cortex 88 (2017) 53–65

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Research report

Influence of the body schema on mirror-touch synesthesia

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ARTICLE INFO

Article history:
Received 4 July 2016
Reviewed 23 September 2016
Revised 20 October 2016
Accepted 14 December 2016
Action editor Georg Goldenberg
Published online 24 December 2016

Keywords:
Mirror-touch synesthesia
Body schema
Frames of reference

ABSTRACT

Individuals with mirror-touch synesthesia (MTS) report feeling touch on their own body when seeing someone else being touched. We examined how the body schema – an on-line representation of body position in space – is involved in mapping touch from a viewed body to one's own body. We showed 45 mirror-touch synesthetes videos of a hand being touched, varying the location of the viewed touch by hand (left, right), skin surface (palmar, dorsal) and finger (index, ring). Participant hand posture was either congruent or incongruent with the posture of the viewed hand. After seeing the video, participants were asked to report whether they felt touch on their own body and, if so, the intensity and location of their percepts. We found that participants reported more frequent and more veridical (i.e., felt at the same somatotopic location as the viewed touch) mirror-touch percepts on posturally congruent versus posturally incongruent trials. Furthermore, participant response patterns varied as a function of postural congruence. Some participants consistently felt sensations on the hand surface that was stimulated in the video – even if their hands were in the opposite posture. Other participants' responses were modulated based on their own hand position, such that percepts were more likely to be felt on the upright, plausible hand surface in the posturally incongruent condition. These results provide evidence that mapping viewed touch to one's own body involves an on-line representation of body position in space.

1. Introduction

The majority of individuals do not experience tactile sensations while observing touch on someone else's body. However, those with mirror-touch synesthesia (MTS) do report feeling tactile sensations on their own body when seeing someone else being touched. In the first reported case of mirror-touch (or vision-touch) synesthesia, Blakemore, Bristow, Bird, Frith, and Ward (2005) imaged a mirror-touch synesthete (C) and twelve non-synesthetes while viewing videos of individuals or inanimate objects being touched. When comparing activity for viewing a person versus an object being touched, they found greater activity in primary and secondary somatosensory cortex for C compared to all controls. In non-mirror-touch synesthetes, regions such as secondary somatosensory cortex and parts of primary

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http://dx.doi.org/10.1016/j.cortex.2016.12.013

somatosensory cortex (e.g., area 2) are active when viewing another person being touched (Blakemore et al., 2005; Bufalari, Aprile, Avenanti, Di Russo, & Aglioti, 2007; Ebisch et al., 2008; Keysers et al., 2004). Holle, Banissy, and Ward (2013) examined an additional ten mirror-touch synesthetes, finding that posterior secondary somatosensory cortex differed in response to viewed touch compared to controls, showing overactivity when watching a face being touched and hypo-activity when watching a dummy being touched. From these results, it has been hypothesized that mirror-touch percepts are caused by the same mechanisms that lead to activation in somatosensory regions after viewed touch in non-synesthetes. However, mirror-touch synesthetes are thought to have an overactive “mirror-touch” system, resulting in suprathreshold sensations after viewing touch on an individual – known as the “Threshold Theory” of MTS.

In understanding the mechanisms of the mirror-touch system, one question of interest is the relationship between the location of the viewed touch and the mirror-touch percept on the synesthete's own body. Previous studies have identified two major subtypes of MTS, in which the spatial mapping between the viewed touch and synesthetic percept is based on different frames of reference. In a somatotopic representation, touch is represented based on its position on the skin surface, irrespective of its position in external space. Whereas in an egocentric, external representation, locations are encoded based on the position of the stimulus in external space (Medina, McCloskey, Coslett, & Rapp, 2014). Banissy and Ward (2007) presented 10 mirror-touch synesthetes videos of a person, facing the synesthete, being touched on either their left or right cheek. Four mirror-touch synesthetes reported sensation on the same skin surface that was touched in the video – such that seeing someone touched on their anatomically-defined left cheek would result in a percept on the mirror-touch synesthete's left cheek. In this *anatomical* subtype of MTS, the synesthete experiences a mirror-touch percept in the same location of the viewed touch in a somatotopic frame of reference. However, six other participants, when viewing someone touched on their anatomically-defined left cheek, perceived touch on their own right cheek. For these individuals with *specular* (or mirrored) MTS, the viewed touch and mirror-touch percept are on the same side in an external reference frame.

To do these mappings, one needs to have a representation of one's own body and the body of the touched individual. A number of studies have provided evidence for an on-line representation of body position in space – often called the body schema or postural schema (Head & Holmes, 1911; Medina & Coslett, 2010). In mirror touch synesthesia, one study examined the relationship between body position and mirror touch synesthesia, finding no effect of viewed face position or hand crossing on synesthetic percept intensity (Holle, Banissy, Wright, Bowling, & Ward, 2011). However, no studies have examined how the synesthete's body schema influences the mapping process from viewed touch to synesthetic percept. In this study, we manipulated the position of the synesthete's body and the viewed body to examine whether and how the body schema influences MTS. More specifically, we examined whether the body schema influenced the frequency and location of mirror-touch percepts, and whether the processes utilized in mapping viewed touch onto one's own body differed across individuals in specific manners.

First, the relationship between the location of the viewed touch and the participant's own body position could influence how *frequently* mirror-touch percepts are experienced. Consider a trial in which the participant views a hand touched on the dorsal surface (palm down) of the index finger of the right hand, with the synesthete's hands positioned palms up (see Fig. 1). In this trial, the posture of the viewed hand is incongruent with the posture of the participant's own hands. If participants are referencing an on-line representation of their body for mapping mirror-touch percepts, one possibility is that this postural incongruency could lead to a decrease in mirror-touch percepts. However, if this mapping is not influenced by the synesthete's own body position, then incongruencies in body posture should have no effect on mirror-touch percept frequency.

Second, changes in body position may also influence, not only the perceived frequency, but the perceived *location* of mirror-touch percepts. Consider the trial previously

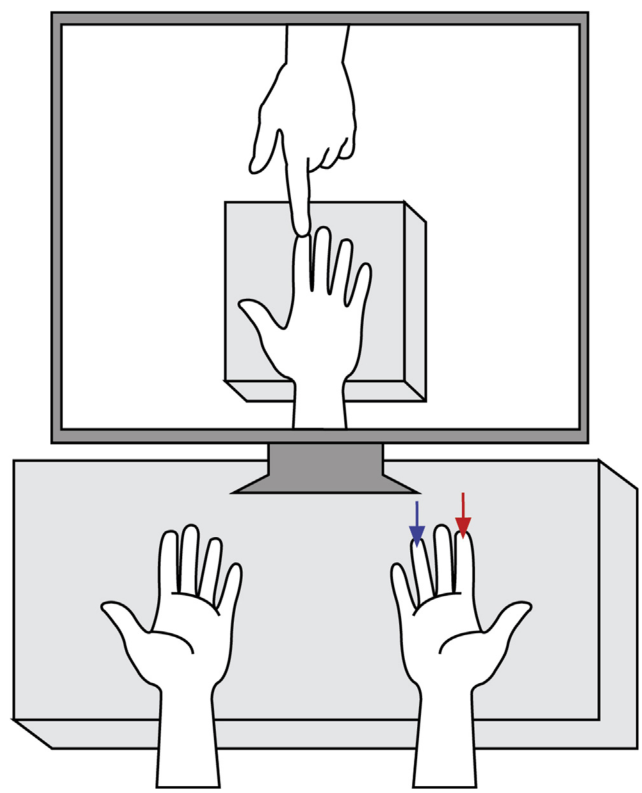

Fig. 1 – Diagram showing participant hand posture on an incongruent trial, in which the participant's hands (bottom) are positioned palms up on a table and the viewed hand (top) is palms down. In the video, the hand is stimulated on the dorsal surface of the index finger of the right hand. The red arrow points to the finger corresponding to the viewed touch. The blue arrow points to a potential response if the location of the viewed touch were encoded in an external, hand-centered representation.

