RESEARCH ARTICLE

"Self pop-out": agency enhances self-recognition in visual search

R. Salomon · M. Lim · O. Kannape ·
J. Llobera · O. Blanke

Abstract In real-life situations, we are often required to recognize our own movements among movements originating from other people. In social situations, these movements are often correlated (for example, when dancing or walking with others) adding considerable difficulty to self-recognition. Studies from visual search have shown that visual attention can selectively highlight specific features to make them more salient. Here, we used a novel visual search task employing virtual reality and motion tracking to test whether visual attention can use efferent information to enhance self-recognition of one's movements among four or six moving avatars. Active movements compared to passive movements allowed faster recognition of the avatar moving like the subject. Critically, search slopes were flat for the active condition but increased for passive movements, suggesting efficient search for active movements. In a second experiment, we tested the effects of using the participants' own movements temporally delayed as distractors in a self-recognition discrimination task. We replicated the results of the first experiment with more rapid self-recognition during active trials. Importantly, temporally delayed distractors increased reaction times despite being more perceptually different than the spatial distractors. The findings demonstrate the importance of agency in self-recognition and self-other discrimination from movement in social settings.

Keywords Self-recognition · Agency · Virtual reality · Body representation · Social psychology · Visual search

Introduction

Ideomotor theories claim that actions are coded in terms of their perceptual consequences (James 1890; Jeannerod 1999), suggesting that action and perception are coded in a common representational form. Accordingly, perceiving others actions may activate representations that are similar to those involved in the planning and execution of own actions. The notion of a shared representation for perception and action has received support from many studies using diverse paradigms. Perceived actions of others have been shown to prime motor actions (Brass et al. 2000) and influence ongoing actions (Kilner et al. 2007). Conversely, our own actions and action intentions have been shown to affect our perception of the actions of others. For example, Jacobs and colleagues have shown that walking interferes with our ability to discriminate perceived walking speeds (Jacobs and Shiffrar 2005). Finally, research in monkeys and in humans has shown neuronal and regional overlap in brain systems responsible for action observation and action execution, termed the "mirror neuron network" (Rizzolatti and Craighero 2004). The shared representation or common coding for perceiving and executing actions has been suggested to have important implications for understanding the intentions of others (Uddin et al. 2007); however,

R. Salomon · J. Llobera · O. Blanke
Center for Neuroprosthetics, School of Life Sciences,
Ecole Polytechnique Fédérale de Lausanne (EPFL),
Lausanne, Switzerland

R. Salomon (✉) · M. Lim · O. Kannape · J. Llobera · O. Blanke
Laboratory of Cognitive Neuroscience, Brain Mind Institute,
Ecole Polytechnique Fédérale de Lausanne (EPFL), SV BMI
LNCO AAB 2 01 (Batiment AAB) Station 15, 1015 Lausanne,
Switzerland
e-mail: roy.salomon@epfl.ch

O. Blanke
Department of Neurology, University Hospital, Geneva,
Switzerland

it poses a challenge for segregation of self-action from the perceived actions of others due to the overlapping representations. Consider a dance troupe in action. They often wear identical outfits and make similar and coordinated movements while monitoring their dance movements in a mirror. Given the strong support for overlap between own movements and those of others, how then can a dancer find her moving image among those of others? This illustrates the complexity of self-recognition (SR) which is a fundamental aspect of our self-consciousness (Bermúdez et al. 1998). Self-representation is construed from integration of multiple afferent sensory signals including visual, tactile, and proprioceptive information (Jeannerod 2003; Lenggenhager et al. 2007) and has been associated with several brain mechanisms especially in the default mode network (Gusnard et al. 2001; Salomon et al. 2009; Salomon et al. 2013). While SR is normally effortless robust and does not require attention, it has been shown to be drastically altered by brain pathology (Blanke and Mohr 2005), psychiatric illnesses (Blakemore et al. 2000) and experimental manipulations (Blanke and Metzinger 2009; Lenggenhager et al. 2007; Tsakiris et al. 2010; Salomon et al. 2012).

