Sense of agency primes manual motor responses

Journal Article

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Abstract

Perceiving the body influences how we perceive and respond to stimuli in the world. We investigated the respective effects of different components of bodily representation – the senses of ownership and agency – on responses to simple visual stimuli. Participants viewed a video image of their hand on a computer monitor presented either in real time, or with a systematic delay. Blocks began with an induction period in which the index finger was (1) brushed, (2) passively moved, or (3) actively moved by the participant. Subjective reports showed that the sense of ownership over the seen hand emerged with synchronous video, regardless of the type of induction, whereas the sense of agency over the hand emerged only following synchronous video with active movement. Following induction, participants responded as quickly as possible to the onset of visual stimuli near the hand by pressing a button with their other hand. Reaction time was significantly speeded when participants had a sense of agency over their seen hand. This effect was eliminated when participants responded vocally, suggesting that it reflects priming of manual responses, rather than enhanced stimulus detection. These results suggest that vision of one's own hand – and, specifically, the sense of agency over that hand – primes manual motor responses.

Sense of Agency Primes Manual Motor Responses

The body is a salient object in the visual world (cf. Gibson 1979). What are the perceptual and cognitive effects of the visual experience of our own body? Studies in both patients with visual extinction (di Pellegrino and Frassinetti 2000) and in healthy participants (Reed et al 2006) have demonstrated attentional enhancement of the space immediately surrounding a viewed hand. These effects are not merely spatial, but are specifically linked to the body, since responses to visual stimuli appearing on or near the hand are facilitated compared to those appearing on a non-hand object (Hari and Jousmäki 1996; Tipper et al 1998; Whiteley et al 2004; Whiteley et al 2008). Furthermore, seeing the hand has specific effects on touch, speeding reaction time (RT) to tactile stimuli (e.g., Tipper et al 1998), and improving tactile acuity (e.g., Kennett et al 2001). It is presently unclear, however, what aspect of seeing the body causes such effects.

The experience of having a body is not monolithic, but is composed of numerous dissociable components (cf. Longo et al 2008). The most common dissociation made between components of the bodily self is that between the sense of *ownership* over one's own body (i.e., the sense that it's 'mine'), and the sense of *agency* over it (i.e., the sense that I can control my body) (Gallagher 2000; Longo et al 2008; Tsakiris et al 2006). One paradigm used recently to investigate such issues is the *rubber hand illusion* (RHI), in which a prosthetic hand touched synchronously with the participant's own hand creates the illusion that the rubber hand is actually theirs (Botvinick and Cohen 1998; Tsakiris and Haggard 2005). An analogous illusion can be created by a video image of the participant's own hand displayed either in real-time, or with a systematic delay (Tsakiris et al 2006). In such situations, viewing both active and passive movements generates a sense of ownership over the viewed hand, but only viewing one's own active movements produces a sense of agency. That is, comparing the effects of active and passive movements of the participants' fingers can shed light on the components of self-representation. Specifically, the sense of ownership results from synchronous – but not asynchronous – video feedback of one's own hand, irrespective of whether the hand is touched, passively moved, or actively moved. The sense of agency, in contrast, results during synchronous – but, again, not asynchronous – video feedback, but only when the finger is actively moved. Tsakiris et al (2006) validated the use of this paradigm as a manipulation of ownership and agency by showing that these aspects of the bodily self induced distinct patterns of proprioceptive biases in the RHI. Whereas the sense of ownership induced a local proprioceptive displacement towards the video image that was confined to the stimulated finger, the sense of agency induced a more widespread global shift of the entire hand.

Thus, it is known that seeing the body has cognitive effects, and also that the representation of the body is composed of dissociable components. Which of these components is responsible for cognitive effects of seeing one's own body? Many experimental designs show an effect of self-representation on basic sensorimotor processing, but cannot reveal whether ownership or agency is responsible (Tsakiris et al 2007). We recently used the RHI to investigate the role of ownership in the enhancement of tactile acuity from seeing one's hand (Longo et al in press-a). Participants observed the same rubber hand in each condition, but tactile enhancement effects were observed only when participants experienced a sense of ownership over the rubber hand. Similarly, Whiteley and colleagues (2008) used the video RHI paradigm to investigate the role of ownership in the enhancement of visual detection of object on one's own hand. Detection of visual stimuli on the hand was significantly faster than detection on an inanimate object only when participants had a sense of ownership over the hand.