mentioned in Fig. 1. In this example, one possibility is that the person reports the stimulus on the same finger that was touched in the video (see Fig. 1, red arrow) – consistent with anatomical MTS. Given that the touch on the video occurs on the left side of the hand in an external, hand-centered frame of reference, a second possibility is that the participant reports a percept on the ring finger of their right hand (see Fig. 1, blue arrow) – consistent with specular MTS. Although it is possible to characterize responses based on anatomical and specular MTS, there are a number of additional dimensions to be considered in mapping touch on the hands. In Fig. 1, the viewed hand is touched on the upward-facing dorsal surface. However, as the participant's hands are positioned with the palmar surface facing up, would the synesthete report mirror-touch percepts on the surface that is more likely to be touched by another hand (palms up)? Or would the percept occur on the same side that was touched on the video (dorsal surface), even though having an actual touch on the synesthete's hands would be implausible (given that it is touching the surface of a table). Also, given that the touch occurs on the right hand, will the participant automatically feel sensation on his/her own right hand? Or is it possible that the mirror-touch percept will be felt on the opposite hand?

Finally, as noted before, there is evidence for two major subtypes of MTS – anatomical and specular. However, other subtypes of MTS are possible. For example, White and Aimola Davies (2012) varied the position (fingers pointing towards or away from the participant) and direction of brushstrokes on a prosthetic hand (e.g., proximal to distal direction on a finger) shown to two specular mirror-touch synesthetes. When the fingers of the prosthetic hand were pointed towards the participant, touch on the left prosthetic hand (on the right side of the participant) resulted in sensation on the synesthete's right hand. However, one participant reported a somatotopic mapping of brushstroke direction, such that a proximal to distal brushstroke was felt proximal to distal on the participant's own hand, whereas that same brushstroke was felt in the same direction encoded in an external frame of reference (distal to proximal) by another participant. This provided evidence that potential mappings from viewed touch to synesthetic experience could vary along multiple dimensions, resulting in a number of potential subtypes of MTS. As noted earlier, when the viewed hand and synesthete's hand are in incongruent postures, participants could either report mirror-touch percepts on the surface stimulated on the viewed hand or on the plausible surface relative to the synesthete's own body (the skin surface positioned upward). Finally, we examined whether synesthetes would all demonstrate the same mapping from viewed to perceived surface, or vary along this dimension?

2. Methods

2.1. Questionnaire and screening

To select participants for further examination, we presented a short synesthesia screener as part of a larger questionnaire to 2351 University of Delaware undergraduate students (976 male, 1373 female, two sex not reported; mean age = 19.3, SD = 1.74) taking Introduction to Psychology over four different semesters. The screener included a number of questions regarding various synesthetic experiences (see Appendix) and included the following question: "Do you ever experience…touch sensations on your body when you see them on another person's body?" Participants responded using a Likert scale ranging from 1 (strongly disagree) to 7 (strongly agree). Any subject who responded "agree" or "strongly agree" to this question (n = 228) was eligible for further testing. We tested 114 participants from this group.

2.2. Experiment

Participants were seated comfortably, arms uncrossed on a table in front of them. The experiment consisted of two blocks, with the participant's hands oriented either palms up or palms down for the first block, taking the other posture for the second block. Posture order was counterbalanced across subjects. A computer monitor was positioned just beyond their hands, with the monitor midline centered with the participant's trunk midline. The participant was told that they were going to watch a series of videos showing an individual's hand being touched, or approached, but not touched. Each block consisted of 64 videos showing a single hand (left or right) positioned palm up or palm down on a table. The hand on the table was shown by itself for approximately 1 sec, followed by a second hand (the touching hand) with its index finger outstretched that would enter the screen. On 75% of trials (48 trials/block), the touching hand would touch the hand on the table for 500 msec (touch trials), whereas on 25% of trials (16 trials/block), the touching hand would move towards the hand on the table, stop above it for 500 msec, but not touch it (no touch trials). For touch trials, we varied characteristics of the viewed touch along the following dimensions: hand touched (left or right), surface touched (dorsal or palmar), initial finger touched (index or ring), and initial segment touched (distal or proximal). For 16 trials, the touch was stationary (two for each condition combination), whereas for 32 trials, the stimulus moved either along the length of the finger or across the fingers (two trials per block for each condition combination). No-touch trials (16 trials per block, two for each condition combination) were balanced for hand shown (left or right), surface shown (dorsal or palmar), and finger approached (index or ring).

After viewing each video, the participant then told the experimenter if they felt any touch on their own hand. If they responded affirmatively, they were then asked how strong the perceived sensation was on a scale from 1 to 10, with 1 being barely perceptible and 10 being the perceived intensity of the touch shown. They were also asked on which hand, surface, finger and finger segment (distal, proximal, or other) was the perceived sensation, along with whether the stimulus was moving and (if so) its direction of movement. These responses were then coded for veridicality – that is, if the mirror-touch percept was felt in the same location as the hand in the video. Veridicality was coded separately for each coded dimension – i.e., stimulated hand, finger, surface, etc. Then, we used separate linear mixed models (using the lmertest package in R 3.2.3) for our dependent variables of interest (frequency and intensity of perceived mirror-touch percepts, and veridicality of mirror-touch percepts on touch trials for hand, surface, and finger location) to examine whether subject hand posture and the location of the stimulus on the viewed hand influenced responses. Model testing began with a null model containing only subject as a random factor. Next, the following fixed factors and interaction terms were entered in a stepwise manner: participant hand posture (palms up/down), video hand posture (palm up/down), the interaction of participant and video hand posture, video hand chirality (left or right), initial video finger touched (index or ring), initial video finger segment touched (distal or proximal), video stimulus movement (stationary or moving), and trial number. These factors were centered to reduce model collinearity, and all models were checked for collinearity using mer-utils.R (https://github.com/aufrank/R-hacks/blob/master/mer-utils.R). Two models would be compared (e.g., the null model and the model with participant hand posture included), and the factor would be included in the final model only if adding it resulted in a significant increase in model fit (tested using analyses of variance (ANOVAs)). Binomial dependent variables were assessed using logit linear mixed models using glmer (family = binomial), while continuous dependent variables were assessed using lmer.

