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RESEARCH ARTICLE

# The plausibility of visual information for hand ownership modulates multisensory synchrony perception

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**Abstract** We are frequently changing the position of our bodies and body parts within complex environments. How does the brain keep track of one's own body? Current models of body ownership state that visual body ownership cues such as viewed object form and orientation are combined with multisensory information to correctly identify one's own body, estimate its current location and evoke an experience of body ownership. Within this framework, it may be possible that the brain relies on a separate perceptual analysis of body ownership cues (e.g. form, orientation, multisensory synchrony). Alternatively, these cues may interact in earlier stages of perceptual processing—visually derived body form and orientation cues may, for example, directly modulate temporal synchrony perception. The aim of the present study was to distinguish between these two alternatives. We employed a virtual hand set-up and psychophysical methods. In a two-interval force-choice task, participants were asked to detect temporal delays between executed index finger movements and observed movements. We found that body-specifying cues interact in perceptual processing. Specifically, we show that plausible visual information (both form and orientation) for one's own body led to significantly better detection performance for small multisensory asynchronies compared to implausible visual information. We suggest that this perceptual modulation when visual information plausible for one's own body is present is a consequence of body-specific sensory predictions.

**Keywords** Multisensory perception · Temporal synchrony perception · Virtual hand · Body representations · Body ownership · Sensory predictions

## Introduction

Our bodies are continually interacting with complex environments. The fundamental question of how the brain enables successful body–environment interactions is related to many areas of research in cognitive science and neuroscience. One important requirement for successful interactions is to identify one's own body and to keep track of its current location in relation to external objects and other bodies. This may, at first glance, seem like a simple task, but in fact, this is a complex process involving the integration of several sources of multisensory information.

Experimental paradigms involving artificial hands (in many cases involving a rubber hand and referred to as the rubber hand illusion paradigm) have highlighted the importance of multisensory cues for the representations of one's own body. Synchronously touching an artificial hand at the same time as the participant's hidden hand induces changes in estimated hand position and the experience of body ownership (Botvinick and Cohen 1998). Such changes in the representation of one's own body can equally well be manipulated by viewing the motion of an artificial hand,

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while one's own hidden hand moves simultaneously (Kalckert and Ehrsson 2012, 2014).

Furthermore, the human body and its parts have typical features that can be used to differentiate them from other objects. One such feature is *the viewed object form or shape* which is regarded an important cue for body ownership (Ehrsson 2012; Tsakiris 2010). The experience of ownership can be induced for a viewed artificial object that is formed like a hand and includes detailed structural hand features such as five separate fingers, but not for objects without a hand shape and without certain structural hand features, e.g. a block of wood (Tsakiris et al. 2010). Secondly, the *viewed body orientation* provides a further important cue for one's own body: viewing a hand with fingers pointing away from one's trunk is anatomically more plausible for one's own hand than viewing a hand with the opposite orientation. The importance of this body ownership cue has been demonstrated also with the rubber hand illusion paradigm (Ehrsson et al. 2004; Holle et al. 2011; Ide 2013).

However, viewing a hand-shaped object in a plausible orientation for one's own hand without synchronous multisensory stimulation, or vice versa, is not sufficient for inducing certain changes in artificial hand illusion paradigms (Holmes et al. 2006; Longo et al. 2008). Accordingly, body ownership models state that body-related cues based on visual sensory input are combined with multisensory temporal information to identify one's own body, estimate its current location and evoke the experience of body ownership (Makin et al. 2008; Tsakiris 2010). However, the exact mechanisms remain unclear. It may be possible that the brain relies on separate perceptual analysis of cues specifying one's own body (e.g. synchrony, form and orientation), which are combined at a later stage of perceptual processing. Alternatively, these cues may interact in earlier stages of perceptual processing. In particular, visually derived body form and orientation cues might influence one's sensitivity to detect temporal delays between two multisensory signals. We investigated this possibility in this study and employed a virtual hand set-up, which allowed us to manipulate the observed form and orientation of the hand as well as to induce small temporal differences between executed and observed movements. In combination with the virtual hand set-up, we employed an unspeeded delay detection task to measure the effects of visual cues on perceptual delay detection thresholds.

Visual cues for one's own body could be associated with relative enhancements or relative diminishments of delay detection performance. Based on more general theories in perception, it is feasible to postulate modulations in both directions. To start with, "predictive brain theories" posit that learned sensory regularities inform the predictions that the brain generates for sensory input. Furthermore, encountered mismatches between predictions and sensory input (prediction errors) are thought to increase the perceptual salience of the incoming information to support the generation of appropriate and adaptive responses (Bubic et al. 2010; Friston 2010). Naturally, viewing one's own body is strongly related to tactile, proprioceptive and visual information occurring synchronously and belonging together. For example, viewing one's own hand move typically concurs with a synchronous proprioceptive movement experience. In contrast, viewing the hand of another person or a different object move is less strongly associated with concurrent proprioceptive feedback. Thus, visually derived information plausible for one's own body could increase the expectation for synchronous multisensory information. Any encountered temporal delays would then become perceptually more salient. This increase in salience in turn would predict better delay detection performance when visual information is plausible for one's own hand compared with when it is implausible.