If indeed, perceived actions and own actions (self-actions) share common representations, it is unclear how we differentiate our own actions from those of others. One mechanism which has been suggested to assist in this segregation is the sense of agency. Self-initiated movements are accompanied by a sense of agency which is the sense that I am the one who is causing an action (Jeannerod 2003). These movements allow us to exploit the sense of agency to rapidly differentiate ourselves from other objects and people in ambiguous situations (Synofzik et al. 2008). The predominant account for our sense of agency is often referred to as the "forward model account". It posits that an "efference copy" is created when we make a movement. This "efferent copy" would be an internal representation of planned motor actions that would be compared to afferent sensory inputs (Wolpert and Kawato 1998b). Current theories of agency suggest that the sensorimotor system adjusts the weights given to efferent and afferent information based upon previous experience and the estimated noise of these signals in order to achieve optimal sensorimotor integration (Wolpert et al. 1995). Thus, if afferent information (e.g. many dancers in similar clothing and movement) contains a high degree of noise, we would expect a higher weighting for efferent information, aiding the recognition of voluntary movements versus passive movements.

Previous investigations have revealed that agency enhances SR (Salomon et al. 2009; Tsakiris et al. 2005). For example, it has previously been shown that when viewing a finger movement either actively or passively participants were at chance at a self-recognition task for the passive movements but showed successful SR for active finger movements (Tsakiris et al. 2005). Presumably, this occurs due to the availability of additional information regarding the precise timing of the movement when it is self-generated. Furthermore, the visual consequences of active movements have been shown to be perceptually salient even when they are task irrelevant (Salomon et al. 2011). Active movements have also been shown to cause changes in temporal judgments. For example, voluntary actions are judged temporally closer to their consequences than passive movements or actions performed by another person (Engbert et al. 2007). While agency is advantageous to SR, the mechanisms by which efferent and afferent signals contribute to SR in a social situation are poorly understood.

SR from movement in a social situation can be viewed as a complex situation of visual search (finding a specific target among distractors). Studies on visual search have highlighted selective visual attention, our ability to focus our perceptual capacities on a specific feature defining the search target, as the central mechanism involved in segregating targets from distractors (Duncan and Humphreys 1989; Wolfe 1994). Visual attention has been shown to be driven by both the salience of the stimuli (bottom–up) and looking for a specific predefined feature (guided or top-down search) (Yantis and Jonides 1984). Studies have shown that some features "pop-out" requiring similar search times for displays with few as well as many distractors (Wang et al. 1994; Treisman and Gelade 1980), while other targets result in "inefficient" search with longer search times for displays with more distractors. The large majority of visual search studies have focused on features defined by specific visual information (e.g. color, shape, or location) all of which are coded within the visual system (Duncan and Humphreys 1989; Wang et al. 1994). It has been suggested that guided search involves an attentional modulation of the specific feature of the search set and has been shown to enhance cortical activity in regions selective to that feature (Corbetta et al. 1990). However, integration of non-visual information such as features pertaining to movement (e.g. agency, motor, or proprioceptive information) has not, to the best of our knowledge, been tested. Here, we asked how sensorimotor cues affect visual search? Specifically, we wished to test whether visual attention can use efferent information to highlight the self among several moving targets.

We employed a novel visual search task using a combination of optical motion tracking with real-time virtual reality (VR) inverse kinematics on several moving avatars to test the contribution of agency to SR. Participants performed a visual search task in a VR environment while their right hand was moved either actively or passively by

the experimenter. They saw by means of a head-mounted display (HMD) either four or six avatars all moving their left hand. One of the avatars in the display was moving exactly like the participant while the others made movements, which were spatially deviated but synchronous in timing to those of the participant. We asked the participants to find the one avatar among the distractors, who was moving like themselves. Thus, in contrast to previous visual search studies, the available afferent visual information (and proprioceptive information) was identical for all search items, whereas additional efferent information was available only for one avatar. In the passive movement condition, no efferent information was available, thus allowing us to test directly the involvement of efferent information in SR. We predicted that SR in the active condition would be more efficient than in the passive condition and that this advantage would increase as we added additional distractors, due to the higher weighting of efferent information in the sensorimotor integration process.

