Visual body form and orientation cues do not modulate visuo-tactile temporal integration

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Keywords: multisensory perception; body perception; temporal integration; temporal order
judgement; Bayesian causal inference

Abstract

Body ownership relies on spatiotemporal correlations between multisensory signals and visual cues specifying oneself such as body form and orientation. The mechanism for the integration of bodily signals remains unclear. One approach to model multisensory integration that has been influential in the multisensory literature is Bayesian causal inference. This specifies that the brain integrates spatial and temporal signals coming from different modalities when it infers a common cause for inputs. As an example, the rubber hand illusion shows that visual form and orientation cues can promote the inference of a common cause (one's body) leading to *spatial integration* shown by a proprioceptive drift of the perceived location of the real hand towards the rubber hand. Recent studies investigating the effect of visual cues on *temporal integration*, however, have led to conflicting findings. These could be due to task differences, variation in ecological validity of stimuli and/or small samples. In this pre-registered study, we investigated the influence of visual information on temporal integration using a visuo-tactile temporal order judgement task with realistic stimuli and a sufficiently large sample determined by Bayesian analysis. Participants viewed videos of a touch being applied to plausible or implausible visual stimuli for one's hand (hand oriented plausibly, hand rotated 180 degrees, or a sponge) while also being touched at varying stimulus onset asynchronies. Participants judged which stimulus came first: viewed or felt touch. Results show that visual cues do not modulate visuo-tactile temporal order judgements. This suggests that a Bayesian causal inference model for the integration of bodily signals fits findings in the spatial, but not the temporal domain. As there are also other conflicting findings regarding audio-visual temporal integration, generally more studies are needed to increase our understanding of the factors that modulate the encoding of temporal information in the brain.

Introduction

Perception of one's body relies on multisensory integration and is dynamically updated based on the available sensory input [1]. Information regarding spatiotemporal correlations between inputs from the different senses is particularly important for self-recognition [2, 3]. For example, experimental work with the rubber hand illusion (RHI) shows that synchronously viewing and feeling touch can cause signals from different modalities to become integrated, resulting in an illusionary experience of ownership over an artificial object [4-7]. Furthermore, visual cues such as form and orientation provide crucial information about whether the observed object is plausible for one's body, which can facilitate or inhibit the emergence of body ownership [6]. For instance, the RHI does not occur when the object lacks certain hand-like features [8], or when it is rotated at an improbable angle in relation to the participant's own body [9, 10]. The mechanism by which these visual cues modulate the integration of multisensory bodily stimuli still remains unclear and further research into this process is fundamental for our understanding of how we perceive our bodies and interact with objects in the world around us.

The brain constantly receives signals from different sensory modalities with some variability between the exact timing or location, and these are either combined into the same multisensory event or kept separate [11, 12]. One proposal is that the processing of multisensory signals relies on a computational mechanisms for causal inference to determine the likelihood that the individual unisensory signals belong to the same object or event, which then influences another mechanism for multisensory integration. Bayesian causal inference models incorporate these two processes and can therefore provide a unified theory for the perception of multisensory events, including their spatial and temporal characteristics [13-17]. On this view, the strength of intersensory coupling can be influenced by previous knowledge that signals belong to one and the same object or event, and repeated experience that signals are statistically likely to co-occur [18-20]. Signals that are likely to 'belong together' (also referred to as the 'assumption of unity'; Welch and Warren [21]) can become partially or completely integrated, which limits access to spatiotemporal conflict between the original signals [22]. These processes of causal inference and multisensory integration explain how the brain perceives signals that are estimated to originate from a common source as the same multisensory event.

A causal inference process might also govern the binding and integration of bodily signals [23]. Depending on whether the brain infers a common cause for inputs or not, it either integrates or segregates spatial and temporal signals coming from visual, tactile and proprioceptive modalities. Visual cues such as body form and orientation could function as causal binding factors as these indicate whether or not inputs originated from the same source (e.g., one's own hand). This could explain why the RHI typically only arises in a plausible context for one's own body and why form and orientation cues can modulate a shift in the perceived location of the real hand towards the spatially separated rubber hand [6, 24]. This 'proprioceptive drift' indicates *spatial integration* of visual information originating from the artificial hand and proprioceptive information about the location of one's own hand [6]. Further, Shimada et al. [5] showed that participants still experienced a strong illusion of ownership even when the visual stimulation on the rubber hand and tactile stimulation on the participant's own hand were presented with a 300 ms delay. This might indicate that the visual presentation of a hand enhances *temporal integration* of visual and tactile stimuli as well. These findings in both the spatial and temporal domain suggest that the assumption of a common cause might indeed modulate the integration of bodily signals.

Findings supporting an effect of causal inference on temporal integration have been reported in the audio-visual domain. For example, in the case of speech perception, Vatakis and Spence [25] showed that temporal lags between auditory and visual stimuli are less likely to be perceived when there is other evidence that the stimuli belong to the same multisensory event. These authors used the method of constant stimuli, and presented participants with videos and sounds at different stimulus onset asynchronies (SOAs). The videos and sounds were either congruent or incongruent in terms of gender (e.g., a female face combined with either a female or male voice, respectively) and phonemic content (e.g., a female pronouncing /ba/ combined with the sound /ba/ or /da/). Participants made unspeeded temporal order judgements (TOJ) about whether the auditory or visual stimulus was presented first and the authors measured the 'just noticeable difference' (JND, the smallest temporal interval at which participants can still reliably distinguish the temporal order of stimuli presented to different modalities). JNDs were larger for both congruent gender and phonemic content compared to incongruent content, which indicates less precision. These results suggest that a plausible context that is consistent with a common cause for auditory and visual speech stimuli can modulate temporal integration.