An alternative hypothesis can be found in multisensory theoretical accounts that have argued that information that increases the "assumption" that sensory signals belong together (known as the unity assumption) increases multisensory integration (Welch and Warren 1980). Both structural (or bottom-up) factors, such as temporospatial correspondences, and other more cognitive (or top-down) factors, such as previous experiences of particular stimuli pairings, can contribute (Welch and Warren 1980). Although it is often difficult to distinguish the contributions of different factors on multisensory integration (Spence 2007), visually derived body information could possibly be a top-down or experience-dependent factor. Visually derived information related to one's own hand is likely to be a strong signal that visual and proprioceptive movement signals belong together and consequently could be associated with a relative increase in the multisensory integration of these signals. Increased multisensory integration could manifest itself as an increased alignment of temporally slightly asynchronous multisensory information (temporal ventriloquism) (see Vatakis and Spence 2007 for a related prediction involving audio-visual speech and temporal order judgements). The consequence of this increased alignment of temporal information would be a reduction in delay detection performance. In other words, this account predicts worse rather than better delay detection performance when visual information is plausible for one's own hand.

We report on three experiments that we conducted to investigate the effect of visually available form and orientation information on movement synchrony perception. In Experiment 1, we investigated the influence of visual form on movement synchrony perception. In particular, we tested whether observing hand movements visualized as a human

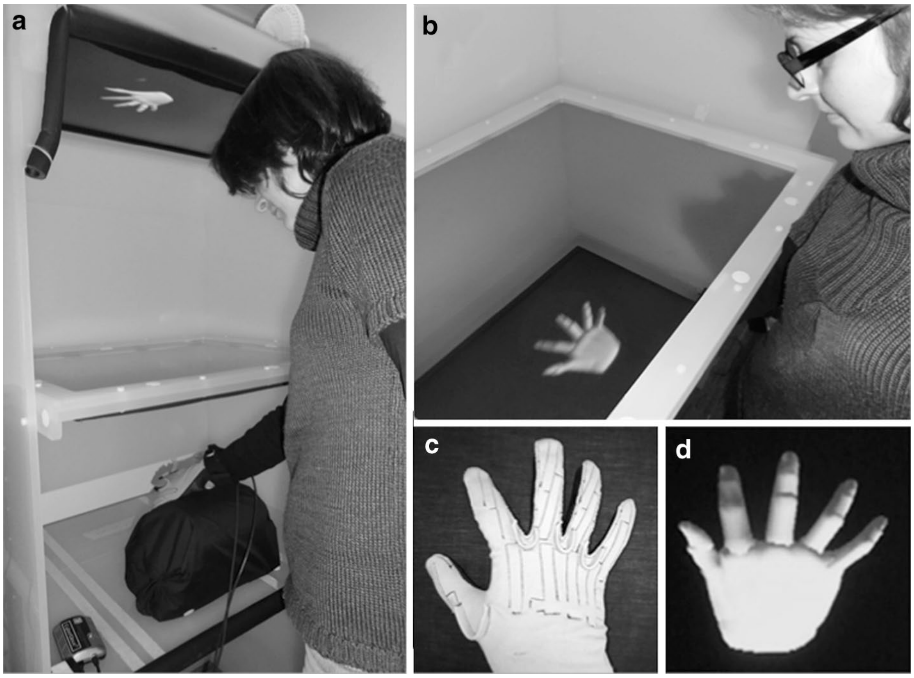

**Fig. 1** Virtual hand set-up. **a** The components of the virtual hand set-up are a glove-based motion capture system, a magnetic motion capture system, a 3D monitor, a semi-silvered mirror and a custom-build frame. **b** Participants view 3D hands or objects projected onto the mirror. The image appears in approximately the same depth as the participant's hand. **c** Depiction of the glove-based motion capture system (CyberGlove Systems). **d** Screenshot of the virtual hand

hand compared to the same movements visualized with moving dots alters participants' sensitivity to detect temporal delays between performed and observed movements. In Experiments 2 and 3, we examined the influence of viewed hand orientation on temporal synchrony perception. Specifically, we tested whether viewing anatomically plausible hand orientations alters temporal delay detection performance when compared with less plausible orientations.

## Experiment 1: Viewing a hand improves movement synchrony perception

In Experiment 1, we investigated whether the viewed *object form* modulates the ability to detect temporal delays between performed and observed movements. Specifically, we recorded and visualized participants detailed hand movements by depicting either a virtual hand or virtual dots. For each visualization condition, we measured delay detection performance for a range of different delays employing a two-interval force-choice task and obtained detection thresholds.

## Method

### Participants

Eleven participants took part in Experiment 1 and received course credit for their participation. Data from one participant were removed due to detection performance below 75 % in the hand condition even for the largest presented delay and consequently an estimated threshold that was more than two standard deviations above the group average. This resulted in ten participants (8 female; mean age = 19.3 years, range 17–22 years, all right-handed).

