RESEARCH ARTICLE

Detecting delay in visual feedback of an action as a monitor of self recognition

Adria E. N. Hoover · Laurence R. Harris

Received: 11 June 2012/Accepted: 7 August 2012/Published online: 25 August 2012 © Springer-Verlag 2012

Abstract How do we distinguish "self" from "other"? The correlation between willing an action and seeing it occur is an important cue. We exploited the fact that this correlation needs to occur within a restricted temporal window in order to obtain a quantitative assessment of when a body part is identified as "self". We measured the threshold and sensitivity (d') for detecting a delay between movements of the finger (of both the dominant and nondominant hands) and visual feedback as seen from four visual perspectives (the natural view, and mirror-reversed and/or inverted views). Each trial consisted of one presentation with minimum delay and another with a delay of between 33 and 150 ms. Participants indicated which presentation contained the delayed view. We varied the amount of efference copy available for this task by comparing performances for discrete movements and continuous movements. Discrete movements are associated with a stronger efference copy. Sensitivity to detect asynchrony between visual and proprioceptive information was significantly higher when movements were viewed from a "plausible" self perspective compared with when the view was reversed or inverted. Further, we found differences in performance between dominant and non-dominant hand finger movements across the continuous and single movements. Performance varied with the viewpoint from which the visual feedback was presented and on the efferent component such that optimal performance was obtained when the presentation was in the normal natural orientation and clear efferent information was available. Variations in

A. E. N. Hoover (⊠) · L. R. Harris
Department of Psychology, Centre for Vision Research,
York University, 4700 Keele Street, Toronto,
ON M3J 1P3, Canada
e-mail: adriah@yorku.ca

sensitivity to visual/non-visual temporal incongruence with the viewpoint in which a movement is seen may help determine the arrangement of the underlying visual representation of the body.

Keywords Cross-modal interactions · Visual perspective · Self recognition · Body ownership · Agency · Continuous and discrete movements

Introduction

We have the awareness that something we are looking at is a part of our own body from experiencing expected sensations correlated with what we are seeing (Gallagher 2000; Tsakiris et al. 2010). Seeing something being touched and feeling synchronous tactile sensations helps create a sense of ownership of the seen item and can even mislead us into thinking that foreign objects, such as rubber hands (the rubber hand illusion; Botvinick and Cohen 1998; Tsakiris et al. 2010; Tsakiris et al. 2005) and other inanimate objects (Armel and Ramachandran 2003), are parts of our own body. Similarly, seeing a finger move after we have attempted to move it helps identify it as belonging to us (Tsakiris et al. 2005). This case involves correlating what is seen with the simultaneous sensory and motor information. Identifying sensory and motor information that comes through very different channels as "belonging together" requires, among other things, that they occur in a certain temporal window (Spence et al. 2004). Temporal congruency promotes binding of the visual, proprioceptive, and efferent signals associated with movement and hence assists in creating a sense of self identification (Gallagher 2000; Tsakiris et al. 2006). We measured the tolerance to disruption of this temporal congruency by introducing a delay in the visual feedback concerning a voluntary movement and asking people to detect the delay. Our logic was that it should be easier to bind visual and motor information if the visual component was aligned with the internal representation of the body in both space and time. This is therefore a potentially more objective measure of body ownership than simply asking someone if something is perceived as being part of their own body.

The effect of perspective

The visual perspective in which we view a body part modulates the ability to recognize it as our own (Conson et al. 2010). We are able to recognize our dominant hand most quickly when it is seen from an "egocentric" or "plausible self" perspective (i.e. the normal view) compared with when it is seen in some anatomically impossible orientation (referred to as viewing from an "allocentric", "other", or "not self" perspective). As well, the ability to identify a hand as left or right hand (Dyde et al. 2011; Fiorio et al. 2007; Parsons 1994) and the effectiveness of the rubber hand illusion (Costantini and Haggard 2007; Holmes and Spence 2007) are likewise reduced if viewed from an allocentric perspective. The fact that perspective makes a difference suggests that there is an internal representation of the body providing an "expected" view that can be matched to what is actually seen. Varying perspective can therefore be used as an experimental tool to assess the nature of the body's internal representation: the view that is matched against proprioceptive and efferent signals.