Methods

Participants

Twenty healthy, right-handed volunteers (13 male, mean age = 23 years, SD = 3 years) participated in the study for pay (20 CHF per hour). Participants had normal or corrected to normal vision. All participants gave informed consent, and the study was performed in accordance with the ethical standards of the Declaration of Helsinki. The study was approved by the local ethics committee: La Commission d'ethique de la recherche Clinique de la Faculte de Biologie et de Medecine—at the University of Lausanne, Switzerland.

Motion capture

An active optical motion capture system was used for tracking and recording the participants' movements (ReActor2, Ascension Technology Corp., Burlington, VT, USA). Four infra-red markers were placed on the participants, on the back of both hands and on both shoulders. Motion capture took place in a 4.11 m × 4.11 m × 2.54 m (length × width × height) tracking arena incorporating 448 detectors positioned in the 12 bar tracking frame. Motion was captured at a sampling frequency of 30 Hz.

Character animation

The 3D character animation was created using XVR virtual reality platform (VRMedia, Pisa, Italy) which maps the infra-red markers worn by the participants onto the virtual avatar. The virtual character was visualized and animated in XVR by using a hardware accelerated library for character animation (HALCA). Stimuli were presented on a V-Real Viewer 3D SVGA head-mounted display (HMD; 800 × 600 resolution, 35 degrees field of view) worn by the participants.

Distractor avatar motions were created by the manipulation of the x- and y-axis in 3D space (reversed x-axis, reversed y-axis, reversed x- and y-axis, and exchanged x- and y-axis, and exchanged x with reversed y-axis). The overall delay of the system, including data acquisition, character animation, and visual presentation, was <80 ms which is below the detection threshold for visuomotor delays (Franck et al. 2001).

Procedure

The experiment was carried out in 4 blocks in random order, with 144 trials per block. Participants were standing upright and saw either 4 or 6 avatars on the HMD facing the participant. One avatar would move consistently with the participant's motions ("self"-avatar), while the other avatars were distractors, which made movements that were temporally identical with the participants' movements, but deviated spatially as defined by the spatial manipulations noted above. Throughout each block, participants either made continuous movements with their right arm (active condition) or their right arm were moved by the experimenter through a pulley system (passive condition; see Fig. 1). Movements in the passive condition were made by a trained experimenter (ML) mimicking the typical movements of the participant. Participants were instructed to focus on a fixation point in the middle of the screen and equidistant to the center of all the avatars displayed. The participants were asked to indicate whether the "self"-avatar was located in the upper or lower half of the screen (upper/lower; two-alternative forced-choice paradigm). They were asked to answer by using a wireless Microsoft XBOX (Microsoft Corp., USA) to give their response.