### Apparatus and movement visualization

Figure 1 depicts the virtual hand set-up we used in this study. The set-up consists of a glove-based motion capture system (CyberGlove Systems) which enables the recording of detailed hand movement by measuring angular changes of 22 hand joints. Additional parts of the set-up include a magnetic motion capture system (Polhemus Fastrak) for wrist movements and a 3D screen (Hyundai TriDef, 60 Hz refresh rate). Custom-built MATLAB software (https://github.com/JasonFriedman/RepeatedMeasures) collects detailed hand posture information and uses this for real-time rendering of hands or objects on the 3D screen. The 3D screen is mounted on the top of a custom-build frame, and the images are reflected in a semi-silvered mirror. Subjects wore polarized glasses such that each eye received a slightly different image to generate the illusion of viewing the stimuli in 3D. The images for each eye were the result of rendering the scene from two viewpoints, horizontally shifted (corresponding to the distance between the eyes). The images appear at approximately the same depth as the participant's own hand which is placed under the mirror and invisible to the participant. We used a high-speed camera to measure the minimum temporal delay between a performed hand movement and an observed virtual hand

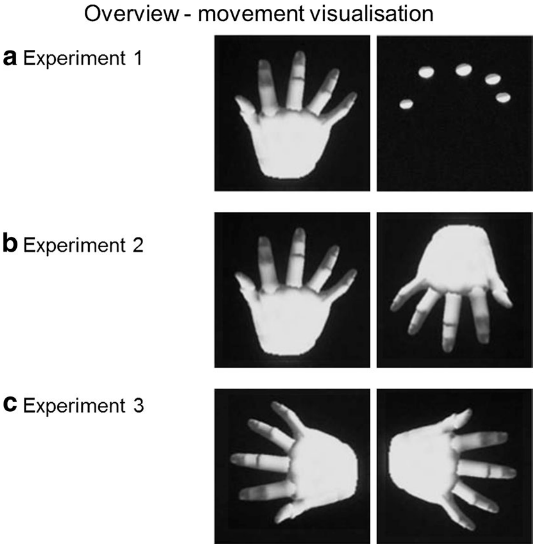

**Fig. 2** Screenshots illustrating the visual displays for each experiment

movement (due to the delays in data acquisition, filtering and rendering of the movement). This revealed a minimum system delay of 80 ms. Temporal delays presented in this study all include this minimum delay. This short time delay was not noticeable to participants, and the observed movement with this system delay appeared to be synchronous. Experiments were run in a dimly lit room.

All experiments involved right hands for movement capture and display. In Experiment 1, captured hand movements were visualized using either a virtual hand or five virtual dots. The virtual hand size was adjusted to approximately match the participants' hands, and the virtual dots were approximately fingertip size. The movement of the virtual dots represented the movements of the five fingertips (Fig. 2a).

### Design and procedure

A two-interval force-choice task was employed. Each trial consisted of two intervals with hands/dots presentations for one second with a one second gap between the presentations. In each interval (as soon as the hand or the dots appeared on the screen), participants were asked to perform a single-index finger flexion movement (about 2 cm). For one interval, the time delay between executed and observed movements amounted to the minimum system delay (80 ms). In the other interval, a time delay was chosen from eight different possible delays (80, 113, 146, 179, 212, 245, 278 and 311 ms). The interval order was randomized; thus, either the first or the second interval could contain a time delay chosen from the eight different delays. Participants were asked to use the left hand to indicate which interval contained a delay (first or second) by pressing one of two keyboard buttons. Performance was close to 50 % accuracy when both intervals contain an 80-ms delay (the minimum typically not-detectable system delay) and increased with increasing temporal delays. The design amounted to eight different trial types which were repeated 20 times. Thus, there were 160 trials per movement visualization condition and in total 320 randomly presented trials.

### Data analysis

The psignifit toolbox for MATLAB (Wichmann and Hill 2001) was employed to fit individual psychometric functions to the proportion of trials in which delays were correctly identified (Weibull function, maximum-likelihood estimation, lower bound fixed to 50 %, lapse rate estimate constrained between 0 and 6 %). We estimated detection thresholds (75 % correct performance level) for individual participants and conditions and subsequently used paired *t* test for statistical comparisons between viewing conditions. Our effect of interest is the difference in detection threshold between the two movement visualization conditions, and we also report Cohen's d as standardized effect size.

Changes in the performed movements themselves could potentially affect the ability to detect delays between performed and observed movements. To investigate the possibility that the viewing conditions affected how movements were executed, we analysed several movement parameters such as the time it took from image presentation to movement onset, movement velocity, the movement amplitude and whether participants missed performing a movement. All movement parameters were analysed for the flexion of the index finger's metacarpophalangeal joint. Movement onset (in ms) is calculated as the time after image onset when the movement velocity first exceeded 5 % of peak velocity. Peak movement velocity (in °/s) is the maximum angular velocity during movement visualization. The movement amplitude was calculated as the maximum joint angle (in °) during image presentation (relative to the starting angle). Movement error is the percentage of trials where no movement was detected (peak velocity did not change more than 5 %).