These results suggest that the sense of ownership facilitates sensory processing. The potential effects of agency, however, are presently unknown. The present study investigated two main questions: (1) what are the effects of ownership and agency over a seen hand on processing of simple visual stimuli appearing near that hand; (2) do such effects reflect facilitation of sensory or of motor processing? Ownership and agency were manipulated using the video RHI paradigm described above. Effects of ownership can be investigated by comparing synchronous and asynchronous video feedback conditions, independent of whether the induction is tactile, or involves passive or active movement. Effects of agency, in contrast, are expected only following synchronous feedback of active movements, but not passive movements or touch.

This paradigm also allows potential effects on sensory or on motor processing to be dissociated. Sensory effects would be expected to be faster when stimuli appear near the hand than farther away, given the known attentional advantage for stimuli appearing in peripersonal space (e.g., di Pellegrino and Frassinetti 2000; Reed et al 2006), and also to be independent of the response effector. If, in contrast, bodily representations prime motor responses, no modulation would be expected as a function of the location of the visual stimulus, but priming might be expected to be specific to the seen effector (in this case, the hand).

Method

Participants

Fourty-four volunteers (28 female, age 18-34) participated. Thirty were right-handed as assessed by the Edinburgh Inventory (Oldfield 1971), M =, 74.97, range: -50 – 100. Participants had normal or corrected to normal vision, and were paid for their participation. Twenty-four participated in the main experiment with manual responses, and twenty in a control experiment with vocal responses. Data from an additional participant was excluded due to experimenter error. Procedures were approved by the local ethical committee.

Apparatus and Materials

The experimental setup is shown in Figure 1. Stimuli were displayed on a 15" flat-panel monitor using LabView 7.0 software (National Instruments, Austin, TX). Participants sat with their head approximately 30 cm from the monitor and placed either their right or left hand behind the monitor. A mirror was attached to the back of the monitor and the mirror image of the hand was recorded by a colour video camera (Sony CCD-V800E) recording at 28 Hz. This video image was displayed on the monitor either with minimal delay (synchronous condition) or systematically delayed (asynchronous condition). In the synchronous condition, the minimal and irreducible delay was approximately 100 ms, while that in the asynchronous condition was approximately 500 ms. Franck et al (2001) found that healthy adults perceived a viewed action as self-generated at delays up to 150 ms, suggesting that the 100 ms delay should not adversely affect illusion of ownership and agency (cf. Blakemore et al 1999).

Participants responded to illumination of small green lights, 1 cm (1.91˚) in diameter, spaced 5.75 cm (10.95˚) apart. A fixation cross was placed midway between the lights.

Design and Procedure

There were 12 experimental blocks, formed by crossing the three methods of inducing ownership (active movement, passive movement, tactile stimulation), the two levels of synchrony (synchronous, asynchronous), and whether the right or the left hand was used to respond. Order of blocks was randomized for each participant. On each block, participants placed either their left or right hand behind the monitor. They wore a black smock which covered their arm such that it was not visible directly, but only indirectly as a video image relayed from the camera to the monitor. The table was covered with black felt. Four bumps on the table which could be felt – but not seen - indicated where to place the tips of the index and little fingers of each hand.

Each block began with a 60 second RHI induction period. In the active condition, participants were instructed to lift and lower their index finger at their own pace. They were instructed to move approximately every 1-2 s, but not rhythmically. In the passive condition, the participant's index finger was lifted and lowered by the experimenter pulling on an invisible thread attached to the finger. The finger was lifted approximately once every one to two seconds, but not rhythmically. In the tactile condition, the participant's index finger was brushed by the experimenter with a paintbrush approximately once every one to two seconds, but not rhythmically. Following the induction period, participants were instructed to fixate the cross and the experimental trials commenced.

For the manual response group, responses were made with the hand that was not being viewed by pressing a mouse button with the index finger as quickly as possible. For half the participants, both lights were always visible, and the imperative stimulus was a change in illumination of one of the lights from grey to bright green. For the other half, the imperative stimulus was the abrupt appearance of one of the lights, fully illuminated. The lights appeared on either the left or right side of the fixation cross. Depending on whether the right or the left hand was the stimulus, one of the lights was always immediately above (but not touching) the tip of the viewed index finger, while the other was farther away in empty space (see Figure 1). The light remained on until a response was recorded, at which time it turned off/disappeared immediately.