Parise and Spence [22] also demonstrated that correspondences between properties in different modalities can promote integration of auditory and visual non-speech stimuli. There

is considerable research showing consistent and systematic mappings (referred to as crossmodal or synaesthetic correspondences) between sensory inputs from different modalities [26-34]. For example, high-pitched tones are consistently judged as corresponding with smaller objects, brighter hues and locations higher in space relative to low-pitched tones [31, 33]. To test whether such correspondences modulate spatial and temporal multisensory integration, Parise and Spence [22] used a TOJ task and presented participants with pairs of spatially or temporally discrepant auditory and visual stimuli that were either matched (e.g., a small circle presented with a high-pitched tone) or mismatched (e.g., a small circle presented with a low-pitched tone). Results showed larger JNDs for matched compared to mismatched stimuli, suggesting reduced access to intersensory conflicts. The authors conclude that crossmodal correspondences between the stimuli increased spatial and temporal integration of auditory and visual signals. Overall, audio-visual research shows that in several cases, provided information thought to influence the likelihood of a common cause results in increased multisensory temporal integration.

Recent findings in body perception suggest that visual form and orientation cues can also modulate the temporal integration of visual and tactile inputs. For instance, when we feel a touch to our hand, we expect to also see a touch to an object that looks like a hand as opposed to a non-hand object. We furthermore observe the touch to a hand located in a set orientation relative to the arm and body, making it clear that it is our hand that is being touched. Hence, the experience of a tactile touch to our hand is most likely to occur together with a visual touch to a plausibly oriented human hand (i.e., one's own hand), indicating that the visual and tactile touch event share a common cause. Ide and Hidaka [35] tested if form and orientation manipulations affect visuo-tactile temporal integration using simple hand images. A light flash on the left index finger of a line drawing of a forward-facing hand, an inverted hand or an arrow (the visual stimulus) was presented with different SOAs relative to a vibration to the tip of a participant's left index finger (the tactile stimulus). Participants judged whether the visual or the tactile stimulus was presented first. Results indicate that a plausible image (forward hand) *decreased* participants' ability to establish the temporal order of stimuli, as indicated by larger JNDs compared to an implausible image (inverted hand and arrow). Hence, this finding is consistent with the observations in the audio-visual domain and suggests that when a visual and tactile stimulus are more likely to have a common cause, this increases temporal integration.

Converging evidence for visuo-tactile integration depending on causal inference comes from Maselli, Kilteni, López-Moliner and Slater [36] who used a virtual reality set-up

to investigate the impact of body contact and visual form on multisensory temporal integration specifically in the context of a body ownership illusion. Participants wore a head-mounted display which streamed a digital 3D replica of the room. By looking down, participants could see a gender-matched virtual body in the same location as their real body. Their first experiment compared a rotating wheel touching a virtual finger with a wheel that was separated from the virtual finger by 6 mm. Participants were asked to determine the temporal order of the visual stimulus (one full rotation of a virtual wheel) and the tactile stimulus (50 ms vibration to the participant's fingertip) presented at different SOAs. The results showed larger JNDs for the touching compared to the not touching wheel condition, implying stronger visuo-tactile temporal integration in the touch condition. This suggests that when a common cause is inferred for the visual and tactile stimuli, this increases temporal integration of bodily signals. A second experiment tested if temporal integration is mediated by body-ownership by replacing the participant's virtual hands with virtual wooden sticks (manipulating body form). Results show that JNDs were larger in the context of a hand compared to a wooden stick. In addition, the virtual hand also increased the experience of ownership. It may be that increased temporal integration due to visual form facilitates ownership, or that the sense of ownership itself leads to increased integration, or both. Either way, together with the result by Ide and Hidaka [35], these findings suggests that a more plausible visual context for one's own body (e.g., indicated by hand form and orientation) increases multisensory temporal integration.

Conflicting findings, however, come from a study by Keys, Rich and Zopf [37]. This study also investigated the effect of viewed hand orientation on temporal integration but with a visuo-tactile asynchrony detection task. In the first experiment, participants viewed model hands in either anatomically plausible or implausible orientations. In a second experiment, the RHI was induced using synchronous touch in addition to the orientation manipulation to strengthen the multisensory cues indicating one's own body. In both experiments, participants detected short delays (40–280 ms) between a visual stimulus (a flash from an LED on the model hand) and a tactile stimulus (a tap to the fingertip of the participant's hidden hand). Each trial had two intervals, one in which the visual and tactile stimuli were synchronous and another where these were asynchronous. Participants indicated whether the asynchronous interval appeared first or second. The authors calculated and compared asynchrony detection thresholds between orientation conditions. They found that visual orientation cues did not influence detection accuracy for small visuo-tactile asynchronies, supported by Bayesian analyses to estimate the strength of evidence for the null result.

There are several potential explanations for the conflicting findings. Keys et al. [37] used an asynchrony detection task whereas the two studies that reported an effect used a TOJ task [35, 36]. Asynchrony detection involves simply detecting a temporal delay (irrespective of order) whereas TOJ tasks involve detecting the specific temporal order of stimuli. Hence it is possible that these tasks pick up on different mechanisms [38] and that only tasks involving temporal order are affected by the plausibility of the context for the multisensory stimuli.