## Results and discussion

The results of Experiment 1 are depicted in Fig. 3. The mean delay detection threshold for viewing a hand was 121.55 ms (SEM = 9.23) and for viewing dots 140.56 ms (SEM = 10.89). These estimated threshold values are comparable to previously reported delay detection thresholds for human hand movements (Hoover and Harris 2012; Leube et al. 2003). Statistical comparisons confirmed that

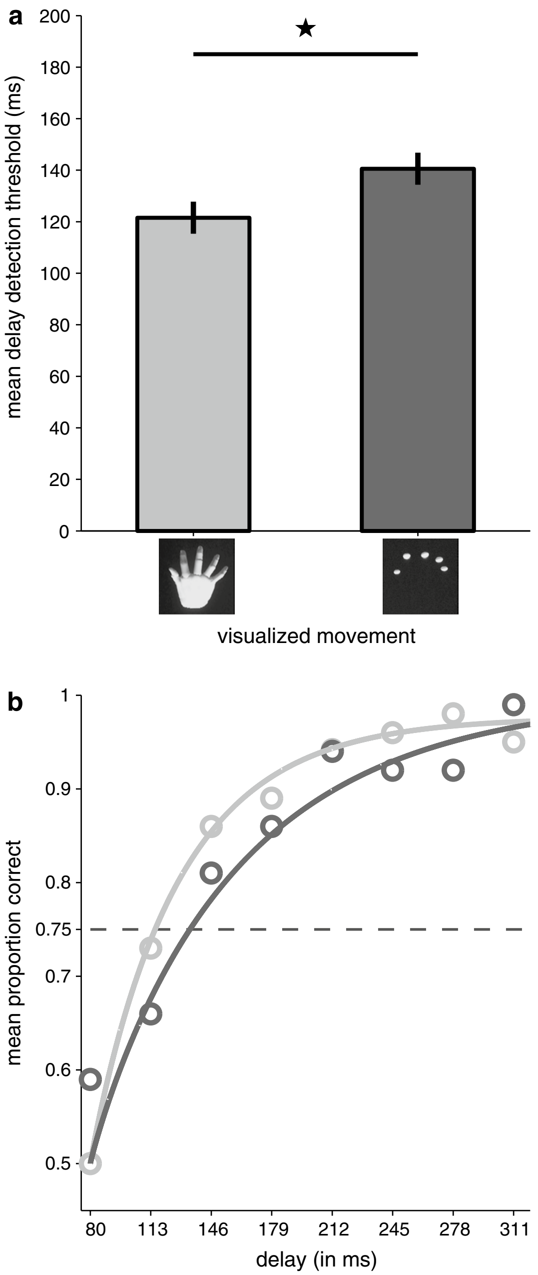

**Fig. 3** Results Experiment 1. **a** Mean delay detection threshold for viewing a hand (*light grey bars*) and dots (*dark grey bars*). Error bars represent within-subjects SEM. **b** Mean proportion correct for individual delays for viewing a hand (*light grey circles*) and dots (*dark grey circles*). Note that a group-fitted estimated psychometric function is displayed only for demonstrative purposes; individual parameter estimations underlie the values depicted in **a**

the sensitivity to detect temporal delays was significantly better (detection threshold difference 19.01 ms, d = .96) when viewing a human hand as compared with viewing dots ($t(9) = 3.05$, $p = .014$).

The movement parameter analysis revealed that none of the movement parameters differed significantly between movement viewing conditions (all $p > .05$): movement onset (hand: M = 345.76 ms, SEM = 15.50; dots: M = 354.24 ms, SEM = 12.32), peak movement velocity (hand: M = 393°/s, SEM = 5.99; dots: M = 395°/s, SEM = 6.33), movement amplitude (hand: M = 44.61°, SEM = 5.30; dots: M = 44.88°, SEM = 5.42) and movement error (hand: M = 4.52 %, SEM = 1.13; dots: M = 4.91 %, SEM = 1.19).

To summarize, in Experiment 1, we found that viewing a hand compared with viewing dots was related to enhanced synchrony perception for performed and observed movements. This result demonstrates a modulatory influence of viewed *object form*, a visual body-specific cue, on synchrony perception. Furthermore, this effect seems unlikely to be related to potential changes in the performed movement itself.

In both visualization conditions, strong cues for movement onset were provided, specifically the movement of the finger endpoint or dot towards the body as a result of the finger flexion. The use of the 3D set-up also meant that depth cues were provided in both cases. However, it is possible that the found perceptual modulation can be explained not only by the presence of different visual form cues (hand versus not hand), but also by different amounts of available visual information. Presenting an entire hand image compared with just the five fingertips provides more detailed three-dimensional shape information, and this could have potentially itself improved the estimation of movement in depth. To deal with this potential confound, in the next two experiments, we investigate the effect of the plausibility of visual information for one's own body by simply changing the orientation of the visualized hand while keeping the available detail of visual movement information constant.

## Experiment 2: Viewed hand orientation modulates movement synchrony perception

In Experiment 2, we investigated the effect of viewed *hand orientation* on synchrony perception. We visualized hand movements by depicting a virtual hand in either an upward (fingers pointing away from the body's trunk) or a downward (fingers pointing towards the body's trunk) orientation (see Fig. 2b).