After testing a number of mirror-touch synesthetes, we noticed that veridicality regarding the location of mirror-touch percepts was far below what was expected, even in congruent postures (see Results). To ensure that simply reporting the location of a viewed touch on a hand across multiple dimensions was not difficult, we ran a control experiment with ten University of Delaware undergraduates who did not report MTS on their questionnaire responses (four males, six females, mean age = 19.4, SD = .96). This experiment was the same as what was given to mirror-touch synesthetes with one important difference. Instead of asking them if they felt the viewed touch, we asked them to report whether they saw the viewed touch and then report its location along the same dimensions as in the experiment with mirror-touch synesthetes.

3. Results

3.1. *Questionnaire responses*

Although not the primary goal of this experiment, we briefly present the data from the synesthesia questionnaire. Using a Bonferroni corrected alpha of .006, there were no differences between males and females in responses to synesthesia questions. Using an uncorrected alpha of .05, two questions differed across sexes: Experiencing taste when observing another person eating or drinking [$t(2185.7) = -2.55$, $p = .011$; $M = 3.03$, $F = 3.22$] and hearing sounds in the environment when touched [$t(2017.9) = 2.25$, $p = .024$, $M = 2.39$, $F = 2.26$]. Next, we did a principal components analysis with varimax orthogonal rotation to examine the relationship between questionnaire responses. In this PCA analysis (Kaiser-Meyer-Olkin Measure of Sampling Adequacy = .867), two components were extracted which accounted for 75.63% of the variance. The first factor (61.5% of variance) consisted of the questions that involved either touch or taste, whereas the second factor (14.1% of variance) loaded on to the grapheme-color and number-color synesthesia questions (see Appendix for factor loadings).

3.2. *Frequency of MTS in the population*

Although all of our participants responded affirmatively to a question regarding having experienced mirror-touch synesthetic percepts, we expected that a fair number would not experience mirror-touch synesthetic percepts in the lab, either because the videos may not have been salient enough to elicit mirror-touch percepts, or simply because of careless questionnaire responses. Before the experiment, we decided to categorize an individual as having MTS if he/she reported mirror-touch synesthetic percepts on >5% of viewed touch trials in the experiment. Only 45/114 reported mirror-touch synesthetic percepts on greater than 5% of viewed touch trials, with 14 participants demonstrating MTS on 0–5% of viewed touch trials, and 55 never once reporting a mirror-touch synesthetic percept (see Fig. 2 for the histogram). The 69 participants below our cutoff experienced MTS on .45% of trials overall.

Using our selected threshold, 1.91% of our population (45/2351) demonstrated mild MTS – though we note that there were 114/228 individuals who reported MTS on the questionnaire but were not tested. This rate is similar to what has previously been reported in the literature (1.6%, see Banissy, Kadosh, Maus, Walsh, & Ward, 2009). We next examined the perceived frequency, intensity, and location of mirror-touch percepts *only* on the individuals who demonstrated MTS on >5% of viewed touch trials. Those analyses follow.

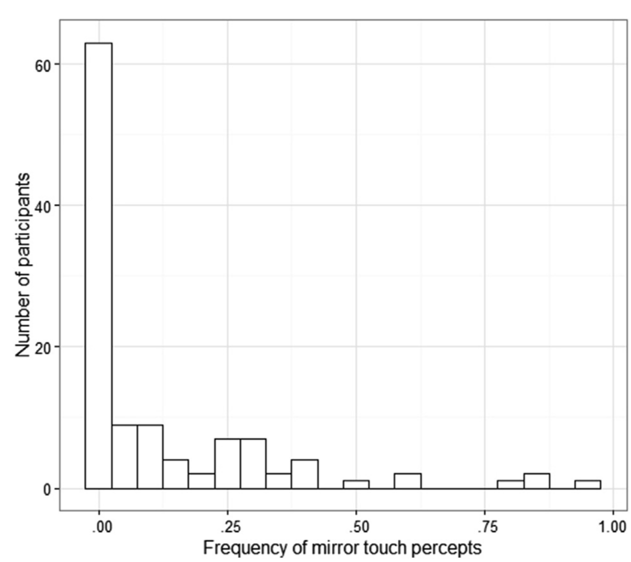

Fig. 2 – A histogram showing the number of participants demonstrating mirror touch synesthesia at different frequencies, with bin size = .05.

3.3. *Frequency and intensity of mirror-touch percepts*

Given that viewed touch and viewed no touch trials were substantially different, we examined what factors influence the frequency and intensity of mirror-touch synesthetic percepts on viewed touch and viewed no touch trials separately. Overall, the mirror-touch synesthetes felt sensations on 30.3% of viewed touch trials. As predicted, there was a significant interaction between participant hand posture and video hand posture ($z = 7.15$, $p < .001$) in the final model, along with a main effect of video hand posture ($z = -4.28$, $p < .001$). Participants were more likely to report mirror-touch percepts when the video hand was stimulated on the palmar (33.0%) versus the dorsal surface of the hand (27.6%). Importantly, participants were far more likely to report mirror-touch percepts when the hand in the video was in the same posture as the participants' hands (34.7%) compared to when they were in opposite postures (25.9%). Next, there was a significant main effect of initial video finger segment touched ($z = 3.45$, $p < .001$), as individuals were more likely to report mirror-touch percepts when the distal (32.4%) versus proximal (28.2%) segment was touched. Participants were also more likely to have mirror-touch percepts for moving (31.2%) versus stationary (28.4%) stimuli ($z = 2.20$, $p = .027$). Finally, there was a main effect of trial ($z = -2.24$, $p = .025$), as the frequency of mirror-touch percepts decreased as the block continued. Examining the perceived intensity of mirror-touch percepts, there were only two main effects: mirror-touch percepts were more intense when their hands were palms down (3.54) versus palms up (3.15, $t = 3.91$, $p < .001$), and were more intense for stationary (3.44) versus moving (3.30) stimuli ($z = -1.96$, $p = .050$).

We also found that mirror-touch synesthetes reported phantom sensations on 14.4% of trials in which the video hand was approached, but not touched (viewed no touch trials). We found no factors that significantly influenced the frequency nor the intensity of phantom sensations on viewed no touch trials. In a separate correlational analysis, we did find a relationship between the percentage of trials in which individuals reported mirror-touch sensations on viewed touch trials and viewed no touch trials, $r(43) = .564$, $p < .001$, suggesting a relationship between reported synesthetic percepts in the two conditions.

Briefly, we found that synesthetes were more likely to report mirror-touch percepts when their hands were in the same posture as the hand touched in the video. Furthermore, participants reported mirror-touch percepts when the touch on the video hand was on surfaces with lower (palmar side of the hand, fingertips) compared to higher (dorsal surface of hand, proximal finger segment) detection thresholds (palm, fingertips). Finally, mirror-touch synesthetes did report sensations, not only on trials in which the hand in the video was touched, but trials in which the hand was approached, but not touched.