There are also differences between these key studies in terms of the ecological validity of the stimuli. As Bayesian causal inference models propose that multisensory integration relies on knowledge that signals belong together [18-20], a realistic pairing between a visual and tactile touch stimulus might be important to observe modulations in multisensory integration. Conversely, a study might potentially fail to pick up on an effect when the stimuli are normally unlikely to co-occur. Maselli et al. [36] used very realistic stimuli, as participants observed a touch to a naturalistic virtual hand and also felt a presumably similar touch. Questionnaire results showed that participants felt as if their index finger was actually being touched by the virtual wheel, suggesting an explicit inference of a common cause. Conversely, in the study by Keys et al. [37], the visual stimulus consisted of a light presented next to a 3D plaster hand which was paired with a tactile stimulus on the participant's own hand. Outside of the laboratory, we don't typically encounter light flashes next to our hands together with a touch and it is possible that these stimuli were not perceived to 'belong together,' which could limit the degree of temporal integration. However, Ide and Hidaka [35] reported an effect with similarly artificial stimuli, consisting of a light presented on a line drawing of a hand paired with a tactile touch, suggesting that these stimuli are sufficiently realistic to modulate temporal integration. Thus, even though more realistic stimuli might result in stronger integration, it remains unclear whether variation in ecological validity can account for the differences in findings.

Finally, Keys et al. [37] used relatively large samples of 30 (Experiment 1) and 31 participants (Experiment 2). This was combined with a clearly defined sampling plan to ensure sensitive data for hypothesis evaluation and a procedure to check for outliers. Studies with high power and a complete analysis strategy are typically more robust and therefore less easily influenced by outliers and analytical flexibility [39-41]. Both Ide and Hidaka (2013) and Maselli et al. (2016) used much smaller samples (12 – including the two authors - and 14 respectively) and it is unclear if these studies used a procedure to check for outliers. Current focus on methodological issues in experimental psychology and other sciences have emphasised the potential for false positive effects when using small sample sizes [39-42].

Thus, this also has the potential to be contributing to conflicting findings whether or not visual cues modulate visuo-tactile temporal integration of bodily signals.

There is also variability between studies investigating the effect of visual cues on the temporal integration of *visuo-tactile* stimuli reviewed above and those exploring *visuo-proprioceptive* bodily signals. Hoover and Harris [43] presented participants with videos of their own finger movements, either from a plausible or implausible perspective. By introducing small delays between the actual movement and visual feedback, they investigated whether visual body orientation cues modulate participants' temporal perception using an asynchrony detection task. Results suggested that viewing a hand from plausible perspective led to greater sensitivity for small temporal delays relative to an implausible viewpoint. Similarly, a study by Zopf, Friedman and Williams [44] using a 3D virtual reality set-up found an effect of both visual form and orientation cues on visuo-proprioceptive temporal perception. These findings suggest that visual form and orientation cues indicating one's own body modulate temporal integration of visuo-proprioceptive inputs, and that these lead to smaller (instead of larger) thresholds to detect temporal delays. In other words, when multisensory inputs are perceived to belong to one's own body, the brain seems to be able to more effectively *segregate temporal signals* coming from visual and proprioceptive modalities, resulting in a *better ability* to detect temporal delays. This different pattern of results raises the possibility that temporal processing of visuo-tactile and visuo-proprioceptive events may depend on different mechanisms (however, note that both studies investigating visuo-proprioceptive processing also used small samples of between 10 and 12 participants). It is therefore important to establish whether visual cues indeed modulate visuo-tactile temporal integration.

Visual cues seem to play an essential role in the spatial and temporal processing of bodily signals, but the exact mechanisms remain unknown due to limited and conflicting findings, especially in the visuo-tactile domain. Here, we investigate the processes underlying visuo-tactile integration of bodily signals, addressing some of the inconsistencies between previous studies. We tested if visual form and orientation cues modulate temporal integration with a visuo-tactile TOJ task, realistic visual and tactile stimuli and pre-registered methods including a sampling plan based on Bayes factor (BF) thresholds for sufficiently large evidence [45, 46] and a procedure for outlier detection. Our research questions were: 1) Does the visual presentation of touch to a human hand compared to a non-body object modulate visuo-tactile TOJs? and 2) Does a plausible hand orientation compared to an implausible orientation modulate visuo-tactile TOJs? We hypothesised that if visual form and orientation

cues increase either temporal *integration* or *segregation*, then we would find larger or smaller JNDs respectively when viewing touch to a hand with a plausible orientation compared to a non-hand object or compared to an implausible orientation. In contrast, the null-hypothesis is that there is no effect of viewing condition on temporal integration as measured by JNDs.

Methods

Preregistration

We preregistered this study including the two hypotheses, planned methods and the data analysis plan before data collection. We followed this plan and describe any exceptions below. All materials, including the presentation script and videos, raw and summary data and analysis scripts, are available at (www.osf.io/4dzrg/?view_only=70b8adadf3ac40bba43857fe595bbbd8, registration date 06/06/2018).

Participants

We planned to test 15 participants before calculating a BF to check if our data were sensitive enough to favour our alternative hypothesis over the null hypothesis or *vice versa* [46]. This initial sample size is based on previous studies that reported an effect of visual form or orientation cues on temporal integration [35, 36, 43, 44]. These studies all had sample sizes between 10 and 14 participants.

Conventionally, a BF larger than 3 indicates that the data provide moderate evidence for the alternative hypothesis and a BF smaller than 1/3 indicates that the data provide moderate evidence for the null hypothesis [47, 48]. A BF smaller than 3:1 (i.e., BF between 1/3 and 3) indicates a lack of sensitivity to support one hypothesis over the other. We specified that we would continue data collection until results for both our research questions reached a BF larger than 10:1, indicating strong evidence [48]. If restricted by time, we planned to accept a BF larger than 3:1 as sufficient evidence. We continued data collected after the first 15 participants as the result for one of the two research questions had not yet

reached a BF larger than 10:1. Then, due to time restrictions, we finished testing before the results converged on a BF larger than 10:1, although they did reach the second level of 3:1.