### Method

Twelve new participants took part in Experiment 2 (3 female; mean age = 23.9 years, range 19–63 years, 11 right-handed) who received $15 for their participation. The methods are as in Experiment 1, except instead of viewing a hand or dots, in this experiment, the movement was visualized either using an upward-oriented or a downward-oriented hand (Fig. 2b).

## Results and discussion

The findings for Experiment 2 are depicted in Fig. 4. Participant's sensitivity to detect temporal delays between performed and observed movements was significantly better (detection threshold difference 17.63 ms, d = .65) when viewing a virtual hand upward oriented as compared with downward oriented ($t(11) = 2.24$, $p = .047$; hand upwards: M = 144.28 ms, SEM = 10.17; hand downwards: M = 161.90 ms, SEM = 10.67).

As in Experiment 1, we analysed several movement parameters. Again, this analysis revealed that none of the movement parameters differed significantly between movement viewing conditions (all $p > .05$): movement onset (hand upwards: M = 351.57 ms, SEM = 20.74; hand downwards: M = 355.71 ms, SEM = 20.90), peak movement velocity (hand upwards: M = 424°/s, SEM = 5.79; hand downwards: M = 421°/s, SEM = 5.85), movement amplitude (hand upwards: M = 52.30°, SEM = 4.62; hand downwards: M = 52.00°, SEM = 4.53) and movement error (hand upwards: M = 6.21 %, SEM = 0.96; hand downwards: M = 6.87 %, SEM = 1.29).

To summarize this experiment, we found that participants reliably detected significantly shorter movement delays when viewing an upward-oriented hand. This result is in line with Hoover and Harris's (2012, 2015) finding that viewed hand orientation modulates movement synchrony perception. In the aforementioned studies, a filmed video of the participant's hand (itself hidden from view) was presented on a screen presented 50 cm in front of the participants. The authors manipulated the viewed hand orientation in four ways: upward orientation, reflection along the *x*-axis (downward orientation), reflection along the *y*-axis (mirrored) or both *x*- and *y*-axis reflection. As in our study, participants were asked to perform finger flexion movements and detect temporal delays between observed and performed movements. Our findings replicate but also extend the previous finding in three ways: first, we find a similar result using a 3D virtual reality set-up instead of a video set-up. Second, we find an effect of hand orientation when the viewed hand is placed in approximately the same spatial location and horizontal–vertical line as the participants' hand. And importantly, by analysing several movement parameters, we showed that the reported effect seems unlikely to be related to potential changes in the performed movement itself.

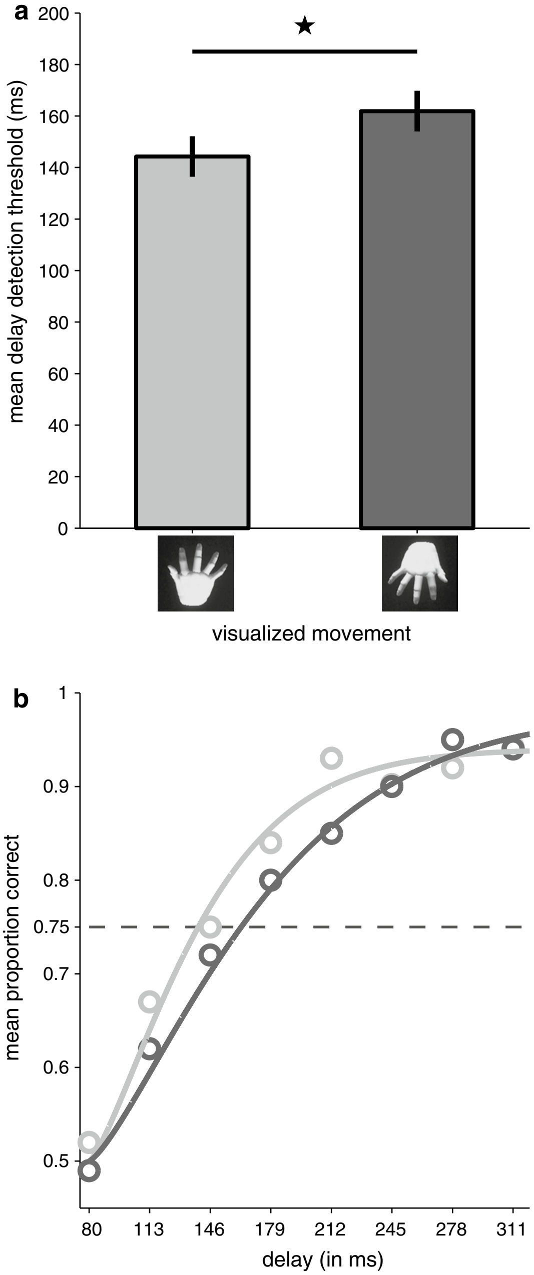

**Fig. 4** Results Experiment 2. **a** Mean delay detection threshold for viewing an upward-rotated right hand (*light grey bars*) and downward-rotated right hand (*dark grey bars*). *Error bars* represent within-subjects SEM. **b** Mean proportion correct for individual delays for viewing an upward-rotated hand (*light grey circles*) and downward-rotated right hand (*dark grey circles*). Note that a group-fitted estimated psychometric function is displayed only for demonstrative purposes; individual parameter estimations underlie the values depicted in **a**