Proprioceptive awareness

The ability to detect the position of a limb from proprioceptive information alone is poor (Graziano 1999; Làdavas et al. 2000). When an arm is moved passively to a new location, such that its position can only be identified by proprioceptive information about joint position and muscle length, participants are significantly less accurate at tracking the arm compared with when a target light is attached to the hand (Mather and Lackner 1981). A proprioceptive map of the body could therefore be expected to be of poor resolution and visual-proprioceptive matching to be broadly tuned. This is not to say that proprioceptive information is unimportant: loss of the proprioceptive system has devastating consequences for movement control and, particularly relevant here, is associated with a loss of body schema (Cole and Paillard 1998). The proprioceptive sense thus gives us some information about the position of a moving finger. However, since we are looking at an active finger movement, not only sensory feedback but also information related to the motor signals is involved (Tsakiris et al. 2005).

Awareness of a motor act

The sense of agency, the feeling that one can control and move one's body (Gallagher 2000; Tsakiris et al. 2010), includes the motor signal (efference copy) as well as sensory feedback (afferent signals) (Farrer et al. 2003). A sense of agency contributes to the sense of ownership, and correlating motor activity with visual feedback is thus an important contributor to this sense. Activity in the visual body areas in the brain (e.g. the extrastriate body area) is correlated with limb movement (Astafiev et al. 2004), providing a neural substrate for the interconnectivity of sensory and motor information in the construction of the representation of the body in the brain. Here, we quantify the important relationship between the sense of agency and sense of ownership without explicitly asking about either. Instead, we look for variations in the sensitivity for detecting a delay between the view of one's finger (ownership, if the perspective is correct) and movement of that finger (agency, if it is thought to be one's own finger).

Varying the efferent contribution: continuous versus discrete movements

Repetitive movements, such as waving one's hand or finger up and down rhythmically, are controlled differently than discrete movements (Spencer 2003). The use of efference copy to specify timing seems to be most explicit for discrete movements (Spencer et al. 2007). We took advantage of this difference in the weighting assigned to efference copy to assess the contribution of efferent control by comparing performances for repetitive and discrete finger motions. We expected performance to be more sensitive for discrete movements.

The dominant hand

Most people show a preference to use one or other hand (Oldfield 1971). The body-specificity hypothesis (Casasanto 2009; Willems and Hagoort 2009; Willems et al. 2010) proposes that right-handed people interact in different ways with their environment than left-handed people and create different representations of "action- and bodyrelated information". Given the extensive use of the dominant hand, right-handers might be expected to be best at tasks that use their right hand and less so when using their non-dominant left hand. If this were true, then we may expect differences in detecting a delayed visual feedback depending on which hand was moving that may be correlated with the reference frame for egocentrically centred body representation. We therefore performed our experiments with both dominant and non-dominant hand movements.

Our project

In order to look at the relative roles of vision, proprioception, and efference copy in identifying self, we varied each of these and used the discrimination of temporal delay as a measure. We used unseen discrete or continuous finger movements and presented participants with a view of their movement from egocentric or allocentric perspective. We measured the sensitivity with which temporal synchrony discriminations between the movement and the sensory feedback could be made and looked for variation in this sensitivity with visual perspective, movement type, and which hand was moving. We hypothesized that when the sensory information matches the internal representation, greater sensitivity in detecting a delay should result.

Methods

Participants

Ten right-handed adults (6 females and 4 males), mean age of 28.9 (\pm 10.7) years, participated in this study. All participants took part in all the experiments using both hands in both the continuous and the discrete movement paradigms. Participants gave their informed consent, which conformed to York University ethical guidelines and the Declaration of Helsinki. Handedness was determined by an adapted version of the Edinburgh Handedness Inventory (Oldfield 1971).

Apparatus

Participants sat on an adjustable chair at a table with their head on a chin rest 50 cm from an LCD display (HP FV583AA 20" widescreen monitor; $1,600 \times 900$ pixels; 5 ms refresh response time) centred at eye level. They placed their hand on the table shielded from view by black cloth. A PlayStation Eye camera (SCEI; resolution 640×480 pixels @ 30 Hz) was mounted on the front of the chin rest and pointed down at their hand (Fig. 1). The camera was angled to capture the view as seen from a "natural" egocentric perspective of the participant as if looking down at their own hand.