For the vocal response group, the participant's task was to say "ta" as quickly as possible into a headset-mounted microphone. Twelve participants responded to the appearance of a light, eight to the illumination of a light. The vocal response was recorded and reaction times were computed offline in Matlab 7.3 (Mathworks, Natick, MA) by finding the first point where the absolute value of the amplitude reached half of its maximum value. To allow sufficient time for vocal responses, a constant trial length of 3,000 ms was used. All other procedures were identical to the manual response condition.

Trials were separated by an interval between 1,000 and 3,000 ms, randomly selected on each trial. There were 60 trials in each block, for a total of 720 trials. For manual responses, trials on which RT was faster than 200 ms or slower than 500 ms were excluded (5.9%). As vocal responses were slower on average, a 600 ms upper bound on RT was used, which produced a similar exclusion rate (6.2%).

Eleven participants in the vocal response group additionally completed a subjective report questionnaire following the main experiment. For each questionnaire item, participants were asked to rate their agreement or disagreement with 10 statements concerning their experience during the various conditions. Responses were made using a 7-point Likert scale, where a score of +3 indicated strong agreement with the statement, -3 strong disagreement with the statement, and 0 neither agreement nor disagreement. Judgments for each statement were made separately for each of the six conditions formed by crossing the induction type (active movement, passive movement, tactile stimulation) and synchrony (synchronous video feedback, asynchronous video feedback) factors. The order of statements was randomized for each participant.

Results

Subjective Reports

Mean responses to the ten subjective report items are shown in Table 1. In order to look generally at the senses of ownership and agency, we collapsed across items related to each of these experiences. To compute an overall measure of ownership in each condition, we averaged across items 1-3, with items 2 and 3 being scored in reverse. To compute an overall measure of agency, we averaged across items 4-6, with item 6 being scored negatively. Mean values for these measures are shown in Figure 2. An ANOVA performed only on data from the synchronous condition revealed a significant main effect of induction type, $F(2, 20) = 11.21$, $p < .0005$, and a main effect of synchrony, $F(1, 10) = 35.24$, $p < .0001$. There was also a significant interaction of induction type and component, $F(2, 20) = 6.03$, $p < .01$.

Significant levels of ownership (i.e., greater than 0, Bonferroni corrected) were observed in the synchronous condition following active movement, $t(10) = 8.48$, $p < .0001$, passive movement, $t(10) = 6.66$, $p < .0001$, and touch, $t(10) = 4.48$, $p < .001$. No such effects were observed in the asynchronous condition, $t(10) = 1.59$, .46, .39, respectively. Significant levels of agency, in contrast, were observed only following synchronous active movement, $t(10) = 13.54$, $p < .0001$, but not following passive movement, $t(10) = 1.66$, touch, $t(10) = 1.81$, nor any of the asynchronous conditions, $t(10) = 2.07$, -1.07, -.85.

Manual Responses

There was a significant main effect of induction type, $F(2, 46) = 4.03$, $p < .05$, and a marginal main effect of synchrony, $F(1, 46) = 3.35$, $p = .08$. More interestingly, there was a significant interaction of induction type and synchrony, $F(2, 46) = 3.30$, $p < .05$ (see Figure 2). The interaction was investigated by simple effects testing, holding each factor constant in turn and looking for effects of the other factor. Simple effects showed a significant facilitation of reactions following active movement of the index finger (298 vs. 306 ms), $t(23) = 3.49$, $p < .002$, which survived Bonferroni correction (see Figure 2). No such effects were found following passive movement (308 vs. 308 ms), $t(23) = 0.01$, or tactile stimulation (307 vs. 308 ms), $t(23) = 0.50$. This pattern suggests that this speedup in RT is a specific effect of the sense of agency over the seen hand, but not the sense of ownership.

When the synchrony factor was held constant in order to compare differences between induction methods in the synchronous condition, RTs were lower in the active movement condition than in the passive and tactile synchronous conditions, $F(1, 23) = 5.14$, $p < .05$ (see Figure 2). No significant difference was observed, in contrast, between RT in the active asynchronous condition and the two other asynchronous conditions, $F(1, 23) = 0.47$. This pattern demonstrates a clear facilitation effect of agency on RT, rather than an interference or distraction effect of asynchronous feedback.