Questionnaires

To assess the subjective difficulty of the task, after the experiment, participants were asked to rate the level of difficulty (from 1 to 10) of the active and passive blocks, and the blocks with 4 and 6 avatars. Participants were also asked to estimate their level of accuracy and rate their confidence in their responses. Participants' subjective assessments of their ability to be moved passively as well as the experimenter's rating of their passivity were also collected. Participants were then debriefed about the experiment.
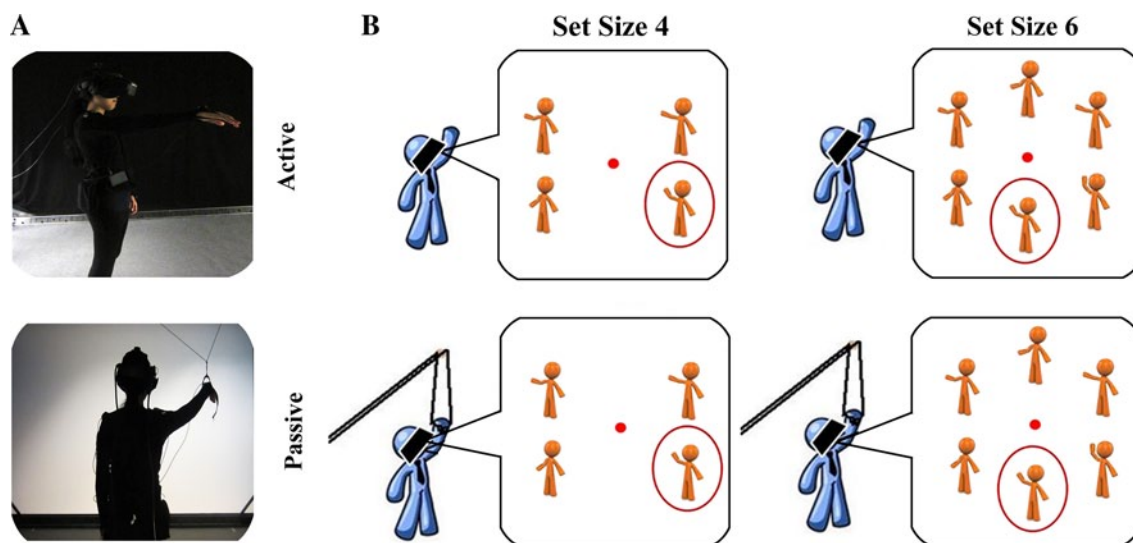
Fig. 1 Experimental design: **a** *Top*. Side view of participant wearing HMD and motion tracking suit. Bottom. Back view of participant in passive condition. Note, in passive condition, the experimenter used a pulley system to move participants' arms. **b** 2 × 2 Factorial design.

Schematic representation of stimuli in all conditions. Note that all avatars were moving synchronously with participants' movements but that all but the target one (marked here by *red circle*) had spatial deviations introduced. *Small central red dot* indicates the fixation point

Movement analysis

To ensure that the movements made during the active and passive blocks were comparable, we collected the motion tracking data during the experiment. We analyzed each participant's motion capture data for each block and for each condition type we calculated the speed, range, location, and acceleration for each of the three-dimensions (x, y and z) as well as the overall curvature. Paired t tests were calculated for the active versus passive movement types.

Statistical analysis

Reaction times (RTs) and accuracy for the SR task were analyzed by means of a repeated measure 2 × 2 ANOVA [set size (4 vs. 6) × movement type (active vs. passive)]. Trials with RTs more or less than 2.5 standard deviations from the participant's mean were discarded (<6 % of trials). RT was calculated only for trials with correct responses (96.9 % of trials). Post hoc comparisons were done using Newman–Keuls test.

Results

Reaction times

Reaction times analysis revealed a main effect for set size ($F(1, 19) = 24.68$, $p = .00009$ $\eta^2 = 0.565$), indicating that responses on the smaller set size were faster (M = 2.98,

SE = 0.21) than in the larger set size (M = 3.85, SE = 0.26). The effect of movement type was also significant ($F(1, 19) = 12.29$, $p = .0023$ $\eta^2 = 0.393$) with active trials showing shorter RTs (M = 3.09, SE = 0.26) than the passive ones (M = 3.74, SE = 0.22). Critically, we also found a significant interaction between the two factors ($F(1, 19) = 4.90$, $p = .039$ $\eta^2 = 0.205$). Follow-up comparisons showed that increasing the set size slowed search when the target was not controlled by the participant (passive condition), with a 1291-ms increase in RT in the 6-relative to 4-item condition ($F(1,19) = 23.985$, $p < 0.0001$ Cohen's $d = 11.005$). In contrast, when the avatars' movements were controlled by the participant (active condition), there was a much smaller slowing of RTs (450 ms.), which was not significant ($F < 1$). These data suggest that search performance is independent of set size when the target motion is controlled by the participant, but dependent on set size during passive movements (see Fig. 2).