Our sample before exclusions consisted of 42 right-handed individuals with normal or corrected-to-normal vision (mean age = 26.5 years, age range = 18 – 58, SD = 9.1 years, 27 female). Our final sample after exclusions is reported in the results section. The only deviation from preregistration is that we listed the subject pool as undergraduate students but also tested participants from the university community who responded to university advertising (e.g., postgraduate students). Participants provided written consent and received $15 per hour for participation. The Macquarie University Human Research Ethics committee approved the study.

Apparatus and stimuli

Participants sat in front of a computer screen and placed their chins on a chinrest, setting viewing distance at 48 cm. Both the hands and sponge presented on the screen were 19 cm high, resulting in a visual angle of 22 degrees. The participant's right hand was placed in front on the table and aligned with the middle of the computer screen. The vertical distance between the top of the participant's hand and the bottom of the hands and sponge on the screen was approximately 15 cm. The participant's hand was hidden from view with a black piece of fabric (see Fig 1A for the experimental setup). Participants placed their left index and middle finger on keyboard keys (H, J).

A Experimental Setup

B Visual Stimuli

Fig 1. Experimental setup and visual stimuli. (A) Participants watched videos of a hand or sponge being touched and indicated whether the seen touch or the felt touch came first by pressing one of two response keys with their left hand. To mask any noise from the tactor, participants listened to white noise via headphones. Viewing distance was kept constant with a chin rest. (B) Screenshots of the videos depicting touch to either a human hand in a plausible orientation (left), a sponge (middle) or a human hand in an implausible orientation (right). Examples of each of the three condition videos can be found on the OSF page for this project: www.osf.io/4dzrg/?view_only=70b8adadf3ac40bba43857fe595bbbd8.

The visual stimuli consisted of videos depicting touch to (a) a human hand in a plausible orientation, (b) a sponge and (c) a human hand in an implausible orientation (see Fig 1B). To avoid confounding factors, we used DaVinci Resolve video editing software to create videos that are identical in terms of the timing, movement and location of the touch. First, we filmed two videos, one of a stationary human hand and one of a stationary sponge. The reason to use actual video footage over a static image was to increase visual realism, for example, due to very small jitter and blood flow in the hand. We used a sponge for the control condition as it depresses to touch in the same way as a hand. The sponge was

matched with the hand (size, light, shade, colour and white balance) so that it differed only in form. To create a realistic touch event, where the surface was slightly indented upon touch, we filmed a black stick touching a green patch (16 mm in diameter) placed on a soft material. This meant that after editing it actually looked as if the hand and the sponge were being touched but the touch was identical across conditions. Another benefit of showing an indentation is that the exact moment of touch stands out more prominently, which is important for the TOJ task. This recreation of real touch could only be achieved by filming the stick touching a coloured surface so that it could later on be etched and separated from the background with the shadows intact. We changed the colour of the green patch to be white in the editing software, so there was less visual difference. We overlaid a hand coming into the screen and touching a white dot with a stick onto the video of the stationary hand and sponge. We created the implausible hand orientation video by flipping the video with the plausible hand orientation and then overlaying the touch video. We cut each video into separate frames using MATLAB (MathWorks, Natick, Massachusetts, U.S.A) so we could control the onset and presentation of the video frames relative to the tactile stimulus across the three conditions. All presented videos consisted of 62 frames (presented for 33.33 ms per frame) resulting in approximately two-second videos. These were presented on an ASUS monitor which was 60 cm wide and 34 cm high with a refresh rate of 60 hz.

Before the start of the experiment, a tactile stimulator was attached to the back of the participant's right hand, just below the junction between the hand and the middle finger (the metacarpophalangeal joint). A printed screenshot of the hand video was initially placed next to the participant's right hand to match the relative location of the tactor as closely as possible to the relative location of observed touch on the screen. The tactile stimulus was a 30 ms pulse of the vibrotactile stimulator, which applied a tap to the back of the participant's hand via an electromagnetic solenoid-type vibrotactile stimulator (diameter: 18 mm and probe height: 12 mm, Dancer Design, St. Helens, UK; dancerdesign.co.uk) and an amplifier (TactAmp 4.2 with a D25 serial port, Dancer Design). The touch stimulus closely matched the visual touch from the stick in the videos in terms of phenomenology and duration. To mask any noise from the tactor, participants listened to white noise via around the ear, closed-back headphones (Sennheiser HD 280 pro, 64 ohm). We presented and controlled stimulus presentation with MATLAB and the Psychophysics Toolbox [49, 50].

Procedure

During each trial, participants watched one of the three videos and felt a touch on their own right hand. The tactile stimuli were presented with one of the following SOAs relative to the visual touch: $\pm 33, \pm 67, \pm 100, \pm 133, \pm 167 \pm 200 \pm 333$ ms (negative values represent a tactile-leading stimulus and positive values a visual-leading stimulus). The task was to determine for each trial whether the visual touch on the screen or the felt touch on one's hand came first (forced choice).