There was no significant main effect, nor any interactions, involving whether the light was near or far from the finger. Comparable RT advantages following synchronous, compared to asynchronous, active movement were observed both when the light appeared near the finger (9 ms), $t(23) = 3.45$, $p < .005$, and when it appeared in empty space (7 ms), $t(23) = 2.47$, $p < .05$. No such effects were observed following passive movement (-1 ms, 1 ms), $t(23) = -0.26, 0.33$, or tactile stimulation (2 ms, 1 ms), $t(23) = 0.60, 0.24$. This pattern suggests that the effect of agency reflects a priming of motor responses, rather than an increase in peripersonal space representation, which would be expected to be larger in the space immediately surrounding the hand.

There was also a significant interaction of hand and synchrony, $F(1, 23) = 4.96$, $p < .05$ (see Figure 3). Across induction types, there was a significant decrease in RT following synchronous stimulation compared with asynchronous stimulation with left-hand responses (7 ms), $t(23) = 3.13.$, $p < .01$, but not with right-hand responses (-1 ms), $t(23) = -.28$, *n.s.*

Vocal Responses

In contrast to manual responses, there was no significant interaction between condition and synchrony, $F(2, 38) = .46$, *n.s.* No significant differences between synchronous and asynchronous conditions were observed in the active (381 ms vs. 377 ms), $t(19) = -0.89$, passive (381 ms vs. 377 ms), $t(19) = -0.74$, or tactile (375 ms vs. 378 ms), $t(19) = 0.37$, conditions. Thus, the selective priming effect of agency observed with manual responses did not appear with vocal responses. For each induction type, we compared the RT advantage for synchronous compared to asynchronous feedback between manual and vocal responses. The synchrony advantage in the active condition we observed with manual responses was significantly reduced with vocal responses, $t(42) = 2.59$, $p < .05$ (Bonferroni corrected). There was no effect of response effector on the difference between synchronous and asynchronous induction for the passive, $t(42) = 0.69$, *n.s.*, or tactile, $t(42) = 0.17$, *n.s.*, conditions. Agency facilitation of RT may therefore reflect motor priming of hand responses, rather than facilitation of stimulus detection. Furthermore, the effector specificity of the effect eliminates the possibility that the effect of agency might result from non-specific attentional arousal.

There was no significant interaction of synchrony and response hand, $F(2, 38) = 0.04$. Nor was there a significant difference between RT during synchronous and asynchronous blocks for either left hand (378 ms vs. 377 ms), $t(19) = 0.11$, or right hand (380 ms vs. 377 ms), $t(19) = 0.62$, responses. Thus, neither of the key effects observed with manual responses occurred with vocal responses, nor was there any trend in their direction.

Discussion

Subjective reports revealed that the sense of ownership over the hand emerged following synchronous, but not asynchronous, video feedback showing active movement, passive movement, and touch. The sense of agency, in contrast, emerged only following synchronous feedback showing active movements. This sense of agency was associated with a decrease in response time for manual – but not vocal – responses. This effector specificity rules out the possibility that the effect of agency might be due to non-specific attentional arousal. Thus, the sense of agency over a seen hand primes manual motor responses.

Ownership and Agency as the Sensory and Motor Reflections of the Bodily Self

The sense of ownership has sensory effects both on tactile stimuli (Longo et al in press), and on visual stimuli appearing on the hand (Whiteley et al 2008). In the present experiment, however, no such effect was observed for visual stimuli which appeared near the hand. Rather, in contrast to the sensory effects of the sense of ownership observed in those experiments, agency in the present experiment primed motor responses. Thus, whereas the sense of ownership over a perceived hand influences sensory processing, the sense of agency influences motor processing. Ownership and agency, then, can be thought of, respectively, as the sensory and motor reflections of the bodily self.

Many studies examining the effects of seeing one's hand have reported enhanced perceptual performance while viewing the hand compared to viewing some other non-hand object (e.g., Kennett et al 2001; Whiteley et al 2004). One concern about this type of manipulation is that there are any number of low-level visual or attentional differences between the visual stimuli which may account for the observed differences. For example, enhancement may arise because the hand is more interesting than the object, or because it is linked to the self. Indeed, Haggard (2006) found comparable visual enhancement of tactile acuity when participants viewed an experimenter's hand as when they viewed their own. In the present study, the hand stimulus was identical across conditions during the RT task, namely a video image of the participant's static hand. Thus, the effects observed in the present experiment, which emerge in the synchronous conditions relative to the asynchronous conditions, cannot be due to the visual stimulus per se, but must result from the context provided by the previous induction period. That is, the induction creates a tonic state consisting of the senses of ownership and agency, which in turn influences visuomotor reactions.