Introducing a delay in the display

The video signal from the USB camera was fed into an iMAC, read by a MATLAB program (version R2009_b), and played through the LCD screen either at a minimal delay or with an added delay of between 33 and 231 ms. To calibrate the system, we had the camera view a flashing LED and compared the voltage across it with its



Fig. 1 Apparatus: participants sat on an adjustable chair at a table 50 cm from an LCD display centred at eye level. They placed their hand on the table shielded from view by a black cloth. A PlayStation Eye camera was mounted on the front of the chin rest and pointed down at their hand. The camera was angled to capture the view as seen from a "natural" egocentric perspective for the participant as if looking down at their own hand. Participants used foot pedals to make responses

appearance on the screen (measured by a light-sensitive diode). This revealed a minimum delay of 85 ms \pm one-half screen refresh duration and confirmed the delay values we introduced by software. With the minimum system delay, motion on the screen appeared simultaneous. The delays presented in the results have all been corrected by the addition of the system delay.

Finger motions

We used either continuous or discrete movements of the index fingers of both the right and left hands. For continuous movements, participants were required to make a repetitive flexion and extension of their index finger of about 2 cm at 2 Hz. The movements began before they saw their hand on the screen and continued until the hand was no longer visible (1 s presentation time). For discrete movements, participants made a single flexion of their index finger through about 2 cm as soon as they saw their hand on the screen. To reduce the between-subject differences in the speed and type of movement, all participants went through a 15-trial practice phase for each session during which the experimenter observed and corrected the movement. We ensured that participants avoided touching the table, other fingers, and/or their hand with their index finger during the movement so as not to introduce other tactile cues.

Manipulating the perspective

Through the use of MATLAB and Psychophysics Toolbox extensions (Brainard 1997; Pelli 1997), participants' movements were displayed on the LCD monitor in one of the four perspectives for each of the delays: (1) self perspective (no axis reflection); (2) *y*-reflection (so that the hand appeared as the opposite hand); (3) *x*-reflection (so that the hand appeared upside down); and (4) *xy*-reflection (so that the hand appeared as the opposite hand presented upside down). Viewing conditions 1 and 2 represent egocentric (or "plausible self") viewing perspectives, and conditions 3 and 4 represent allocentric (or "other") perspectives. Examples of these views are shown as insets in Fig. 2.

Procedure

To explore the temporal synchrony discrimination, a 2AFC discrimination paradigm was used. Each trial consisted of two presentations: a minimum-delay presentation (duration 1,000 ms) and a delayed presentation (duration 1,000 ms) separated by an inter-stimulus interval (ISI) of 100 ms. Whether the delayed presentation or the minimum-delay presentation was displayed first was randomly chosen by MATLAB. There were eight possible differences in visual delays between the two presentations in any given trial: 0,

Fig. 2 Continuous movement: Plots of the mean proportion correct as a function of the imposed visual delay for the dominant (right) (a) and nondominant (left) (b) hands. The curves are for self perspective (black solid line and filled circles), y-reflection (black dashed and filled squares), x-reflection (grey solid line and grey circles), and xy-reflection (grey dashed line and grey triangles). The data expressed as mean sensitivity scores (d')are plotted as bar graphs for the dominant (c) and non-dominant (d) hands. Viewing condition indicated by the insets beneath each column. All error bars are the SE of the mean

33, 66, 99, 132, 165, 198, and 231 ms. Participants indicated which presentation was delayed using foot pedals (left = first presentation; right = second presentation).

Experiments were run in a counterbalanced block design where either continuous or discrete movements of either the left or right hand were tested in four blocks. For each block, the eight differences in visual delay were presented eight times for the four viewing conditions in a random order, resulting in a total of 256 trials. After the first 128 trials, participants were given a break. Each session of 128 trials lasted approximately 15 min. Each experiment was repeated for left and right hands and for continuous and discrete movements, resulting in a total of $256 \times 4 = 1,024$ trials. The entire experiment took 2 h to complete.