3.4. *Influence of body posture on percept location*

Along with reporting whether they felt touch when viewing the videos, participants also reported the perceived location of the mirror-touch percepts on their own body. Examining the veridicality (whether they felt mirror-touch percepts on the same location as shown in the video) of their responses, we were interested in three questions. First, how veridical were the mirror-touch percepts along different stimulus dimensions (e.g., stimulated hand, finger, surface)? Second, what factors (including the participant's own hand posture) influenced the perceived location of their mirror-touch percepts? Third, do participants differ in whether their own body posture influences the location of mirror touch percepts?

We ran separate logit linear mixed models for finger, hand, and surface veridicality, adding the same factors and interaction terms as in the previous models. Given that we could only assess veridicality for trials in which the video hand was touched, this analysis includes only video touch trials. For finger veridicality only two variables were significant in the final model: initial finger stimulated [as participants were more veridical for when the video index (82.2%) versus ring (76.1%) finger was touched ($z = 2.79$, $p = .005$)], and moving/stationary stimulation (more veridical for stationary (85.1%) versus moving (76.5%) stimuli). Although participants made more veridical responses for finger when the hands were congruent (81.6%) versus incongruent (76.0%), the video hand surface by subject hand posture interaction was not significant when added to the model ($z = 1.78$, $p = .075$). Hand veridicality – whether the participant felt the mirror-touch percept on the same hand (left, right) as in the video – was relatively poor, as responses were veridical on only 64.9% of trials. For hand veridicality, there was a main effect of video hand posture, as sensations were more veridical when the hand in the video was palm down (67.8%) versus palm up (62.5%; $z = 2.23$, $p = .026$). There was also a significant video hand surface by subject hand posture interaction ($z = 4.23$, $p < .001$) as participants felt the mirror-touch percept on the veridical hand on 70.1% of trials in congruent postures, versus only 58.0% of trials in incongruent postures. For surface veridicality – whether the mirror-touch percept was felt on the same hand surface (dorsal or palmar) as in the video – there was a main effect of video hand posture, as participants were more likely to make veridical responses when the video hand was touched on the palmar (85.1%) versus the dorsal (76.5%) surface of the hand ($z = -3.73$, $p < .001$). Importantly, there was a highly significant video hand posture by participant hand position interaction ($z = 11.8$, $p < .001$), as participants were more likely to make veridical responses when the video hand and actual hand were in congruent (93.4%) versus incongruent (64.8%) postures. For finger segment veridicality, participants made veridical responses on 92.8% of trials. The only significant factor predicting finger segment veridicality was whether the stimulus was stationary (95.4%) versus moving (91.8%; $z = -2.23$, $p = .026$). Finally, we note that for moving stimuli, participants were quite veridical in reporting moving direction for stimuli that went along (95.3%) versus across (64.3%) fingers. Given that the viewed hand was always in the same orientation as the participant's hands, this veridicality for along finger moving stimuli was expected. Decreased veridicality for judging movement directionality across fingers was likely due to a decrease in veridicality in representing the hand, surface, and finger that was initially stimulated.

As predicted, the veridicality of localization percepts was strongly influenced by participant hand posture, as individuals were significantly more likely to feel the mirror-touch percept on the veridical hand and hand surface when their own hands were in the same posture as the viewed hand. However, veridicality overall was relatively inaccurate, especially with regards to the stimulated hand. One possibility is that participants, when attending to the location of the stimulus on the skin surface (e.g., the stimulated finger) fail to code information about which hand and/or hand surface was stimulated. Therefore, we examined performance of control, non-synesthetic participants in identifying the location of touch. These participants were randomly selected from the individuals who responded “disagree” or “strongly disagree” to the questionnaire entry on mirror touch synesthesia. Controls were quite accurate overall, identifying the stimulated hand on 98.4% of trials, surface on 97.0% of trials, and finger on 93.8% of trials. As with the mirror-touch synesthetes, we also did model testing to examine if any stimulus or subject factors influenced the accuracy of their reports. There were no factors that predicted overall response accuracy, correct hand, or correct surface. For correct finger, participants were significantly more accurate when their own palms were up (95.7%) versus down (91.8%; $z = 2.54$, $p = .011$) and when viewed stimuli were first presented to the index (96.0%) versus ring (91.3%) finger ($z = 2.87$, $p = .004$). Importantly, controls showed no postural congruency effects for identifying the correct finger, surface, or hand (see Fig. 3).

As noted in previous studies (Banissy & Ward, 2007; White & Aimola Davies, 2012), individuals with MTS can be categorized based on the reference frame utilized in transforming viewed touch into percepts onto the synesthete's own hand. As an example, a synesthete is positioned facing an individual who is touched on her left cheek. An individual with anatomical MTS would feel touch on the viewed skin surface – that is, the touch would be encoded in a somatotopic reference frame. This is contrasted with specular MTS, where the synesthete feels touch on the same side that the touch occurred in an external reference frame. In this example, the viewed touch occurs on the right side of the participant's face relative to the synesthete, and then the synesthete feels touch on that side.

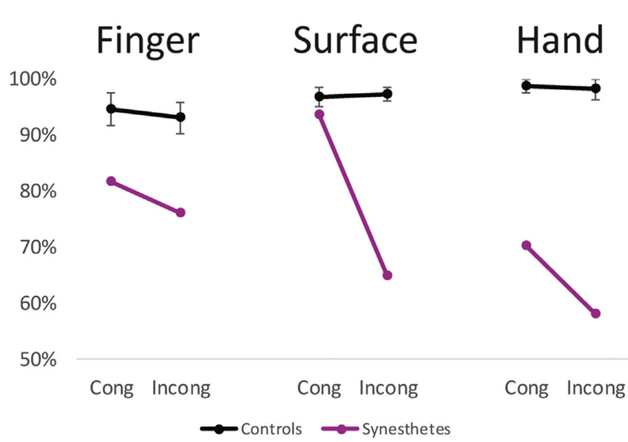

Fig. 3 – Percentage of veridical trials for stimulated finger, surface, and hand (chirality) for mirror-touch synesthetes (purple) and controls (black) on posturally congruent and incongruent trials. Error bars show a 95% CI for control performance.

However, mapping mirror-touch sensations to the hand provides additional dimensions to consider. In the example in which a mirror-touch synesthete views another person being touched on the left cheek, there are two likely response locations (assuming that the participant does not localize to a completely different body part) – either on the participant's own left cheek (anatomical MTS) or on the same side relative to a reference frame projected from the viewer – the right cheek (specular MTS). Contrast this with viewing an individual being touched on the dorsal surface (palms down) of the index finger of the right hand, with the synesthete's hands palm up. If we limit potential responses to either the index or ring finger, there are eight potential responses that could be made, with different response patterns reflecting different frameworks for mapping viewed touch on another individual to one's own body.