Ownership and the Right Hemisphere

While no overall effect of ownership was observed on motor responses, there was an interaction between ownership with hand laterality. Ownership appeared to prime left-hand responses, but interfere with right-hand responses. While this effect was unanticipated, it is consistent with several previous studies that have found a left-hand advantage for responding to self-related stimuli (e.g., Keenan et al 1999; Keenan et al 2001; Platek et al 2003). Such effects suggests that the effect observed in the present experiment is not a specific effect of body ownership as such, but rather a generic effect of self-related stimuli. Keenan and colleagues (Feinberg and Keenan 2005; Keenan et al 2001) suggest a general right-hemisphere bias for self-related information, which reduces motor thresholds for the left hand. Indeed, right-hemisphere biases have been observed in numerous neuroimaging studies examining such diverse self-related stimuli as autobiographical memory (Craik et al 1999), self-face recognition (Sugiura et al 2000), self-voice recognition (Nakamura et al 2001), and the senses of body ownership (Tsakiris et al 2007) and agency (Ruby and Decety 2001; for review see Decety and Lamm 2007).

Tonic vs. Event-Based Agency

Up to now, we have discussed agency over the hand as a tonic background context, acquired during the induction period. However, we also experience a more punctate sense of agency over particular actions, the sense that ‘I did that’. This feeling is present when we make deliberate actions, but absent for involuntary movements, such as twitches. In the present paradigm, the sense of agency over the hand is caused by repeated instances of self-generated movements with synchronous visual feedback, which are known to be perceived as self-caused (e.g., Blakemore et al 1999; Franck et al 2001). Thus, repeated experience of transitory agency over individual actions creates a generalized and tonic sense of agency over the effector producing those actions. The causes and the effect, however, appear to have rather different cognitive effects. Event-based agency modulates the perceived timing of events. The perceived time of stimuli caused by self-generated actions – but, again, not involuntary movements – is shifted towards the time of the movement (Haggard et al 2002), while the perceived time of the movement, in turn, is shifted towards the time of the effect. Furthermore, there is some evidence that perceiving an action attributed to one’s own body may reduce the excitability of the motor system (Schütz-Bosbach et al 2006), an effect opposite that observed for tonic agency in this study. Thus, there are cognitive effects both of tonic agency over an effector (as in the present study) and punctate agency over a specific action, though these effects are rather different.

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Figure Captions

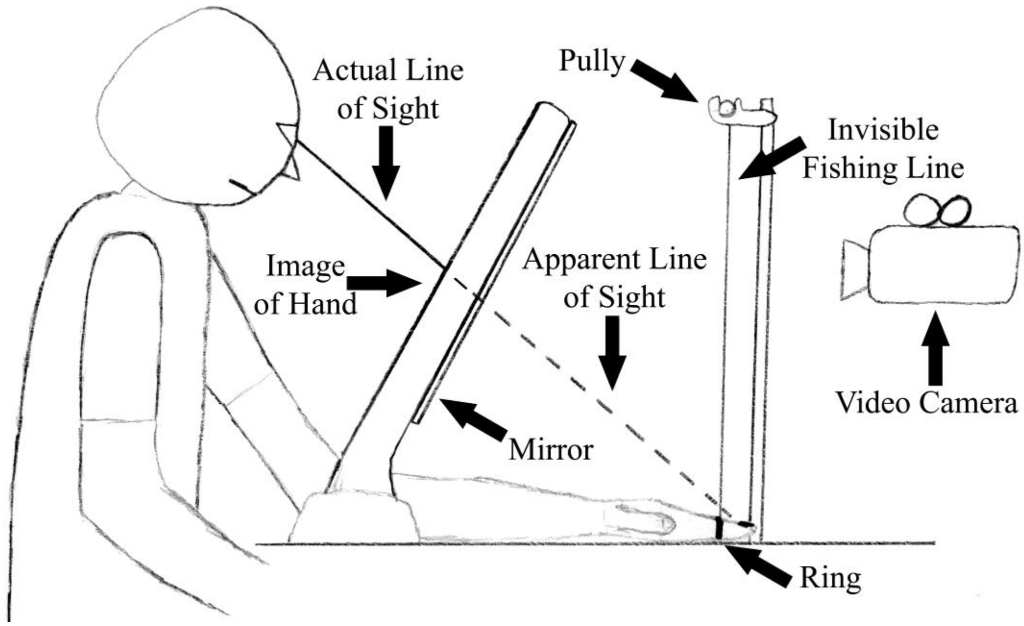
Figure 1: Experimental setup.