Data analysis

To assess the performance for each visual perspective, we fitted a sigmoidal function to the proportion of times participants correctly chose the delayed presentation as a function of the delay using

$$y = 0.5 + \frac{0.5}{1 + e^{-\left(\frac{x - x_0}{b}\right)}},\tag{1}$$

where x is the delay, x_0 is the 75 % detection threshold, and b is the standard deviation. The sensitivity (d') values were



calculated from the 2AFC discrimination data by dividing the data into trials where the minimum delay was presented first and those where it was presented second. The hit rate was taken from the trials in which the delay was correctly identified as presented in the first presentation; the falsepositive rate was taken as the rate at which the delay was incorrectly identified as occurring in the first presentation when it actually occurred in the second. These rates were converted into Z scores, and the difference was converted to a d' score (Macmillan and Creelman 1991).

The statistical analysis comprised repeated measures analysis of variances (ANOVAs). For all tests, alpha was set at P < 0.05. All multiple comparisons were made with the false discovery rate P value correction (Benjamini and Hochberg 1995).

Results

Detecting visual delays using continuous movement (thresholds)

Figure 2a, b shows the mean proportion correct plotted as a function of delay for the data averaged across the ten participants. For the statistics, each participant's performance was analysed separately. The 75 % of threshold values were extracted from these curves and converted to absolute thresholds by adding the system delay (85 ms). The mean thresholds are shown in Table 1.

A 2 (hands) × 4 (viewing conditions) repeated measures ANOVA revealed a significant main effect of viewing condition ($F_{(3,27)} = 10.308$, P < 0.001, $\eta_p^2 = 0.534$) and no effect of hand ($F_{(1,9)} = 0.183$, P = 0.678, $\eta_p^2 = 0.020$). Pairwise comparisons showed that participants had lower thresholds for detecting an imposed delay while viewing their movement in the self perspective compared with the "other" perspective (*x*- and *xy*-reflections) (P < 0.001 and P = 0.005, respectively). Participants also had lower thresholds for detecting the delay when viewing their movement in *y*-reflection compared with the "other" (P = 0.005 and P = 0.021, respectively;

 Table 1
 Mean thresholds and standard errors for all conditions tested using continuous movements

	Dominant (right) hand (ms)	Non-dominant (left) hand (ms)	
Self perspective	145 ± 7	140 ± 15	
y-reflection	156 ± 16	146 ± 15	
x-reflection	168 ± 8	202 ± 16	
xy-reflection	193 ± 13	183 ± 16	

Values were obtained by adding the system delay (85 ms) to the imposed delay

Fig. 2a, b). In other words, when movements were seen in a "plausible self" (self and y-reflection) perspective, participants detected shorter delays (mean threshold $149 \pm 13 \text{ ms}$) compared with when movements were seen in an "other" perspective (mean threshold $187 \pm 13 \text{ ms}$).

Detecting visual delays in continuous movement (sensitivity)

The same data used for the threshold analysis were converted into sensitivity scores (d'; see "Methods"). A 2 (hands) \times 4 (viewing conditions) repeated measures ANOVA revealed a significant effect of perspective $(F_{(3,27)} = 15.256,$ $P < 0.001, \eta_p^2 = 0.629$) and no effect of hand $(F_{(1,9)} =$ 0.067, P = 0.802, $\eta_p^2 = 0.007$) on sensitivity scores. Pairwise comparisons confirmed the threshold analysis showing that participants were more sensitive at detecting a delay when viewing their movement in the self perspective compared with the "other" perspective (P < 0.001 and P = 0.004, respectively). Participants were also more sensitive at detecting the delay when viewing their movement in v-reflection compared with the "other" (x- and xv-reflections) viewing conditions (P = 0.003 and P = 0.015, respectively). Regardless of the hand used, participants performed better (i.e. they could detect shorter delays) when their continuous, repetitive movement was viewed from a "plausible self" perspective compared with when it was viewed from an "other" perspective (Fig. 2c, d).

Discriminating visual delay in discrete movement (thresholds)

Figure 3a, b shows the mean proportion correct for detecting a delay in the visual feedback for discrete movements plotted as a function of delay averaged across the ten participants. For the statistics, each participant's performance was analysed separately. As for the continuous movement analysis, the system delay was added to these values to obtain absolute threshold values. The mean 75 % threshold values are shown in Table 2.