There are at least two potentially relevant differences between viewing a hand with fingers pointing away from the trunk and viewing a hand with fingers pointing in the opposite direction. First, the hand orientations differ in terms of visual anatomical plausibility. Viewing a hand in an upright orientation is anatomically more plausible and also more commonly viewed for one's own hand as compared to the opposite orientation. Alternatively, in Experiment 2, the hand orientation conditions differed in terms of current spatial congruency between visual and proprioceptive information. Viewing a hand in an upright orientation was spatially better matched to the actual hand posture, while the opposite downward hand orientation was incongruent (i.e. moving the index finger, on the left side of the hand, caused a movement on the right side of the rendered hand). Previous research has shown visual–proprioceptive mismatches can influence somatosensory and multisensory perception (Folegatti et al. 2009; Pavani et al. 2000). Thus, both factors, the visual plausibility and the spatial congruency, could potentially account for the perceptual modifications we have found in Experiment 2. When interpreting their results, Hoover and Harris (2012) conclude that the "plausible self"-perspectives modulate the sensitivity to detect movement delays. However, in their study, the delay detection thresholds increased from self-perspective to *y* reflection to *x* reflection and *xy* reflection. These orientations entailed changes both in anatomical plausibility and in the relative amount and type of spatial congruency.

We conducted Experiment 3 to conclusively investigate whether the visual plausibility of viewed hand orientation for one's own body modulates movement synchrony perception while keeping the degree of spatial mismatch between current visual and proprioceptive information constant. Specifically, we visualized the movement using a virtual hand either oriented towards the body (right hand with a leftward orientation, anatomical plausible) or oriented away from the body (right hand with a rightward orientation, anatomical less plausible) (Fig. 2c). In both cases, the viewed hand orientation is spatially incongruent to the participant's hand with a 90° offset and an angular rotation around the wrist.

## Experiment 3: Plausibility of viewed hand orientation for one's own body improves movement synchrony perception

In Experiment 3, we tested the effect of anatomical plausibility of the viewed hand orientation on movement synchrony perception. We manipulated the anatomical plausibility of a viewed right virtual hand to be one's own hand (orientations towards the left versus the right) while controlling the amount and type of current orientation incongruence between visual and proprioceptive hand information (in both cases 90° and an angular rotation around the wrist) (Fig. 2c).

### Method

Eleven participants took part in Experiment 3 who received $15 for their participation. Data from one participant were removed due to detection performance below 75 % in both conditions even for the largest presented delay and consequently estimated thresholds that were more than two standard deviations above the group average. This resulted in ten participants (4 female; mean age = 21.3 years, range 18–27 years, all right-handed). The methods are as in Experiment 1 and 2, except that in this experiment, movements were visualized either using a leftward-oriented or using a rightward-oriented hand (Fig. 2c).

### Results and discussion

The results of Experiment 3 are depicted in Fig. 5. Participant's sensitivity to detect temporal delays between performed and observed movements was significantly better (detection threshold difference 18.16 ms, d = .72) when viewing a human-like virtual hand in an anatomically plausible orientation for one's own hand compared with viewing an anatomically less plausible orientation ($t(9) = 2.29$, $p = .048$; hand leftwards: M = 148.11 ms, SEM = 17.97; hand rightwards: M = 166.27 ms, SEM = 21.45).

The analysis of the movement parameters revealed that these did not differ significantly between movement viewing conditions (all $p > .05$): movement onset (hand leftwards: M = 324.60 ms, SEM = 18.39; hand rightwards: M = 318.74 ms, SEM = 19.72), peak movement velocity (hand leftwards: M = 383°/s, SEM = 5.45; hand rightwards: M = 383°/s, SEM = 5.51), movement amplitude (hand leftwards: M = 38.04°, SEM = 2.59; hand rightwards: M = 38.31°, SEM = 2.68) and movement error (hand leftwards: M = 5.41 %, SEM = 1.36; hand rightwards: M = 5.78 %, SEM = 1.66).

Thus, Experiment 3 demonstrates that plausibility of the viewed hand modulates movement synchrony perception and that viewing a hand in an anatomically plausible view is related to enhanced sensitivity to detect temporal delays between performed and observed movements. In this experiment, anatomical plausibility was the significant modulator of the effect, whereas spatial congruency was kept constant and amounted in both tested conditions to a 90° rotation. Furthermore, there were no significant condition differences for the analysed movement parameters, suggesting that the found effect cannot be explained by potential changes in the performed movements itself.