To test for possible learning effects during the blocks, we divided each block into three epochs of 48 trials. We analyzed the RT using a repeated measure 2 × 2 × 3 ANOVA (set size (4 vs. 6) × movement type (active vs. passive) × epoch (first/second/third). The results revealed a main effect of epoch ($F(2, 38) = 6.2462$, $p = .00451$ $\eta^2 = 0.24$). Post hoc analysis revealed that this effect was driven by significantly higher RTs in the first epoch (M = 3.66, SE = 0.26) than in the second (M = 3.42, SE = 0.23, $p < 0.03$) and third epochs (M = 3.28, SE = 0.21, $p < 0.003$). No interaction of epoch with any of the other conditions reached significance (all $p > 0.12$).
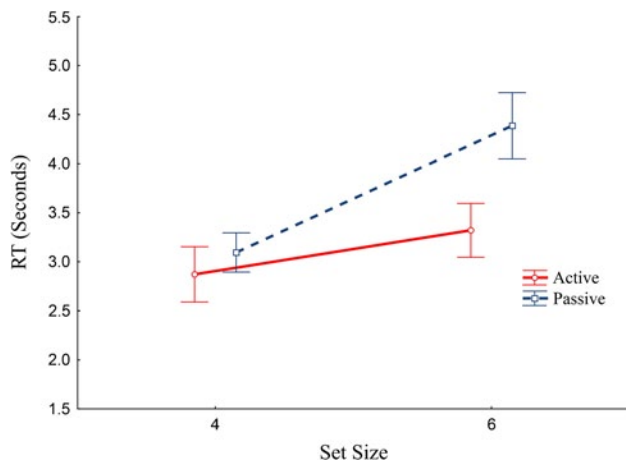
Fig. 2 Reaction times by condition. RTs for all conditions. Note that search slope (difference between set size 4 and 6) for passive movements ($p < 0.0001$) is much steeper than for active movements (n.s). *Error bars* denote SE

Fig. 3 Difficulty ratings by condition. Participants' post hoc difficulty ratings of the task by condition type. Note that participants were unaware of the advantage during the active condition but were sensitive to the additional difficulty in the larger set size. *Error bars* denote SE

Accuracy

Mean accuracy was 96.9 %. A main effect for set size was found ($F(1, 19) = 7.3862$, $p = .01366$, $\eta^2 = 0.28$) with more errors in the larger set size (M = 96.02, SE = 0.91) than in the smaller set size (M = 97.89, SE = 0.42). No other effects were found (all $F < 1$).

To test for possible learning effects during the blocks, we divided each block into three epochs of 48 trials. We analyzed the accuracy rates using a repeated measure $2 \times 2 \times 3$ ANOVA (set size (4 vs. 6) $\times$ movement type (active vs. passive) $\times$ epoch (first/second/third). The results revealed a main effect of epoch ($F(2, 38) = 3.3610$, $p = .04529$, $\eta^2 = 0.15$). Post hoc analysis revealed that this effect was driven by significantly lower accuracy rates in the first epoch (M = 96.48 SE = 0.69) than in the second (M = 97.22, SE = 0.56, $p < 0.03$) and third epochs M = 97.23 SE = 0.56, $p < 0.03$). No interactions between epoch and other conditions were found (all $p > 0.4$).

Difficulty ratings

Post-experimental ratings of the difficulty of the different condition types revealed that participants found the conditions with larger set size to be more difficult than the conditions with the smaller set size (M = 6.79, SE = 0.36 and M = 4.58, SE = 0.32, respectively, $t = 4.9$, $p = 0.000008$, Cohen's $d = 2.24$) (see Fig. 3). No difference was found in the difficulty ratings for active and passive movement conditions (M = 5.58, SE = 0.44 and M = 5.58, SE = 0.50, respectively, $t < 1$, n.s).