Figure 2: Subjective report data for ownership and agency. Ownership scores reflect the mean response to questionnaire items 1-3 (items 2 and 3 scored in reverse); agency scores reflect the mean response to questionnaire items 4-6 (item 6 scored in reverse). Error bars are one SEM.

Figure 3: Induction-type by synchrony interaction. Reaction time was selectively speeded following synchronously displayed active movements. Error bars are one SEM.

Figure 4: Effects of synchrony (difference in reaction time between asynchronous and synchronous conditions) by response hand and induction type. Synchrony effects were larger for left-hand than for right-hand responses. Error bars are one SEM.

Figure 1: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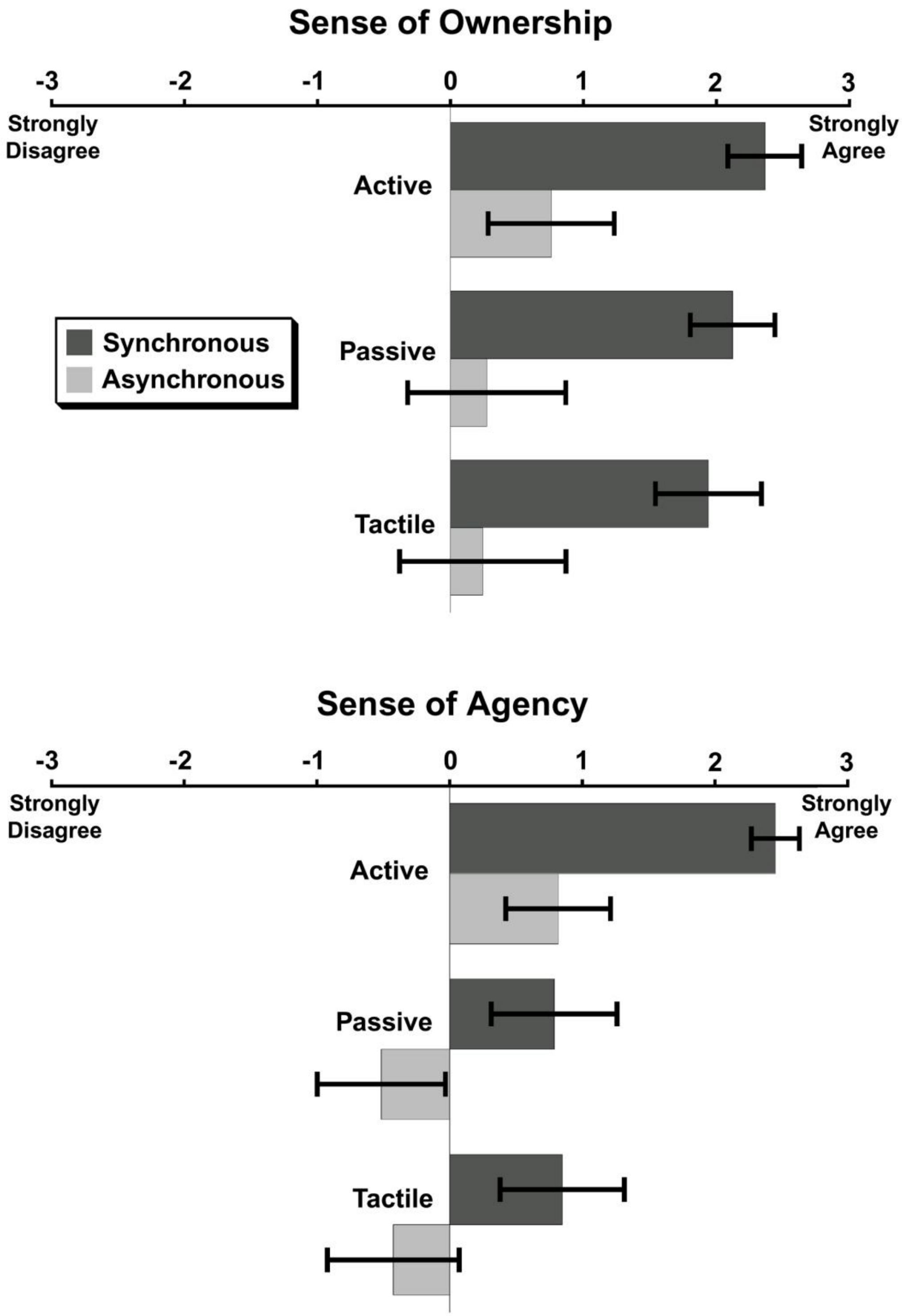
Pully
Invisible
Fishing Line
Image
of Hand
Apparent Line
of Sight
Video Camera
Mirror
Ring