Participants responded by pressing the H or J key on a keyboard with the middle and index finger of the left hand. A yellow and blue sticker (corresponding to either 'visual-first' or 'tactile-first') were placed over the H and J response keys and these were counterbalanced across participants to eliminate the effect of any response bias. This meant that half the participants responded to the 'visual-first' cue with their index finger and to the 'tactile-first' cue with their middle finger and for the other half of participants this was the other way around. A note describing the responses was placed next to the response keys as a reminder for the participants. Inter-trial timing was jittered to reduce the likelihood of participants getting into a routine response. The next trial started 800~1200 ms after a response was recorded. There were scheduled breaks and a participant could choose to take a break or continue the experiment by pressing the space bar. To keep participants focused and reduce expectancy effects, we varied the exact moment at which the visual touch happened in each video. Each trial consisted of 62 frames but we randomly moved the start and end frame by 0 - 5 frames forwards or backwards in the sequence. The five frames on either side of these 62 frames depicted a stationary hand or sponge (before and after the stick has come in for the touch) so for each trial a video showed a complete touch action.

For each of the three conditions, there were 20 trials with 14 different SOAs resulting in 840 trials in total presented in a random order. Prior to the experiment, participants performed a practice block to become familiar with the task and the button responses. For the practice block, the participants completed 84 trials with each SOA presented twice per condition (randomly intermingled).

Before starting the task, participants removed any jewellery from their hands. The practice run and experiment combined took approximately one hour to complete. During the experiment participants did not receive feedback on their performance. After the experiment, participants filled out three questionnaires which took another 20 minutes (see additional measures section below).

Data analysis

For our main analysis, we compared the mean JNDs between the experimental conditions across the group. To calculate each participant's individual JNDs, we first calculated the proportion of 'visual-first' responses for each SOA in each condition. For example, 0 = 0% 'visual-first'/100% 'tactile-first' responses and 100 = 100% 'visual-first'/0% 'tactile-first' responses. We then fitted a sigmoid function (cumulative Gaussian distributions) to the proportion of 'visual-first' responses using maximum likelihood estimation using the MATLAB Palamedes toolbox (Prinz & Kingdom, 2009; www.palamedestoolbox.org). We then calculated each participant's JND for each of the three conditions from the fitted psychometric functions, using the formula: JND = (75% point - 25% point)/2. We also calculated participants' point of subjective simultaneity (PSS) which is the SOA at the 50% crossover point (the same number of 'visual-first' and 'tactile-first' responses), which means that participants were maximally unsure about the temporal order of the visual and tactile stimuli [51]. The PSS is reported for completeness but does not provide relevant information about the strength of coupling between the visual and tactile stimuli [22].

We excluded data sets for participants based on three criteria: (1) a JND larger than three standard deviations from the group mean in any condition; (2) any of the three curves (representing the three conditions) failing to converge on a solution for fitting a sigmoid function; or (3) incomplete data due to a technical error or failure to perform the task.

We performed Bayesian t-tests, which require a specification of the theory which is tested against the null hypothesis (i.e., the probability of different effects given the alternative theory [46]). We specified a plausible predicted effect size based on previous reports where hand form and/or orientation lead to either increased or decreased temporal integration. We took the average of the mean delay detection improvement (decreased temporal integration) reported by Zopf et al. [44] (18 ms) and Hoover and Harris [52] (22 ms) resulting in 20 ms. Our theory allows effects to go in either direction as the study by Ide and Hidaka [35] found an effect of increased temporal integration of approximately 12 ms (see their Fig 2). However, we postulate that the first two studies found a relatively larger effect due to more ecologically valid stimuli. As our study also incorporates realistic stimuli we set our predicted effect size at 20 ms in either direction. The effect sizes in previous studies comparing different hand orientations and hands with objects are roughly the same (see the effect sizes in Zopf et al. [44] comparing a hand versus dots, 19 ms [Experiment 1] and plausible hand orientation versus implausible hand orientation, 18 ms [Experiment 2]). Hence

we used the same informative prior for both our hypotheses and specified a normal distribution with the mean set to zero, the standard deviation set to 20 and the tails set to two-sided. We calculated the BF in MATLAB with a script downloaded from Dienes' online calculator (http://www.lifesci.sussex.ac.uk/home/Zoltan_Dienes/inference/Bayes.htm). An informative prior (as opposed to a non-informative or default prior) contains information that is relevant to the estimation of the model and consequently the choice of prior can impact the final estimates [53]. To check to what extent our final estimates depend on our informative prior, we also performed a robustness check with the statistical software JASP (www.jasp-stats.org) using JASP's range of default priors.

We planned to sequentially plot the BFs as data were collected, which does not require any corrections for multiple comparisons [54]. This produces a visual impression of when the BFs are converging on a specific level of evidence which favours one hypothesis over another [55]. Furthermore, to visualise data, we used R including the package ggplot2 [56].

Additional measures and exploratory analyses

Mirror-touch synaesthesia (MTS) is a condition where observing touch to another person results in an experience of touch on the observer's own body [57]. It is possible that multisensory interactions are generally enhanced in synaesthesia (including MTS) which could potentially result in increased temporal integration [58, 59]. To ensure we are able to detect and exclude MTS participants, we used short synaesthesia questionnaires. The first questionnaire screened for synaesthesia in general, the second for MTS specifically (adapted from Ward, Schnakenberg and Banissy [60]). Our adapted MTS screener consisted of 20 of the Ward et al. [60] short video clips depicting touch to a human or an inanimate object and four videos of someone scratching their chest or upper arm. After each video participants were asked whether they experienced anything on their body, how they would describe the sensation and where on their body it was felt. We planned to analyse the data both with and without potential mirror-touch synaesthetes to see if this influenced the outcome.

Finally, we planned to explore if, in our sample, stronger temporal integration for the hand condition compared to the sponge condition (as evidenced by large JNDs) correlated with higher empathy scores. Ward et al. [60] tested for different categories of empathy: cognitive empathy (predicting others' thoughts and feelings), social skills (being able to interact with others appropriately) and emotional reactivity (intuitively understanding how

people feel). They found that the latter was increased in MTS. This type of empathy could also be related to increased temporal integration in non-synaesthetes. To explore this, we had participants fill out a short empathy questionnaire [61], which was divided into the same three categories as previously used by Ward et al. [60].