A 2 (hands) × 4 (viewing conditions) repeated measures ANOVA of the discrete movement data revealed a significant main effect of viewing condition ($F_{(3,27)} =$ 8.850, P < 0.001, $\eta_p^2 = 0.496$) and no effect of hand ($F_{(1,9)} = 0.680$, P = 0.431, $\eta_p^2 = 0.070$; Fig. 3b). Pairwise comparisons showed that participants had lower thresholds when detecting a delay while viewing their movement in the self perspective compared with the "other" perspective (P = 0.002 and P < 0.005, respectively). Participants also had lower thresholds when detecting the delay when viewing their movement in the y-reflection compared with the "other" (xy-reflection) viewing condition (P = 0.057; Fig. 2a, b). Further, there was a near-significant difference Fig. 3 Discrete movement: Plots of the mean proportion correct as a function of the imposed visual delay for the dominant (right) (a) and nondominant (left) (b) hands. The curves are for self perspective (black solid line and filled circles), y-reflection (black dashed and filled squares), x-reflection (grey solid line and grey circles), and xy-reflection (grev dashed line and grev triangles). The data expressed as mean sensitivity scores (d')are plotted as bar graphs for the dominant (c) and non-dominant (d) hands. Viewing condition indicated by the *insets* beneath each column. All error bars are the SE of the mean



 Table 2
 Mean thresholds and standard errors for all conditions tested using discrete movements

	Dominant (right) hand (ms)	Non-dominant (left) hand (ms)
Self perspective	123 ± 7	139 ± 8
y-reflection	140 ± 8	140 ± 8
x-reflection	144 ± 7	144 ± 8
xy-reflection	148 ± 7	148 ± 8

between the self and y-axis reflection within the "plausible self" perspectives (P = 0.058). In other words, when movements were seen in the self perspective, participants detected shorter delays (mean threshold 131 ± 7 ms) compared with when movements were seen in all other perspectives (mean threshold 144 ± 8 ms).

Discriminating visual delay in discrete movement (sensitivity)

The same data used for the timing analysis were analysed as sensitivity scores (*d*'; see "Methods"). Unlike for the continuous movement data, a 2 (hands) × 4 (viewing conditions) repeated measures ANOVA revealed a significant interaction between which hand was used (dominant or non-dominant) for the discrete movement and viewing condition ($F_{(3,27)} = 6.724$, P = 0.002, $\eta_p^2 = 0.428$). Participants performed differently across the viewing

conditions depending on the hand with which they performed the movement. To break down the significant interaction, 2×2 interaction contrasts were run. The contrasts confirmed that participants performed differently in the self perspective and y-axis reflection conditions for the dominant and non-dominant hands by revealing a significant interaction ($F_{(1,9)} = 13.190, P = 0.005, \eta_p^2 = 0.594$). The difference in sensitivity scores between the self perspective and y-axis reflection conditions was greater for the dominant hand than for the non-dominant hand (Fig. 3c, d). This difference was also reflected in the threshold data listed in Table 2. In fact, there were no differences between the different viewing conditions for the non-dominant hand. When the non-dominant left hand was y-reflected so that it was seen as the dominant right hand, it appeared to inherit the right hand's advantage whereby participants showed higher sensitivity (first two bars in Fig. 3d). Further, when comparing the dominant and non-dominant hands across the x-axis and xy-axis refection conditions, we find only a significant main effect of condition where performance was best (regardless of hand) in the x-axis reflection condition $(F_{(1,9)} = 5.847, P = 0.039, \eta_p^2 = 0.394).$

Continuous versus discrete movements

From the above data, a difference between continuous and discrete movements appeared when comparing the "self"



Viewing Condition

395

with the y-reflection condition. Therefore, we looked in more detail at these conditions. Figure 4 compares the d'scores obtained from continuous movement with those from discrete movements for the dominant (Fig. 4a) and non-dominant (Fig. 4b) hands. A $2 \times 2 \times 2$ repeated measures ANOVA on the d' scores revealed a significant three-way interaction between the movement (continuous or discrete), hand used (dominant or non-dominant), and visual perspective (no reflection or y-reflection), $F_{(1,9)} =$ 16.560, P = 0.003, $\eta_p^2 = 0.648$. That is, the effect of perspective depends on the type of movement and the hand used. To break down this three-way interaction, we ran pairwise comparisons to compare performance across the different movements for both hands and both conditions. There were significant differences between continuous and discrete movements for all comparisons except for the nondominant hand in the self perspective condition (dominant hand: self perspective P = 0.004 and y-axis reflection P = 0.022; non-dominant hand: self perspective P =0.396 and y-axis reflection P = 0.023). Overall, participants were most sensitive at detecting a delay when viewing their dominant hand making a discrete movement.