Figure 2:


Sense of Ownership
-3
-2
-1
0
1
2
3
Strongly Disagree
Strongly Agree
Active
Passive
Tactile
Synchronous
Asynchronous
Sense of Agency
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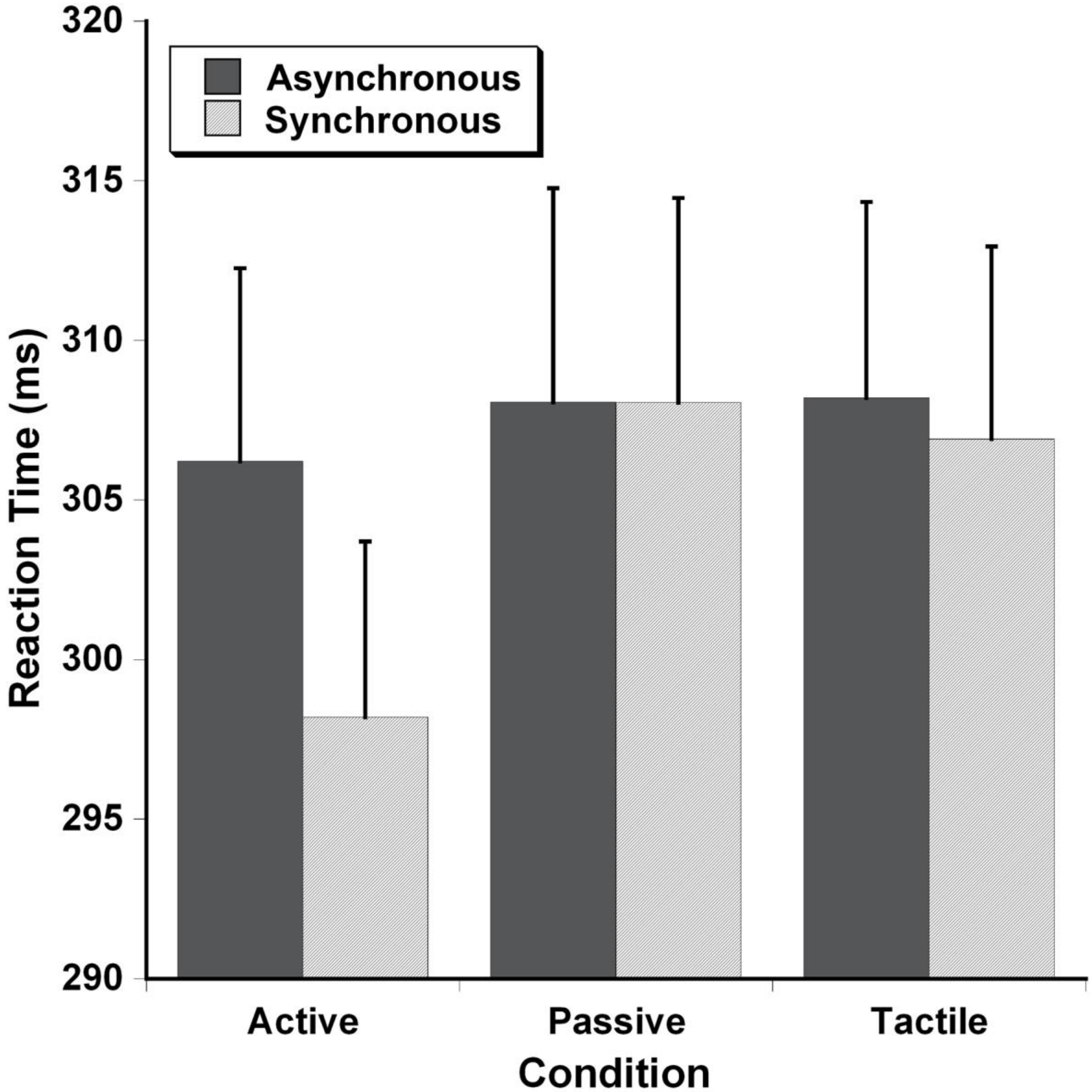
-2
-1
0
1
2
3
Strongly Disagree
Strongly Agree
Active
Passive
Tactile