In attempting to find different patterns of MTS in our population, we first examined whether our participants could be described as having anatomical or specular MTS. We defined individuals with “anatomical” MTS as those who made veridical responses for the stimulated finger on >80% of trials in both congruent *and* incongruent postures, with at least >5% MTS percepts in each posture. We then defined two separate “specular” MTSs. In a hand-centered specular MTS, we encoded the location of the perceived mirror-touch sensation relative to a hand-centered midline, and then examined whether the synesthete's mirror-touch percept was on the same side of the hand as the touch viewed in the video. For trunk-centered specular MTS, we coded whether the participant's mirror touch sensation was on the same hand (left hand, right hand) as the touch viewed in the video. Our criteria for both specular MTSs was localization of mirror-touch percepts on the same side (in either a hand- or trunk-centered external reference frame) as the viewed hand on >80% of trials in both congruent *and* incongruent postures. Although 16 participants met our definition of anatomic MTS, surprisingly, none of our participants demonstrated either hand- or trunk-centered specular MTS based on these criteria.

Our prior analyses provided evidence for changes in the frequency of mirror-touch percepts based on the *postural* congruency between the video and synesthete's hands. Therefore, we next examined whether mirror-touch synesthetes could be categorized based, not on a strict anatomical/specular distinction, but on whether their perceived response location is constrained based on their own body posture. For example, Fig. 3 shows the percentage of trials in which participants respond veridically to the stimulated finger, hand, and surface in the video in the congruent and incongruent postures, averaged over all participants with MTS (purple). An interesting pattern evident is the prevalence of non-veridical responses (responses that differ in at least one dimension – e.g., finger, hand, surface – from the viewed touch) that are felt on the correct surface in congruent versus incongruent postures. In the congruent posture, 93.4% of non-veridical responses are still felt on the viewed surface, as compared to only 64.8% in the incongruent posture. This clearly shows an effect of the participant's own body posture on response location for hand surface.

We then considered whether participants differed based on whether the location of their mirror-touch percepts took into account their own body posture. For example, some participants could consistently localize the mirror-touch percept to the same hand surface that was touched in the video *regardless of their own body posture*. For example, let's say these individuals viewed a hand facing palms up, and their hands were palms down. These individuals would report feeling sensation on the palmar surface, even though stimulation of this surface would be implausible given their own hand posture. We will call these individuals *surface constrained* mirror-touch synesthetes. We contrast this with individuals whose responses are influenced by their own hand posture, demonstrating a bias towards mirror-touch percepts on the "plausible" surface – that is, the hand surface facing upward in the participant – even when the video hand and real hand posture are incongruent. We will call these individuals *plausible* mirror-touch synesthetes. We defined individuals as having "surface constrained MTS" if they met the following criteria: >80% somatotopic responses (e.g., veridical hand surface and finger) in *both* posturally congruent and incongruent conditions. Individuals with "plausible mirror-touch synesthesia" were those who demonstrated a significant decrease (as assessed using a chi-square test) in the frequency of surface constrained responses in incongruent versus congruent postures. Using these criteria, we found 17 participants who demonstrated surface constrained MTS, 17 who demonstrated plausible MTS, and two who fit the criteria for both. (These were two individuals who, together, made surface constrained responses on 75/75 trials in the congruent condition, and 56/65 in the incongruent posture.) Using an unpaired t-test (equal variances not assumed), there was no difference in the frequency of mirror touch synesthesia in the surface constrained (35.9%) versus the plausible (27.1%) subtypes, $t(22.1) = 1.19$, $p = .247$. Figs. 4 and 5 shows a hypothetical trial in which either a surface constrained subtype synesthete or a plausible subtype synesthete views the index finger of the right hand (dorsal surface) touched, along with participants' response profiles when their hands were either congruent (Fig. 4) or incongruent (Fig. 5) with the video hand. Comparing response localization across groups, there was a clear difference in performance. Those in the surface constrained group made veridical surface responses on 97.3% of congruent trials and 95.1% of incongruent trials. Participants in the plausible group made veridical surface responses on 90.2% of congruent trials, but only 38.1% of incongruent trials.

4. Discussion

In this study, we examined how the postural schema influences various aspects of mirror-touch synesthetic percepts, with three main findings. First, mirror-touch synesthetes reported more sensations when the viewed hand and participant's hands were in congruent versus incongruent postures. Second, this congruency influenced the location of mirror-touch percepts. Participants were less likely to veridically map the location of the viewed touch onto the "correct" hand and hand surface in incongruent versus congruent postures. Third, we found that participants varied in localizing the surface on which mirror-touch percepts were experienced. Some synesthetes reported mirror-touch percepts on the same surface as the viewed touch, regardless of their own hand position. However, other participants' mirror-touch percepts were modulated based on their own hand position. When the participant and viewed hands were in incongruent postures, they demonstrated a tendency to experience percepts on the hand surface that was facing upward. These findings all provide evidence that the participant's own body posture influenced their mirror-touch percepts.

First, we found more mirror-touch percepts when the viewed hand and the synesthete's hands were in congruent versus incongruent postures. There are two non-exclusive accounts that have been put forth to explain MTS. First, individuals without synesthesia demonstrate both activation in somatosensory regions (Keysers et al., 2004) and enhancement in tactile perception (Serino, Pizzoferrato, & Ladavas, 2008) when viewing someone else being touched – but typically do not feel touch on their own body when viewing someone else being touched. However, there are examples in which viewed touched is felt in non-synesthetic individuals. In these studies, viewed touch (e.g., lasers, viewed touch with Semmes–Weinstein filaments) is presented to rubber hands or mirror images of the participant's own hands (Durgin, Evans, Dunphy, Klostermann, & Simmons, 2007; Hoermann, Franz, & Regenbrecht, 2012; Honma, Koyama, & Osada, 2009; Takasugi et al., 2011). Other studies have shown that the relationship between one's own body posture and the position of viewed body parts influences the effectiveness of both the rubber hand (Costantini & Haggard, 2007; Tsakiris & Haggard, 2005) and mirror box (Liu & Medina, submitted for publication) illusions. In both the rubber hand and mirror box illusion, the position of the viewed hand is compared to the position of the participant's actual hand, and the viewed hand is more likely to be embodied if there is sufficient positional congruence between the hands. In these studies, it has been suggested that the rubber or mirror hands, typically being near the participant's actual hand, become embodied and incorporated into the participant's own body schema. Embodiment of the viewed hand at some level may boost activation in this "mirror-touch" system, resulting in these illusory tactile percepts when seeing mirror and rubber hands touched in normal individuals. The Threshold Theory proposes that mirror-touch synesthetes have increased activation in this "mirror-touch" system, resulting in suprathreshold somatosensory activation and mirror-touch percepts. Why do individuals with MTS have increased activation when viewing touch on another individual?