Discussion

The current study has shown significant variation in the ability to detect temporal asynchrony between a movement and visual feedback concerning that movement that depended on the visual perspective (egocentric or allocentric), the nature of the movement (continuous or discrete), and the hand used to make the movement (dominant or non-dominant). Performance varied with the perspective from which the visual feedback was presented and on the efferent component such that optimal performance was obtained when the presentation was in the normal natural orientation and clear efferent information was available. In other words, participants were most sensitive when viewing the dominant hand in its natural ("self") perspective making a discrete movement. For this condition, participants could make a reliable discrimination between the minimal delay of 85 ms (which appeared simultaneous) and 85 + 38 = 123 ms (the mean threshold for the perception of delay). When participants were viewing the dominant hand in its natural perspective making a continuous, repetitive motion (with less access to an efference copy command), the corresponding mean threshold was 85 + 59 = 134 ms, indicating a 21-ms improvement attributable to the availability of a clear onset of the movement (efference copy).

Viewing Condition

An unnatural perspective reduces the ability to detect a delay

Perception of the relative timing of visual and non-visual cues to hand motion depends on whether one is viewing from a "self" (egocentric) or "other" (allocentric) perspective. All conditions provided the participant with an efference copy of their movement, which is deemed as intrinsically important in identifying agency and self (Gallagher 2000; Tsakiris et al. 2006). However, when movements were viewed in a "plausible self" perspective, there was a higher sensitivity to delay between visual and non-visual cues, suggesting an enhanced sense of ownership (Gallagher 2000) and a better ability to match the image presented on the screen in an egocentric perspective to the visual motion expected. Participants performed best (regardless of the type of movement) when the hand was viewed in the self or plausible self perspective. This is in line with previous research which revealed that the rubber hand illusion was not effective when the observer saw the rubber hand in a spatially or anatomically incongruent posture (Costantini and Haggard 2007; Holmes and Spence 2007). The pattern of performance for our cross-modal task replicates a similar pattern of performance found in the detection of self while viewing static images in which

performance was best when images were presented in a self (or egocentric) perspective (Conson et al. 2010). However, this study used only a subjective method of report. We conclude that variation in temporal synchrony discrimination provides quantitative evidence for an internal representation of the body providing an "expected" perspective that can be matched to what is actually seen.

The contribution of a clear efferent component

Discrete motion is associated with more efferent activity and a sharper onset of that activity than is present while maintaining a repetitive, continuous movement (Spencer et al. 2007). Sensitivity for detecting a delay in visual feedback was greater for discrete movements, thus suggesting a role of efference copy ("forward model"; Wolpert 1997). Delays could be detected on average 22 ms earlier if the movement was discrete. We thus conclude that having such a clean efferent component may have made it possible to detect shorter delays between the "efferent plus proprioceptive" and the visual feedback. This is reminiscent of the 29-ms advantage for detecting an active rather than a passive finger movement measured by Winter et al. (2008) and Lau et al. (2004). Of course this advantage would have been constant across perspectives.

Dominant versus non-dominant hand

Participants were most sensitive at detecting a delay when viewing their dominant hand making a discrete movement compared with a continuous movement. Further, we found that participants showed less of a difference in performance between the "plausible self" conditions (self perspective and *y*-reflection) during a discrete movement when performing that movement with the non-dominant hand. Thus, subjects were best at cross-modal asynchrony detection when moving their dominant hand in a discrete movement. This is consistent with previous self recognition experiments which indicated superior recognition of movement of the dominant hand (Conson et al. 2010) and the body-specificity hypothesis (Casasanto 2009).

