping of remembered visual space in an open-loop pointing task, *J. Neurosci.* 18, 1583–1594.
- Hill, A. L. (1972). Direction constancy, Percept. Psychophys. 11, 175–178.
- Ho, C. and Spence, C. (2007). Head orientation biases tactile localization, *Brain Res.* 1144, 136–141.
- Jones, S. A. H., Cressman, E. K. and Henriques, D. Y. (2010). Proprioceptive localization of the left and right hands, *Exper. Brain Res.* 204, 737–783.
- Klatsky, R. L., Loomis, J. M., Beall, A. C., Chance, S. S. and Golledge, R. G. (1998). Spatial updating of self-position and orientation during real, imagined, and virtual locomotion, *Psych. Sci.* **9**, 293–298.
- Katz, D. (1925/1989). The World of Touch, L. E. Krueger (Ed. and Trans.). Lawrence Erlbaum Associates, Hillsdale, NJ, USA.
- Lederman, S. J., Klatzky, R. L., Chataway, C. and Summers, C. (1990). Visual mediation and the haptic recognition of two-dimensional pictures of common objects, *Percept. Psychol.* 47, 54–64.
- Lewald, J. (1997). Eye-position effects in directional hearing, Behav. Brain Res. 87, 35-48.
- Lewald, J. and Ehrenstein, W. H. (2000). Visual and proprioceptive shifts in perceived egocentric direction induced by eye-position, *Vision Research* **40**, 539–547.
- Loetscher, T., Bockisch, C. and Brugger, P. (2008). Looking for the answer: the mind's eye in number space, *Neuroscience* 151, 725–729.
- Millar, S. (2008). Space and Sense. Psychology Press, Hove, New York, USA.
- Millar, S. and Al-Attar, Z. (2002). The Müller-Lyer illusion in touch and vision: implications for multisensory processes, *Percept. Psychophys.* 64, 353–365.
- Millar, S. and Al-Attar, Z. (2004). External and body-centered frames of reference in spatial memory: Evidence from touch, *Percept. Psychophys.* 66, 51-59.
- Morgan, C. L. (1978). Constancy of egocentric visual direction, *Percept. Psychophys.* 23, 61–68.
- Pavani, F., Husain, M., Ladavas, E. and Driver, J. (2004). Auditory deficits in visuospatial neglect patients, *Cortex* 40, 347–365.
- Pierce, A. H. (1901). *Studies in Auditory and Visual Space Perception*. Longmans, Green, New York, USA.
- Pritchett, L. M. and Harris, L. R. (2011). Perceived touch location is coded using a gaze signal, *Exper. Brain Res.* 213, 229–234.
- Röder, B., Föcker, J., Hötting, K. and Spence, C. (2008). Spatial coordinate systems for tactile spatial attention depend on developmental vision: evidence from event-related potentials in sighted and congenitally blind adult humans, *Eur. J. Neurosci.* 28, 475-483.
- Röder, B., Rösler, F. and Spence, C. (2004). Early vision impairs tactile perception in the blind, *Curr. Biol.* 14, 121–124.
- Rossetti, Y., Tadary, B. and Prablanc, C. (1994). Optimal contributions of head and eye positions to spatial accuracy in man tested by visually directed pointing, *Exper. Brain Res.* 97, 487– 496.

- Titchener, E. B. (1909). *Lectures on the Experimental Psychology of Thought*. MacMillan, New York, USA.
- Weerts, T. C. and Thurlow, W. R. (1971). The effects of eye position and expectation on sound localization, *Percept. Psychophys.* 9, 35–39.
- Yamaguchi, M. (2007). Integration system of head, eye and retinal position signals for perceptual direction, *Optical Review* 14, 411–415.