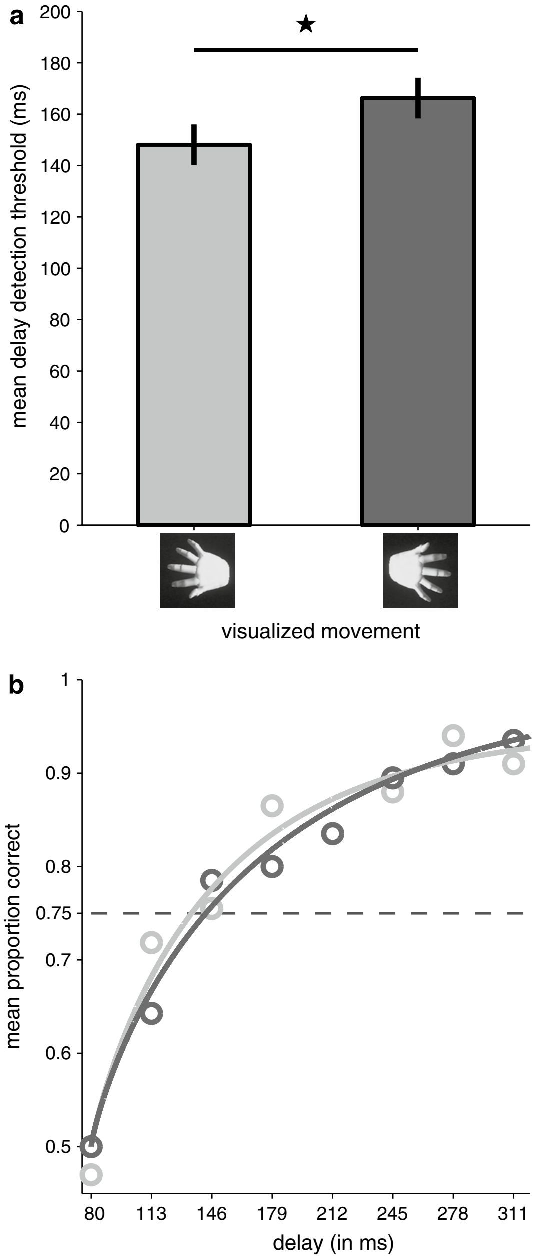

**Fig. 5** Results Experiment 3. **a** Mean delay detection threshold for viewing a leftward-rotated right hand (*light grey bars*) and rightward-rotated right hand (*dark grey bars*). *Error bars* represent within-subjects SEM. **b** Mean proportion correct for individual delays for viewing a leftward-rotated hand (*light grey circles*) and rightward-rotated right hand (*dark grey circles*). Note that a group-fitted estimated psychometric function is displayed only for demonstrative purposes; individual parameter estimations underlie the values depicted in **a**

## General discussion

We found that body-specifying visual cues such as the viewed object form (Experiment 1) and the viewed body orientation (Experiments 2 and 3) modulate synchrony perception. First, we demonstrated superior sensitivity to detect temporal delays between performed and observed movements when viewing an object form that is plausibly a body, such as a hand as compared with dots (Experiment 1). Second, we found enhanced temporal synchrony perception when viewing hand orientations plausible for one's own body (Experiments 2 and 3). Overall, our findings demonstrate that the plausibility of visual information signalling one's own body significantly modulates and in particular enhances perceptual sensitivity for temporal asynchronies in multisensory body-related movement signals. These effects cannot be explained by potential differences in the amount of presented depth information (matched in Experiments 2 and 3), by potential differences in visual–proprioceptive conflict (matched degree of conflict in Experiment 3) or by potential condition-dependent changes to the performed movement itself (excluded in all three experiments).

The relative enhancement of perceptual sensitivity for multisensory temporal delays when visual information is plausible for one's own hand can be explained by sensory predictions and modulations of perceptual salience (Bubic et al. 2010; Friston 2010). Visual body information is commonly associated with synchronous visual–proprioceptive and visual–tactile events. Consequently, visual information plausible for one's own body is likely associated with a relative increase in expectations for such events to be synchronous. Encountered multisensory temporal delays that do not match such predictions could consequently be particularly highlighted (relative to sensory information that matches predictions or is less strongly predicted). If this notion is correct, then visual hand information should not influence delay detection performance of two sensory events for which temporal synchrony is not strongly associated with visual body information. Future research could investigate this prediction.

In contrast, the relatively enhanced delay detection performance when visual information is plausible for one's own hand argues against the idea that visual hand information, as an experience-dependent factor and strong signal for visual–proprioceptive unity, increases multisensory temporal integration. Possibly, visual hand information is not a factor that influences the "assumption of unity" for visual–proprioceptive signals. Alternatively, it might be possible that experience-dependent or statistical factors, while being able to influence many aspects of multisensory perception, do not modulate multisensory temporal integration (or temporal ventriloquism). For example, in the audio-visual domain, this is a much debated issue. Whereas some authors have argued on the basis of their findings that specific natural common or synesthetic audio-visual associations modulate audio-visual temporal binding (Parise and Spence 2008, 2009; Vatakis et al. 2008; Vatakis and Spence 2007), others have not found evidence for an effect of common audio-visual associations on temporal binding (Keetels and Vroomen 2011; Vatakis and Spence 2008). More research is needed to increase our understanding of how the brain encodes temporal information for commonly associated sensory inputs.