In normal individuals, tactile sensations for visual stimulation occur in conditions where the viewed hand is either embodied or within peripersonal space of their actual hand. It has been proposed that mirror-touch synesthetes are impaired at distinguishing self from others (see Ward & Banissy, 2015 for a discussion). This potential deficit could have a number of causes, including differences in ownership (Cioffi, Banissy, & Moore, 2016; Derbyshire, Osborn, & Brown,

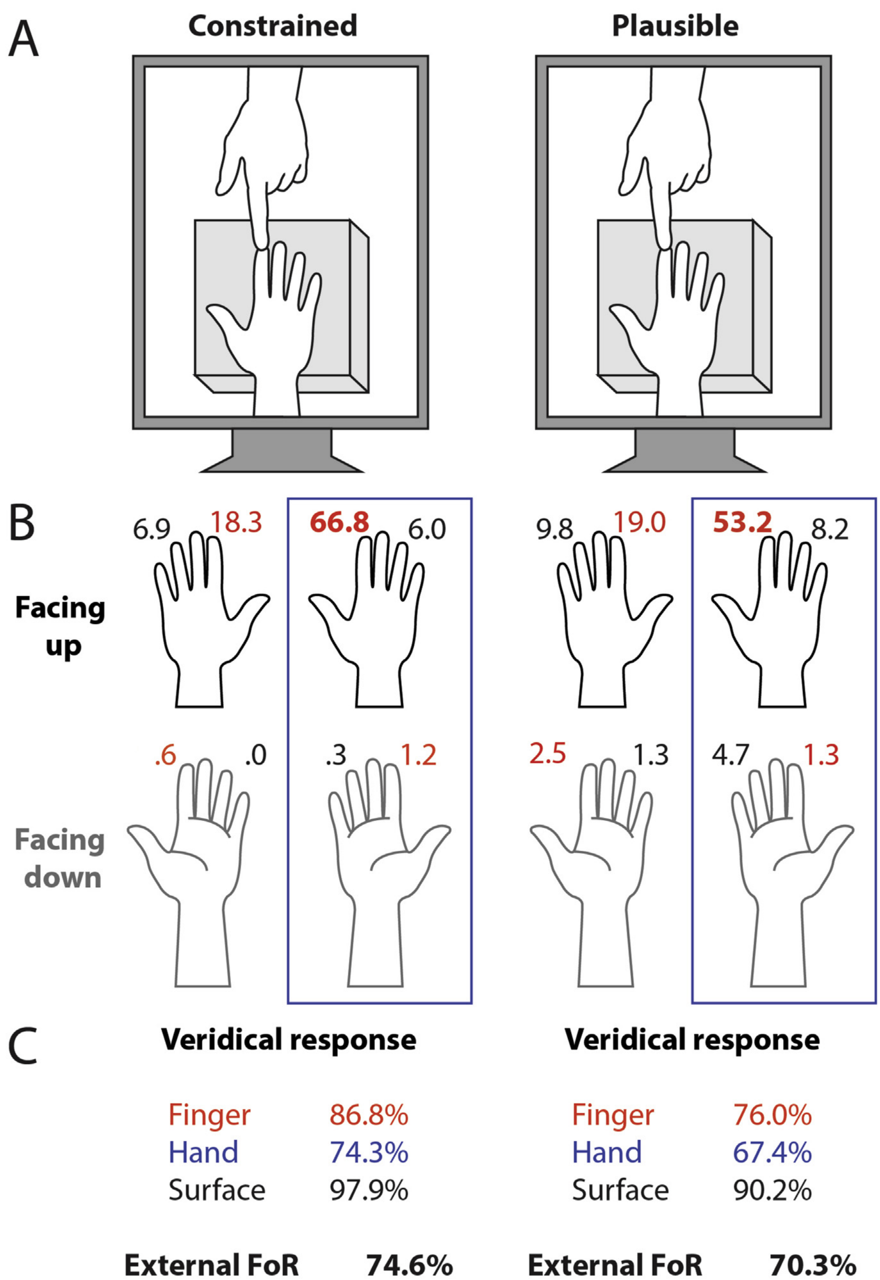

Fig. 4 – A. Shown is an example trial in which the video hand is stimulated on the dorsal surface of the right hand, index finger. B. Shown are the percentage of responses based on veridicality with viewed finger, surface, and hand in the *congruent posture*. Participants could report touch on the hand surface facing up (black) or the hand surface facing down (grey). On the left is the response profile for the *constrained* subtype, with the *plausible* subtype on the right. For example, 66.8% of responses for the constrained subtype were "correct" percepts (shown in bold) on the veridical finger, surface and hand; whereas 18.3% of responses were veridical responses for finger (index) and surface (dorsal), but not hand (the video right hand was stimulated, the synesthete reported a percept on their left hand), and there were no responses that were perceived on the non-veridical surface, finger and hand. As a visual aid, veridical responses for finger are shown in red. C. Shown are the percentage of veridical responses overall for finger, hand and surface, along with the percentage of congruent responses in an external, hand-centered reference frame. For example, the surface constrained subtype experienced mirror-touch percepts on the same finger touched in the video on 86.8% of trials (regardless of whether the percept was accurate for stimulated hand or surface), whereas the plausible subtype reported veridical responses for finger on 76.0% of trials.

2013) and agency (Cioffi, Moore, & Banissy, 2014) over one's own body, increased weighting of visual inputs in multisensory integration of the body, or other factors. Broadly consistent with the self-other account, we propose that at some level, the "self" representation involves an online position of one's own body in space – i.e., postural schema. When the viewed hand and synesthete's hands are in the same posture, they are more visually similar and potentially more