Results

Exclusions

Data from six participants were removed due to a JND larger than three standard deviations from the group mean for at least one of the three conditions. For four out of the same six participants (but not for any of the others) a curve failed to converge on a solution for a sigmoid function for a given condition. Two participants had incomplete datasets due to a technical error and one participant failed to perform the task. After the exclusion of these nine participants, there were 33 participants (mean age = 26.3 years, age range = 18 – 55, SD = 8.3 years, 20 female) included in the analysis.

Just-noticeable difference (JND)

We calculated the average proportion of 'visual-first' responses (derived before fitting the data) and plotted this against SOAs for the three conditions. As can be seen in Fig 2A, the averaged proportions were similar across the three conditions. Fig 2B depicts both participants' individual JNDs (derived from individual data fits) and the group mean JNDs for the three conditions. This shows that the mean JNDs are very similar for the three conditions: hand plausible orientation mean JND = 104 ms, SD = 45 ms, 95%CI [88, 119], hand implausible orientation mean JND = 102 ms, SD = 42 ms, 95%CI [87, 116] and sponge mean JND = 102 ms, SD = 46 ms, 95%CI [86, 118]. Fig 2C depicts the condition differences. The mean difference for the plausibly orientated hand versus sponge comparison was 1.39 ms, 95%CI [-3.50, 6.28] and for the plausibly versus implausibly orientated hand comparison this was 1.48 ms, 95%CI [-4.94, 7.88]. Fig 2C also shows that there was considerable variability for the JND differences between participants, with differences ranging from -40 to 29 ms for the form and -29 to 32 ms for the orientation comparison.

Fig 2. 'Visual-first' responses and JND results. *(A) Averaged proportion of 'visual-first' responses plotted against SOAs for the three conditions. The averaged 'visual-first' responses for the different conditions are very similar. Note that we fitted sigmoid functions to the data of each participant and then calculated JNDs for each participant and condition. (B) Bar graph showing mean JNDs for each of the three conditions with JND estimates from individual participants indicated by scatter points. The vertical bars represent 95%CI. (C) Bar graphs showing the mean JND differences for the two comparisons. JND differences from individual participants are indicated by scatter points and show high between-subject variability (ΔJND form = JND hand plausible orientation – JND sponge and ΔJND orientation = JND hand plausible orientation – JND hand implausible orientation). The vertical bars represent 95%CI.*

Bayes factors and robustness check

We calculated the BF with a Bayesian t-test to test if visual cues in terms of form and orientation modulate visuo-tactile temporal integration. First, to test for the effect of form, we compared the group mean JND between the plausible hand orientation and sponge condition. Fig 3A depicts the development of the BF as a function of the number of participants tested. As data accumulates with more participants being tested, evidence converges and the BF increasingly supports the null hypothesis indicated by values smaller than 1 [62]. Results indicate moderate evidence (BF = 0.178) that body form did not have an influence on the precision of TOJs. In other words, the data were 5.61 (1/0.178) times more likely under null hypothesis than the alternative hypothesis. It is interesting to note that the BF in Fig 3A (plausible hand orientation versus sponge) does cross the BF > 10 threshold with less than twenty subjects. However, this is likely due to noise as data points have not converged, potentially because of the variability in the data [55]. This emphasises the importance of having larger sample sizes. We next tested if hand orientation modulates visuo-tactile TOJs by comparing the group mean JND between the plausible hand orientation and implausible hand orientation (see Fig 3A). A Bayesian t-test indicates moderate evidence (BF = 0.144) that the JND for the two conditions is not different. In other words, the data were 6.94 (1/0.144) times more likely under null hypothesis than the alternative hypothesis.

Fig 3. Sequential plotting and robustness check of the Bayes factors. *We compared the two conditions: plausible hand orientation versus sponge (left panel) and plausible hand orientation versus implausible hand orientation (right panel). (A) Sequential plotting of the BF which shows that the BFs start to converge at N = 20 (plausible hand orientation versus sponge) and N = 24 (plausible hand orientation versus implausible hand orientation), which in both cases provides moderate evidence to support the null hypothesis. (B) BF robustness check in JASP using the program's default prior which shows a similar pattern of results. (C) Assessment of the robustness of the BF to different parameter settings in JASP, which shows that the qualitative conclusion does not change across a range of different parameter specifications.*

To check the impact of the prior on our analysis, we also performed an analysis and robustness check in JASP using the default priors. Fig 3A shows a sequential plot of the BF based on our set prior and Fig 3B incorporates JASP's default prior, which demonstrates a very similar pattern of results. Fig 3C is also based on an analysis in JASP and shows that as the prior becomes wider (the scale parameter r increases), the BF increasingly favours the null hypothesis. Overall, the analyses with JASP indicate that evidence for the null hypothesis is stable across a range of specified parameters which suggests that our analysis is robust.

Point of subjective simultaneity (PSS)

In addition, for completeness, we also calculated each participant's PSS for the three conditions. The mean results show that overall there was a slight 'visual-lead' bias in that simultaneity was perceived as maximal (i.e., maximally unsure about temporal order) when the tactile event slightly preceded the visual one (plausible hand orientation = -12.02 ms, implausible hand orientation = -7.95 ms, sponge = -20.16 ms). We explored condition differences using a Bayesian analysis in JASP which indicates insensitive evidence for a PSS difference (plausible hand orientation vs. sponge, BF = 1.42, plausible hand orientation vs. implausible hand orientation, BF = 0.29). Please note that PSS data do not provide information regarding the strength of temporal integration [22].