Special body-related multisensory brain mechanisms could potentially be related to the multisensory perceptual changes we report. Converging evidence from monkey electrophysiology studies (Graziano et al. 2004), human brain imaging studies (Brozzoli et al. 2011; Gentile et al. 2011; Makin et al. 2007) and neuropsychological patient studies (di Pellegrino et al. 1997; Farne et al. 2000) supports the notion for specialized multisensory mechanisms related to the hand. For example, neurons in the parietal and premotor cortex selectively respond to tactile, visual and proprioceptive stimulation related to the hand, such as touch on the hand and visual stimuli near the hand (Graziano et al. 1997; Hyvarinen 1981; Rizzolatti et al. 1981). Visual information of one's hand can modulate the responses of such multisensory neurons (Graziano 1999). Future work could further investigate the potential links between these special hand-related multisensory mechanisms and the multisensory perceptual modulations we found.

In this study, we found that visual body-related cues modulate the processing of multisensory temporal synchrony—in particular we have argued that visual information plausible for one's own hand is associated with a relative highlighting of small temporal asynchronies. This relative enhanced multisensory temporal processing when visual information is plausible for one's own body is possibly functionally relevant for distinguishing one's own body from other bodies. Indeed, it has previously been shown that small temporal differences between observed and performed movements (when many other possible cues such as hand form, hand orientation and skin texture are kept constant) can inform the participant's decision as to whether they are viewing one's own hand movement or somebody else's (Salomon et al. 2009; Tsakiris et al. 2005). Perceptual interactions between different sensory self-related inputs are likely relevant for understanding the mechanisms that underlie the formation and updating of distinct representations for one's own body. A recent predictive coding account of self-recognition indeed included the notion that self-specific contextual information (such as visual body form and orientation) may increase the expectations for certain multisensory information and consequently evoke prediction errors (or surprise) and relative increases in the salience of perceptual information when unexpected sensory information is encountered (Apps and Tsakiris 2013). Our findings support the notion that self-specific body form and orientation information increase the expectation for synchronous multisensory information and that encountered small asynchronies are consequently relatively highlighted. Future work could further investigate whether in addition to temporal discrepancies, spatial multisensory discrepancies are also especially highlighted when self-specific visual information is present. The experience of illusory body ownership in the rubber hand illusion could furthermore be the consequence of an active inference as one means to minimize the encountered prediction errors that result from perceptual interactions between different self-related information (Seth 2013).

As described in the introduction, viewing an artificial hand moving synchronously with one's own hidden hand may modulate representations of one's own body and induce, for example, the experience that the artificial hand belongs to one's own body. In this study, we tried to minimize actual changes to body representations because such adaptive changes are related to changed multisensory processing itself (Zopf et al. 2010). Rather, we were particularly interested in studying the perceptual processing of body-related visual and multisensory stimuli prior to any potential adaptive effects. We minimized changes to representations of one's own body by presenting short intervals in which the hand was viewed (1 s). The experience of ownership is typically only induced after at least a few seconds of stimulation (Ehrsson et al. 2004). Furthermore, stimulation that could induce ownership (such as synchronous movement and viewing hands in orientations typical for one's own hand) was randomly mixed with stimulation that typically does not induce ownership (such as asynchronously perceived movement, viewing dots or hands in orientations not typical for one's own hand).

So far we have reasoned that visually derived body information modulates the processing of visual–proprioceptive temporal information. Theoretically, these modulations could be achieved through influencing comparisons between position changes of one's own hand and observed position changes over time (i.e. comparison of proprioceptive and visual afferent feedback). Alternatively, the effect of viewing a hand could only encompass comparisons involving sensory predictions based on an efference copy of the planned movement and the visual movement feedback (i.e. comparisons of efferent information and visual feedback) (MacDonald and Paus 2003). Active movement (as used in this study) allows for efferent and afferent comparisons, whereas passive movements are externally produced and only generate afferent multisensory signals. If visually derived plausible hand information only involved comparisons using efferent information, then one would not expect any significant delay detection improvements when employing passive movements. Furthermore, if visually derived hand information only modulated efferent but not purely afferent mechanisms, then viewing a plausible hand would result in better detection performance when using active movements as compared with passive movements. Shimada et al. (2010) conducted an experiment in which a hand was viewed in a plausible orientation for one's own body and in which the authors measured movement delay detection performance for both active and passive movements. Participants viewed a video-recording of the hand and simple finger movements were visually presented after movement execution with different delays. The authors found that active movements did not significantly alter the time window for reporting the presence of temporal delays when compared with passive movements (Shimada et al. 2010). This finding suggests that the presence of efferent information does not modulate the effect of viewing a hand on synchrony perception. Together with the findings in this study, this strengthens the explanation that viewing a hand in a plausible orientation for one's own body leads to relative enhanced processing of multisensory afferent information.

In conclusion, we found that participants were significantly better at detecting temporal asynchronies between observed and performed finger movements when viewing a virtual hand in an anatomically plausible posture for one's own hand, compared to viewing dots or hand orientations implausible for one's own hand. Thus, our study provides evidence that multisensory processing is modulated by visually derived body form and orientation information. We suggest that this perceptual modulation is a consequence of body-specific sensory predictions.

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