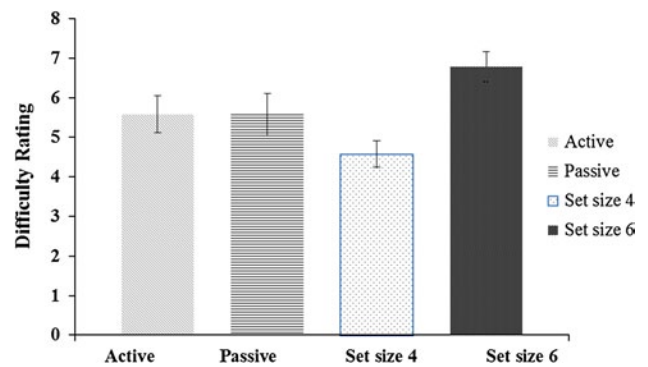Participants' post-experimental assessment of their accuracy showed a high correlation with their measured accuracy rates ($r = 0.57$, $p = 0.0041$). Furthermore, participants' judgments of their confidence in their responses (M = 7.45, SE = 0.28) strongly correlated with their perceived accuracy ($r = 0.7327$, $p = 0.00004$), suggesting that participants had good insight into their task performance.

Movement analysis

The results of the analysis of the motion capture data indicated no significant differences in speed, range, or location for any of the dimensions (all $p > 0.2$) or any difference in curvature ($p > 0.5$). Finally, subjective ratings of their ability to remain passive and release control in the passive blocks were high (M = 8.04, SE = 0.25) as were the corresponding ratings of the experimenter (M = 8.58). These ratings also showed a high correlation $r = 0.57$, $p = 0.0042$. These measures suggest that participants were able to allow passive movement of their hand and did not make self-movements during the passive blocks.

Discussion

The results of experiment 1 show that when the avatar's movements were actively controlled by the participant's self-movements, reaction times were shorter and did not increase as the number of distractors in the search display increased. However, reaction times for SR during passive movements increased with additional distractors. The inclusion of additional distractors in the display caused a significant and proportional increase in the RTs only in the passive condition suggesting a serial search strategy. Conversely, the additional distractors added in the active condition had a non-significant impact on the RTs showing a flat search slope, which suggests a parallel search capability.

As the results showed a strong effect of set size on self-recognition, we were interested if these results were related only to a visual search context or would they be present in a discrimination task using only two avatars. Additionally, we wanted to compare the effects of distractors using the participants' own movements delayed in time.

Experiment 2

Introduction

Movements which are part of one's own motor repertoire have been shown to be processed differently than other's movements (Calvo-Merino et al. 2005; Casile and Giese 2006). For example, Casile and Giese (2006) showed that non-visual motor training of novel movements improved perceptual discrimination following the training. This suggests that movements that are part of our motor repertoire are processed differently. We therefore hypothesized that using the participants' own movements with a small temporal delay as a distractor would increase the difficulty of SR compared to spatial distractors. Hence, to test the effects of temporal delays and further test the replicability and robustness of our results, we performed another experiment in which only two avatars were presented. As in the primary experiment, one avatar's motion was identical to that of the participant's. The second avatar's motion was either the participant's motion with a spatial deviation (as in primary experiment) or the participant's motion delayed by 1, 2 or 3 s. We expected to replicate the active versus passive difference for self-recognition. We therefore hypothesized that the distractors which are the participant's own movements delayed in time would, despite being perceptually more different than the spatial deviations (due to having both a spatial incongruence and a temporal asynchrony from the participant's current motions), cause larger interference to self-recognition.

Methods

Participants

Twenty-four, right-handed participants (9 male, mean age = 22.5 years, SD = 2 years) participated in the study for pay (20 CHF per hour). Participants had normal or corrected to normal vision. All participants gave informed consent, and the study was performed in accordance with the ethical standards of the Declaration of Helsinki. The study was approved by the local ethics committee: La Commission d'ethique de la recherche Clinique de la Faculte de Biologie et de Medecine—at the University of Lausanne, Switzerland.