Questionnaires (planned exploratory research)

To assess MTS, participants filled out a screening questionnaire. Two participants had a score >7 (they scored 10 and 12), which Ward et al. [60] suggest is a potential indication of MTS. To ensure that the data from these two participants did not influence our outcome, we also calculated the BFs without data from these two participants, which did not change the pattern of results (mean difference plausible hand orientation vs. sponge = 1.53 ms, BF = 0.19, mean difference plausible hand orientation vs. implausible hand orientation = 1.89 ms, BF = 0.17). The short synaesthesia questionnaire did not pick up other types of synaesthesia in any of the participants.

We also explored if stronger temporal integration effects for the hand condition compared to the sponge condition (as evidenced by large JNDs) correlated with higher

empathy scores. A Bayesian analysis demonstrated positive correlations for cognitive empathy (r = 0.36, BF = 1.69) and social skills (r = 0.39, BF = 2.47) but not for emotional reactivity (r = -0.14, B = 0.29). However, the BFs indicate a lack of sensitivity and more research is needed to further investigate this.

Discussion

To successfully interact with the environment the brain needs to establish which unisensory signals belong to the same object or event despite small intersensory spatiotemporal conflicts that may be present [11, 12]. A Bayesian causal inference model proposes that multisensory perception relies on causal inference to establish which unimodal inputs share a common source and should therefore be integrated (or otherwise segregated). This framework might also apply to the processing of spatial and temporal signals from visual, tactile and proprioceptive modalities to establish body ownership [23]. However, limited empirical evidence exist regarding the temporal integration of bodily signals.

In this study we tested with a TOJ task if viewing touch to a hand with a plausible hand orientation compared to a non-hand object and compared to a hand with an implausible orientation modulates visuo-tactile temporal integration. We hypothesised that if visual form and orientation cues influence either temporal *integration* or *segregation*, this would result in larger or smaller JNDs respectively when comparing the three conditions. Results show that group mean JNDs were the same across our three conditions. Bayesian analysis further indicates moderate evidence that neither body form (BF = 0.178) or orientation (BF = 0.144) had an influence on the precision of TOJs. These findings suggest that plausible visual cues do not modulate integration (or segregation) of visual and tactile bodily inputs.

We addressed several key differences between previous studies that investigated the effect of visual cues on visuo-tactile temporal integration [35-37]. The two studies that reported evidence for an effect used a TOJ task whereas Keys et al. [37] who reported evidence for no effect used an asynchrony detection task which may have picked up on different mechanisms [38]. To test whether the null finding by Keys et al. [37] was specific to the task, we used a TOJ task and also found evidence that there is no effect. This suggest that visual object plausibility does not modulate visuo-tactile temporal integration across different types of tasks.

The previous three studies also differed in terms of the ecological validity of stimuli and it is possible that Keys et al. [37] failed to detect an effect due to an unrealistic visual stimulus (a model plaster hand). Ide and Hidaka [35] presented participants with a light presented on a line drawing of a hand and did report an effect. We used a comparatively more realistic visual stimulus than these two studies (a video of a human hand being touched) and thus discrepancies between previous studies are unlikely to be simply due to variance in ecological validity.

Finally, both Ide and Hidaka (2013) and Maselli et al. (2016) used smaller sample sizes (12 – including the two authors - and 14 respectively) than the current study (33 after exclusions) and Keys et al. [37] (30 and 31 for two experiments). Our results show large individual differences between JNDs, ranging from -40 to 29 ms for the form comparison and -29 to 32 ms for the orientation comparison (see Fig 2C) and this was also the case in the study by Maselli et al. [36] (range of JNDs between ~-50 to ~100 ms for Experiment 1 and ~-50 to ~50 ms for Experiment 2, see their Fig 2B and 3A; Ide and Hidaka [35] did not report on individual participant data). Noise due to data variability may strongly affect outcomes on a TOJ task, especially when sample sizes are small [39, 40, 63]. To make sure our experiment produced sensitive data to either support our alternative or null hypothesis we based our sample size on Bayesian analysis and defined a procedure to check for outliers. Our results therefore provide compelling evidence that there is no effect of visual cues on visuo-tactile temporal integration of bodily signals.

An additional difference between the studies [35-37] is the spatial disparity between the visual and tactile stimulus, but this is unlikely the cause for the inconsistency in findings. In the study by Maselli et al. [36] for example, the real and virtual hand spatially overlapped, and they found stronger temporal integration for the trials where the visual stimulus (virtual wheel) appeared to touch the participant's hand compared to the not touching condition. Ide and Hidaka [35] on the other hand, presented visual and tactile stimuli at a 30 – 50 cm distance from each other and also reported an effect. In comparison, the distance between the visual and tactile stimuli in the current study (approximately 15 cm) and the Keys et al. [37] study (12.5 cm) was much smaller. Further, studies with the RHI show that the illusion of body ownership and spatial integration effects (proprioceptive drift) still occur despite a distance between the participant's own hand and the observed rubber hand. Spatial disparity is therefore unlikely to account for the reported null findings that visual cues do not modulate visuo-tactile temporal integration.

Our findings contrast previous studies that investigated the temporal processing of visuo-proprioceptive bodily stimuli. Hoover and Harris [43] and Zopf et al. [44] demonstrated that visual form and orientation cues led to greater sensitivity to detect small temporal delays. This suggests that visual plausibility allows the brain to better segregate visual and proprioceptive temporal inputs. Thus it appears that different mechanisms underlie the temporal processing of visuo-tactile and visuo-proprioceptive bodily inputs.