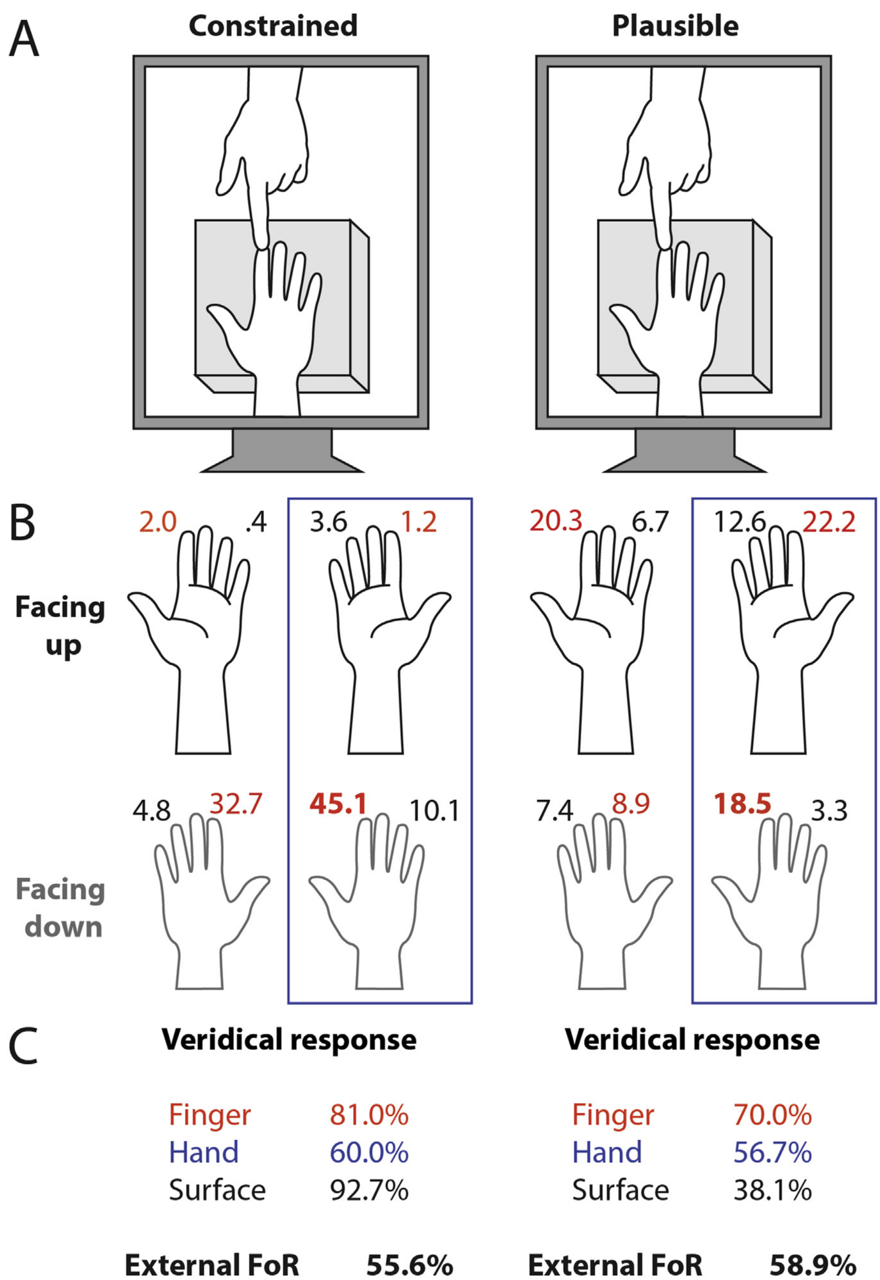

Fig. 5 – Same as Fig. 4, except for trials in the *incongruent posture*, such that a veridical response for stimulated surface is on the hand surface facing down (grey). Note that for the constrained subtype, the vast majority of percepts (92.7%) were on the veridical surface. Whereas for the plausible subtype, the majority of responses were on the palmar surface (facing up), even though the hand in the video was touched on the dorsal surface.

confusable. Although systems for self-other discrimination in non-mirror-touch synesthetes may easily differentiate between a video hand versus one's own hand, a deficit in such a system could lead to increased confusability when the hands are in the same posture in mirror-touch synesthetes. If the viewed hand is embodied in some manner, it could result in feeling viewed touch in the same manner in which non-synesthetes feel visual stimuli presented to embodied rubber/mirror hands.

To clarify, we are not stating that it is necessary for one's postural schema and the viewed body part to be positionally congruent to elicit mirror-touch percepts. Various studies have found that mirror-touch percepts are elicited when viewing touch on hands in impossible postures relative to the synesthete (e.g., White & Aimola Davies, 2012), and we found a substantial number of mirror-touch percepts in incongruent conditions. Interestingly, illusory tactile sensations in non-synesthetes after visual stimulation of a rubber/mirror hand still occur even when the rubber/mirror hand is an incongruent (Honma et al., 2009) or impossible (Durgin et al., 2007) posture. Both findings in mirror-touch synesthetes and studies of referred sensations in non-synesthetes provide evidence that postural congruence, or even postural plausibility, are not necessary components to elicit these phantom percepts. However, our findings do demonstrate that congruency between an on-line representation of the body (i.e., the postural schema) and the viewed body part are a factor that contributes to the frequency of mirror-touch percepts.

Second, we found that the synesthete's body position influences *where* the mirror-touch percept is felt. To veridically map the location of touch viewed on another individual to one's own body, a number of processes are necessary to accurately represent the location of touch on the viewed body and then transform the location of the viewed touch to a representation of one's own body. This transformation can, in theory, involve multiple types of body and spatial representations. In representing the location of stimuli on the body, two general categories of spatial representation have been proposed – somatotopic representations which code the location of stimuli on the skin surface, and external representations which represent location in external space relative to a midline projected from the viewer. However, these somatotopic and external representations have various subtypes. In our study, we examined how changes in body position influenced the location of mirror touch percepts in a somatotopic, finger-based representation; a trunk-centered representation, an external hand-centered representation, and an external, "surface-centered" representation. Next, we review evidence regarding how transformations along these spatial dimensions were influenced by body posture and other factors.

First, there is clear evidence that participants utilized somatotopic, finger-based representations in mapping viewed touches onto their own body. First, participants made veridical responses for finger on a large majority of trials (79.2%), and we did not observe a significant change in veridical finger responses on congruent versus incongruent trials. As shown in Fig. 1, when the viewed hand and synesthete's hands are in incongruent postures, stimuli can be encoded in a somatotopic, finger-based (Fig. 1, red arrow) or external, hand-centered (Fig. 1, blue arrow) frame of reference in which the midline is along the long axis of the middle finger. If participants were encoding stimulus location in an external, hand-centered frame of reference, then one would predict significantly less veridical finger responses in incongruent versus congruent postures. However, postural congruency did not significantly influence the veridicality of finger responses. Furthermore, no participants demonstrated specular MTS when defined using an external, hand-centered reference frame, and (overall) participants made external, hand-centered responses on only 57.0% of posturally incongruent trials. These results all provide evidence that, in our experiment, mirror-touch percepts were more veridically mapped using a somatotopic, finger-based representation, but not an external, hand-centered representation.

A second possibility is that participants would accurately map mirror-touch percepts from the viewed hand to the stimulated hand. Participants did make more veridical responses when the hands were posturally congruent versus incongruent. This provides additional evidence that individuals referenced their own body posture in mapping mirror touch sensations to their hands. However, mirror-touches were veridically localized to the stimulated hand at a rate far less than for finger responses, even when the viewed and participant hands were in congruent postures. This potential dissociation between finger and hand responses may be consistent with past findings suggesting differential encoding of location on the fingers versus the rest of the body. For example, Haggard, Kitadono, Press, & Taylor-Clarke (2006) presented suprathreshold tactile stimuli on participants' fingers, and asked them to identify which finger and hand was stimulated in different postures (e.g., fingers interwoven *vs* vertically oriented). Hand posture did not influence finger identification, but did influence stimulated hand identification, with performance poorer in the interwoven hand condition. They proposed that identifying a stimulated finger can be done utilizing a strictly somatotopic representation, whereas identifying the stimulated hand involves a representation of external space. One possibility is that mapping stimulus location from one body to another preferentially involves somatotopic, finger-based representations compared to representations of hand chirality. However, a second possibility is that task difficulties led to this difference in veridical finger versus hand percepts. In our task, only one hand was shown on the screen, such that the chirality of the viewed hand would need to be identified by its shape as opposed its position relative to the body or the other hand. It is possible that difficulties in encoding the stimulated hand resulted in the poor performance. Although this may be the case, it is moderately surprising given that control participants were quite skilled at identifying the touched hand using the same paradigm, and that there were a large number of non-veridical responses for hand chirality even in congruent postures – a condition in which hand identification is not difficult. Nevertheless, the lack of more obvious cues regarding hand chirality may have resulted in increased attention towards the finger touched versus the hand touched, which could explain the poorer performance for hand veridicality. Future research will be needed to see additional information regarding hand chirality (e.g., seeing two hands on the screen at the same time) results in increased veridicality for hand responses.