It is possible that when participants perform a continuous movement (typical for bimanual tasks Swinnen 2002), they consider the right and left hands as yoked or working in tandem. Under these conditions, the advantage would be compatible with our observation that participants did not show a difference between the two "plausible self" (self and *y*-reflection) perspectives during continuous movements performed with the non-dominant hand. In contrast, during the discrete movements, which are typical of goaldirected movements, participants may consider the left and right hands as different/separate. Goal-directed movements are typically initiated and performed by the dominant hand because they often require greater precision (Bryden et al. 2000).

Our results provide further evidence that handedness could possibly define the reference frame for egocentrically centred body representation and create different representations of "action- and body-related information" (Conson et al. 2010). Past neuroimaging research has shown that the dominant hand provides the basis for left- and righthanders having different patterns of activation in areas of the visual cortex that are specifically related to body (Willems et al. 2010; Willems et al. 2009a; Willems et al. 2009b).

Neural correlates of self recognition

The discovery of an area in the brain responsive to views of the body (extrastriate body area-EBA; Downing et al. 2001) has provided a possible neural substrate for how the body may be represented in the brain. The EBA responds selectively to views of human body parts regardless of whether they are presented as photographs, line drawings, stick figures, silhouettes, or still images depicting bodies in motion (see review in Peelen and Downing 2007). It does not respond selectively based on perspective, lending doubt as to whether it may be involved in representing one's own body. However, EBA activity has been correlated with motor imagery of the movements of a limb, suggesting the integration of visual, efference, and proprioceptive information tantalizingly suggestive of an involvement in creating a representation of one's body in the brain (Astafiev et al. 2004). We suggest that the EBA may be particularly active during the combination of agency and ownership employed in this study, possibly underpinning the enhanced sensitivity to discrepancy between motor and visual correlates of finger movements when viewed from the natural perspective. Another area that might be involved in the recognition of these finger actions is in the parietal. Reduction in activity in parietal and frontal cortices has been correlated with difficulties in recognizing self actions in schizophrenia (Maruff et al. 2005).

Conclusion

We manipulated the recognition of "self" by varying the visual perspective in which participants saw their movements and the quality of efferent information available by varying the nature of the movement. Overall, we find that egocentric perspectives of self are very important. We are able to discriminate asynchrony from our proprioceptive information and visually presented information more efficiently when our movements are seen in a plausible self perspective and when efferent information is most distinctive during a discrete movement. Further, there is a clear difference in whether the dominant hand provides an advantage in detecting asynchrony during a discrete movement compared with a continuous movement. Together, these data contribute to the evidence for the roles of both vision and information about posture/movement from proprioceptive and motor systems in the development of representations of self (body schema).

Acknowledgments This work was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) grant to LRH. AENH held a PGS-D2 NSERC graduate scholarship.

References

- Armel KC, Ramachandran VS (2003) Projecting sensations to external objects: evidence from skin conductance response. Proc R Soc Lond B Biol Sci 270:1499–1506
- Astafiev SV, Stanley CM, Shulman GL, Corbetta M (2004) Extrastriate body area in human occipital cortex responds to the performance of motor actions. Nat Neurosci 7:542–548
- Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. J R Stat Soc Series B Stat Methodol 57:289–300
- Botvinick M, Cohen J (1998) Rubber hands "feel" touch that eyes see. Nature 391:756
- Brainard DH (1997) The psychophysics toolbox. Spat Vis 10: 433–436
- Bryden PJ, Pryde KM, Roy EA (2000) A performance measure of the degree of hand preference. Brain Cog 44:402–414
- Casasanto D (2009) Embodiment of abstract concepts: good and bad in right- and left-handers. J Exp Psychol Gen 138:351–367
- Cole J, Paillard J (1998) Living without touch and peripheral information about body position and movement: studies with deafferented subjects. In: Bermudez J (ed) The body and the self. MIT Press, Cambridge, pp 245–266
- Conson M, Aromino AR, Trojano L (2010) Whose hand is this? Handedness and visual perspective modulate self/other discrimination. Exp Brain Res 206:449–453
- Costantini M, Haggard P (2007) The rubber hand illusion: sensitivity and reference frame for body ownership. Conscious Cogn 16:229–240
- Downing PE, Jiang Y, Shuman M, Kanwisher N (2001) A cortical area selective for visual processing of the human body. Science 293:2470–2473
- Dyde R, MacKenzie K, Harris L (2011) How well do you know the back of your hand? Reaction time to identify a rotated hand silhouette depends on whether it is interpreted as a palm or back view. J Vis 11:868
- Farrer C, Franck N, Georgieff N, Frith CD, Decety J, Jeannerod M (2003) Modulating the experience of agency: a positron emission tomography study. NeuroImage 18:324–333
- Fiorio M et al (2007) Defective temporal processing of sensory stimuli in DYT1 mutation carriers: a new endophenotype of dystonia? Brain 130:134–142
- Gallagher I (2000) Philosophical conceptions of the self: implications for cognitive science. Trends Cogn Sci 4:14–21
- Graziano MS (1999) Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. Proc Natl Acad Sci USA 96:10418–10421