A Bayesian causal inference model for body ownership suggests that evidence for a common source promotes temporal and spatial integration of visual, tactile and proprioceptive inputs [23]. Hence, findings in the temporal domain that show no effect on temporal integration (the current study and [37]) and those showing temporal segregation [43, 44], do not fit within this general framework. On the other hand, studies with the RHI do suggest that plausible visual cues can promote spatial integration of visuo-proprioceptive bodily signals. In addition, findings from crossmodal congruency tasks also show effects of visual form and orientation cues on visuo-tactile spatial interactions which might also indicate spatial integration [64-67] (although this is debated as effects could merely occur on a response level [68, 69]). Therefore, evidence for a Bayesian causal inference framework for the integration of bodily signals comes predominantly from the spatial domain (see Table 1 for findings regarding temporal and spatial integration or segregation) and the model needs to be further developed to also take the temporal findings into account.

Table 1. Selected papers that directly test visual context (form and orientation) effects on temporal and spatial integration of visual, tactile and proprioceptive bodily inputs.

Studies	Form[a]	Orientation	Method[b]	N/expt.	Temporal effects Visuo-tactile	Visuo-proprioceptive	Spatial effects Visuo-tactile[c]	Visuo-proprioceptive
Current study	✓	✓	TOJ	33	No integration or segregation			
Keys et al. [37]		✓	SJ	30, 31	No integration or segregation			
Ide and Hidaka [35]	✓	✓	TOJ	12	Integration			
Maselli et al. [36]	✓		TOJ	14	Integration			
Zopf et al. [44]	✓	✓	SJ	10, 12, 11		Segregation		
Hoover and Harris [43]		✓	SJ	10		Segregation		
Igarashi et al. [66]	✓		CCT	22			Integration	
Igarashi et al. [67]		✓	CCT	8, 12			Integration	
Pavani et al. [64]	✓	✓	CCT	10, 10			Integration	
Tsakiris et al. [8]	✓		JHP (RHI)	40				Integration
Holmes et al. [24]	✓	✓	Reaching	18, 21, 24, 12, 12				Integration
Tsakiris and Haggard [6]	✓	✓	JHP (RHI)	8, 8, 10,14				Integration
Costantini and Haggard [9]		✓	JHP (RHI)	16				Integration

[a] Significant ($p < 0.05$ or equivalent) report of visual form and/or orientation cues influencing temporal and spatial integration/segregation.
[b] Temporal order judgement (TOJ) task, synchrony judgement (SJ) task, crossmodal congruency task (CCT), judgement of hand position (JHP), rubber hand illusion (RHI).
[c] The research into visuo-tactile spatial interactions, referenced here, involves crossmodal congruency tasks, and it is not clear whether these results also indicate spatial integration or merely an effect at the response selection level.

Conflicting findings regarding the effect of causal inference on temporal integration have also been reported in the audio-visual domain. Studies show that in the case of human speech perception, auditory and visual stimuli are more likely to become temporally integrated when there is evidence for a common cause [25, 70]. Further, Parise and Spence [22] demonstrated that certain correspondences between properties in different modalities can increase spatial and temporal integration of auditory and visual stimuli not related to human speech. Other studies however, have not been able to find a causal inference effect on temporal integration of auditory and visual non-speech stimuli. Vatakis et al. [70] used a TOJ task and presented participants with matched and mismatched audio-visual stimuli which consisted of: 1) one call-type made by two different monkeys, 2) two different call-types from the same monkey, 3) a person versus monkey 'cooing,' and 4) speech sounds produced by a male and a female person. Results show that participants' performance was only affected in the case of human speech stimuli, not when observing matched versus mismatched monkey calls or human imitations of monkey calls. Another study by Vatakis and Spence [71] presented participants with auditory and visual musical and object action stimuli that were either matched (e.g., seeing a piano being played and hearing the sound of a piano) or mismatched (e.g., seeing a piano being played and hearing the sound of a guitar). They also found no significant difference in participants' performance between matched versus mismatched videoclips. Together, these findings suggest that contextual information could modulate audio-visual temporal integration, but that this might be limited to certain stimuli. Thus, to better understand multisensory processing, more research is needed across different modalities to clarify how certain properties between multisensory events affect temporal integration.

Conclusion

Our study provides compelling evidence, supported by Bayesian analysis, that visual form and orientation cues do not modulate *temporal integration* of *visuo-tactile* bodily signals. This contrasts previous studies that showed that visual plausibility resulted in enhanced *segregation* (as opposed to integration) of *visuo-proprioceptive* bodily signals. Thus, it appears that the underlying temporal mechanisms are different for visuo-tactile and visuo-proprioceptive integration. Bayesian causal inference models propose that evidence for a common source promotes both spatial and temporal integration of multisensory inputs.

Studies with the RHI indeed show that a plausible context can promote the inference of a common cause (one's body) resulting in *spatial integration* of *visuo-proprioceptive* signals. The current and previous findings, however, suggests that a plausible context does not result in increased temporal integration of bodily signals and hence a Bayesian causal inference model for body-ownership needs to be further developed to also take the temporal findings into account. Research into the effects of higher-level cues such as context on temporal integration is limited and conflicting in the multisensory literature. Thus generally, more research is needed to provide better insight into the factors that influence how multisensory events are integrated in time. The current study emphasises the importance of rigour in our methodologies and analyses to advance our understanding of the processes that underlie multisensory integration.

Acknowledgements

RZ is supported by a Discovery Early Career Research Award from the Australian Research Council (ARC; DE140100499). ANR has research funding from the ARC (DP12102835 and DP170101840).

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