Although we did not find strong effects for external hand-centered, or hand chirality mapping, we did observe a substantial decrease in the veridicality of mirror-touch percepts in incongruent versus congruent postures for stimulated surface. Furthermore, our participants differed based on whether postural congruency influenced the surface on which these mirror-touch percepts were felt. In the surface constrained subtype, participants consistently felt sensations on the skin surface that was stimulated in the video – regardless of their own body posture. In contrast, the response patterns of participants in the plausible subtype were influenced by their own body position – demonstrating a significant increase in the number of mirror-touch sensations on the upward facing hand surface in the incongruent condition. The existence of the plausible subtype provides additional evidence that, for some individuals, an on-line representation of their own body (postural schema) is utilized in mapping mirror-touch sensations. The surface constrained subtype shares a number of similarities with the "anatomical" subtype of MTS previously reported in the literature – in which participants map mirror-touch percepts utilizing a somatotopic frame of reference. However, we did not find any participants who demonstrated specular MTS, which may be surprising given that the majority of mirror-touch synesthetes in the literature (see Banissy et al., 2009) are of the specular subtype. Instead, we found a number of participants who demonstrated plausible MTS. Why would some mirror-touch synesthetes map sensations in a "plausible" manner? And why are there so few "specular" mirror-touch synesthetes in our population, in contrast with past literature?

Given how little we know about the process in mapping touch from one body to another, our answer is speculative. In the typical example used to contrast specular from anatomical MTS, a mirror-touch synesthete views touch on the cheek of an individual facing them. In specular MTS, the location of touch is mapped in an external frame of reference, such that viewing touch on an anatomically-defined right cheek is felt on the anatomically-defined left cheek of the synesthete. This mapping does not involve any transformations across the primary face axis in an external frame of reference – touch on the (externally-defined) left side of the viewed face is then mapped on to the left side of the synesthete's face. Whereas in anatomical MTS, it is necessary to transform the location of touch to the other side in an externally-defined reference frame. Information about the spatial location of stimuli on the body in different reference frames can be weighted differentially given attentional and task demands (Badde, Röder, & Heed, 2015). When transforming the location of tactile stimuli on someone else's body, individuals may weight somatotopic or external information more strongly. Interestingly, the vast majority of previous cases of MTS are of the specular subtype (Banissy et al., 2009). This may suggest that mappings that involve less transformations in external space are preferred in some manner, resulting in more individuals demonstrating the specular subtype. In our study, the mapping between skin surfaces (dorsal *vs* palmar) can involve either a transformation in an external frame of reference to maintain somatotopic veridicality for surface (surface constrained subtype), or a simpler mapping in external space between the two bodies that maintains tactile location on the upright surface (plausible subtype). Both the plausible subtype in our study and the specular subtype may both be caused by increased weighting towards mapping touch in externally-based representations, and individuals in the plausible subtype may show specular mirror touch synesthesia on simpler mappings with less transformations (e.g., mapping viewed touch on one's face). A second factor that may explain our results is contextual factors. Since participants have their hands resting on a table, it is highly unlikely that the stimulus (coming from the hand of another individual) would be coming through the bottom of the table on incongruent trials. If context is taken into account in mapping mirror-touch percepts, this could explain why some participants demonstrate a plausible subtype. We also note that we only tested participants in one session on this specific task. Although we did divide participants based on subtypes of MTS, we do not know whether these subtypes are stable over time. One possibility is that these subtypes are specific to a particular session, such that increased attention to somatotopic or external factors could change the subtype within individuals. Future research will be necessary to explore this possibility.

Finally, we will briefly discuss two unexpected results in our experiment. First, we found that mirror-touch sensations were more frequent for viewed touch on the palmar surface versus dorsal surface, and on the distal versus proximal segment of the finger. The palmar surface of the fingertips has more mechanoreceptors, are more sensitive, and have larger cortical representations compared to the proximal segment of the fingers and the dorsal side of the hand. One possibility is that MTS is more likely to occur on overrepresented skin surfaces. Second, we found that participants reported feeling touch on approximately 15% of trials in which a finger approached, but did not touch, the viewed hand. Interestingly, a recent study showed higher tactile sensitivity when the stimulated versus unstimulated hand is approached by an experimenter (Van der Biest, Legrain, De Paepe, & Crombez, 2016). The approaching hand could increase activation in somatosensory cortex for the approached hand, resulting in mirror-touch percepts in those with overactive mirror-touch systems. We believe that these findings can be explored in more detail in future studies to understand the mechanisms that underlie MTS.

To conclude, we found that the frequency and location of mirror-touch synesthetic percepts are influenced by the synesthete's own body posture. Mirror-touch synesthetes experience more frequent and more veridical percepts when their hands are in the same posture as the hand in the video. Responses were most veridical for the stimulated finger versus hand or surface, providing some evidence for stronger somatotopic, finger-based mapping of stimulus location from the viewed body to the synesthete's body. Furthermore, participants varied in how they mapped the location of the stimulated surface onto their own body. In the incongruent posture, some consistently reported percepts on the same surface that was touched in the video (surface constrained subtype), whereas others demonstrated a tendency to report sensations on the upright surface (plausible subtype). In total, the results provide strong evidence that viewed touch is mapped onto an online representation of the participant's own body position in space.

Acknowledgments

We would like to acknowledge Emily Baumert, Caitlin Duckett, Yuqi Liu, Stephanie Rodgers and Megan Ziegler for their work on this project, and Chelsea Martin for her illustrations. This research was supported by the National Science Foundation under Grant No. 1632849 and the University of Delaware Research Foundation under Grant No. 13A00851.

Appendix

For each question in the questionnaire, the average Likert scale rating for males and females, the percentage of participants who responded "agree" or "strongly" agree with the statement, and the factor loadings for the principal components analysis in Section 3.1.

Question (Do you ever experience…)	Male	Female	% agree	% str. agree	Factor 1	Factor 2
…the letters of the alphabet having specific colors	2.1	2.04	2.09	1.15		.921
…numbers (e.g., 1, 4, 8) having specific colors.	2.06	1.95	1.92	1.02		.925
…touch sensations on your body when you see them on another person's body.	2.89	2.95	7.76	1.96	.817	
…spontaneous visual sensations (that are not in the environment) when you are touched.	2.61	2.61	4.14	1.36	.815	
…hearing sounds (that are not in the environment) when you are touched.	2.39	2.26	2.39	.68	.74	
…when touched on your body, feeling touch sensations on other locations of your body that were not touched.	2.73	2.83	6.27	2.34	.833	
…feeling touch sensations on your skin even though you were not touched.	2.95	3.01	8.36	2.30	.819	
…taste sensations when you observe another person eating or drinking.	3.03	3.22	9.00	2.73	.754	

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