- Holmes NP, Spence C (2007) Dissociating body image and body schema with rubber hands. Exp Brain Res 166:489–497
- Làdavas E, Farnè A, Zeloni G, di Pellegrino G (2000) Seeing or not seeing where your hands are. Exp Brain Res 131:458–467
- Lau HC, Rogers RD, Haggard P, Passingham RE (2004) Attention to intention. Science 303:1208–1210
- Macmillan NA, Creelman DC (1991) Detection theory: a user's guide. Cambridge University Press, New York
- Maruff P, Wood SJ, Velakoulis D, Smith DJ, Soulsby B, Suckling J, Bullmore ET, Pantelis C (2005) Reduced volume of parietal and frontal association areas in patients with schizophrenia characterized by passivity delusions. Psychol Med 35:783–789
- Mather JA, Lackner JR (1981) The influence of efferent, proprioceptive, and timing factors on the accuracy of eye-hand tracking. Exp Brain Res 43:406–412
- Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9:97–113
- Parsons LM (1994) Temporal and kinematic properties of motor behavior reflected in mentally simulated action. J Exp Psychol Hum Percept 20:709–730
- Peelen MV, Downing PE (2007) The neural basis of visual body perception. Nature Rev Neurosci 8:636–648
- Pelli DG (1997) The VideoToolbox software for visual psychophysics: transforming numbers into movies. Spatl Vis 10:437–442
- Spence C, Pavani F, Maravita A, Holmes N (2004) Multisensory contributions to the 3-D representation of visuotactile peripersonal space in humans: evidence from the crossmodal congruency task. J Phys 98:171–189
- Spencer RMC (2003) Disrupted timing of discontinuous but not continuous movements by cerebellar lesions. Science 300:1437– 1439
- Spencer R, Verstynen T, Brett M (2007) Cerebellar activation during discrete and not continuous timed movements: an fMRI study. NeuroImage 36:378–387
- Swinnen SP (2002) Intermanual coordination: from behavioural principles to neural-network interactions. Nat Rev Neurosci 3:348–359
- Tsakiris M, Haggard P, Franck N, Mainy N, Sirigu A (2005) A specific role for efferent information in self-recognition. Cognition 96:215–231
- Tsakiris M, Prabhu G, Haggard P (2006) Having a body versus moving your body: how agency structures body-ownership. Conscious Cogn 15:23–432
- Tsakiris M, Carpenter L, James D, Fotopoulou A (2010) Hands only illusion: multisensory integration elicits sense of ownership for body parts but not for non-corporeal objects. Exp Brain Res 204:343–352
- Willems RM, Hagoort P (2009) Hand preference influences neural correlates of action observation. Brain Res 1269:90–104
- Willems RM, Ozyürek A, Hagoort P (2009a) Differential roles for left inferior frontal and superior temporal cortex in multimodal integration of action and language. NeuroImage 47:1992–2004
- Willems RM, Toni I, Hagoort P, Casasanto D (2009b) Body-specific motor imagery of hand actions: neural evidence from right- and left-handers. Front Hum Neurosci 3:39
- Willems RM, Hagoort P, Casasanto D (2010) Body-specific representations of action verbs: neural evidence from right- and left-handers. Psychol Sci 21:67–74
- Winter R, Harrar V, Gozdic M, Harris LR (2008) The relative timing of active and passive touch. Brain Res 1242:54–58
- Wolpert DM (1997) Computational approaches to motor control. Trends Cogn Sci 1:209–216