Figure 3: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300
295
290
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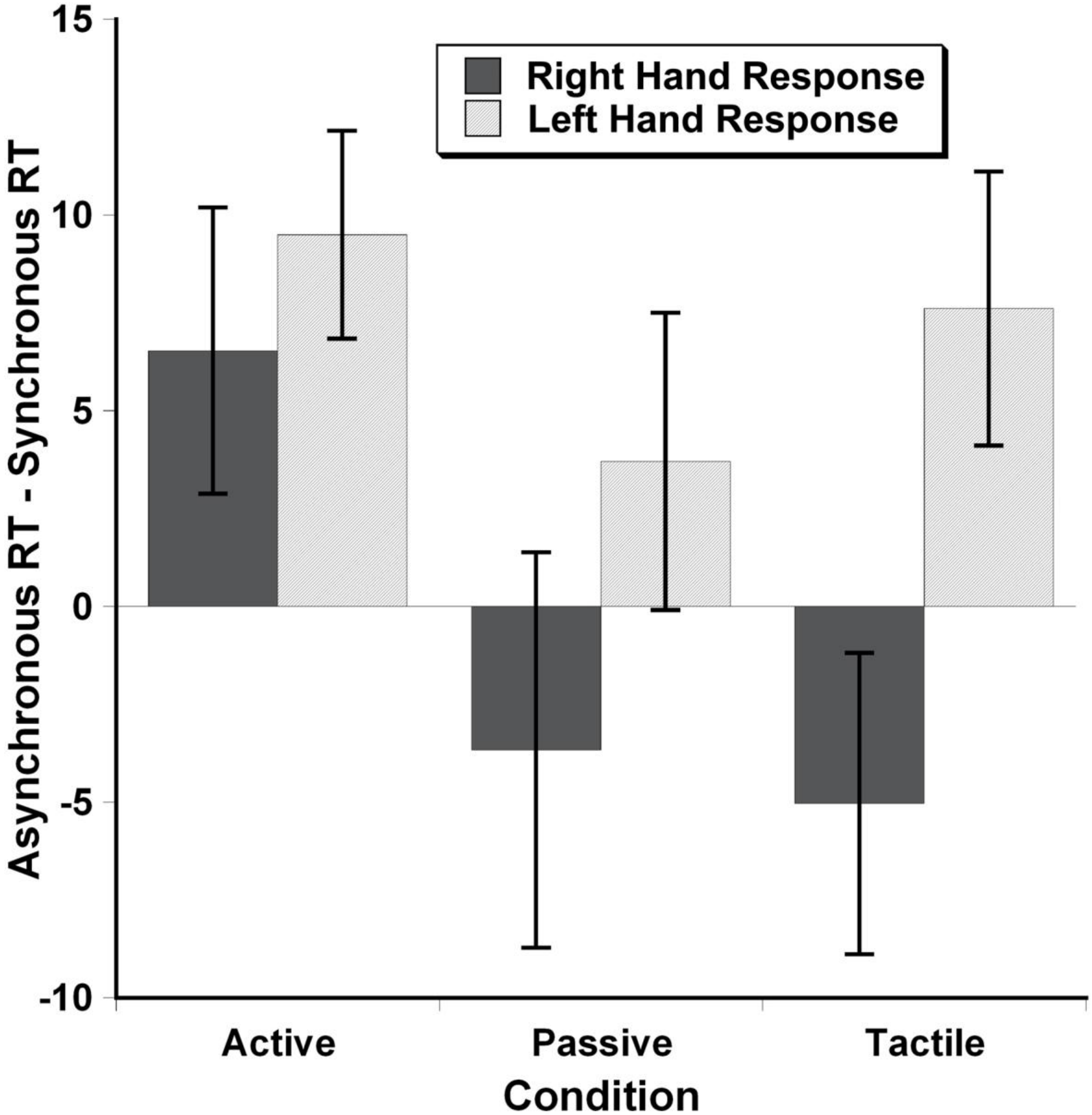
Active
Passive
Tactile
Condition

Figure 4:


Right Hand Response
Left Hand Response
Asynchronous RT - Synchronous RT
15
10
5
0
-5
-10
Active
Passive
Tactile
Condition