Experimental design

The experimental setup was identical to that of the primary experiment except for the number of avatars (2 only, vs. 4 or 6 in main experiment), and the type of distractors used. The spatial distractors were taken from the first experiment and included x-axis reversal, y-axis reversal, and x- & y-axis reversal. The temporal distractors were the participants' own movements recorded in a buffer and then projected to the avatar. The avatars were placed to the left and the right of the fixation cross. The location of the self-controlled avatar and the distractor were randomized as were the order of active and passive blocks.

Results

Reaction times were analyzed as in primary experiment and then subjected to a repeated measures ANOVA with factors movement type (active vs. passive) × distractor type (spatial vs. temporal). The results showed an effect of movement type ($F(1,23) = 5.6$; $p = 0.02$, $\eta^2 = 0.19$), active trials showing shorter RTs (M = 2.91, SE = 0.17) than the passive ones (M = 3.33, SE = 0.28). The effect of distractor type was also significant ($F(1,23) = 7.1$; $p = 0.01$, $\eta^2 = 0.23$), with trials with a spatial distractor showing shorter RTs (M = 3.01, SE = 0.2) than the passive ones (M = 3.23, SE = 0.23) (Fig. 4). No interaction between the two factors was found $p > 0.1$.
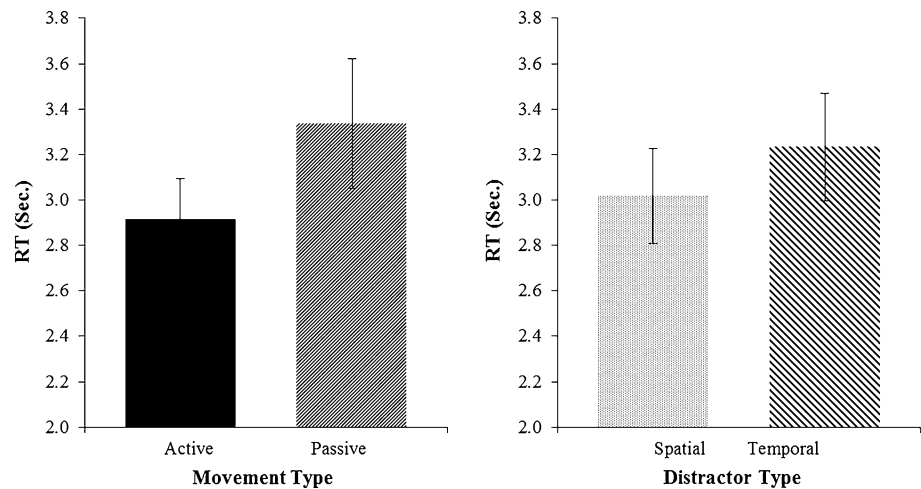
Accuracy was analyzed using a similar ANOVA as RTs. Only the effect of distractor type was significant ($F(1,23) = 5.4$, $p = 0.02$, $\eta^2 = 0.19$) with higher accuracy for the trials in which the distractor was a spatial distractor (M = 0.95, SE = 0.006) compared with trials in which the distractor was a temporal one (M = 0.92, SE = 0.01).

Comparison of the participants' movements with those of the distractors showed that for the spatial distractors (as used in primary experiment), there was a strong correlation for both velocity and acceleration changes (~0.9). However, the temporally shifted distractors showed a low correlation with the participants' movements (~0.1).

Discussion

As predicted, we found more rapid self-recognition when the participant controls the avatar's movements. This was found in a display of only two avatars, thus extending the results of the primary experiment to a smaller display size. Furthermore, the results showed that the temporal distractors which are perceptually more different than the spatial ones, as they are not temporally synchronized to the subjects' motion, increased the difficulty of self-recognition as shown in both accuracy and reaction times. This broadens the finding of the primary experiment to show that

they generalize to other distractor types. Additionally, this finding extends previous findings showing differential recognition for previously authored actions (Knoblich and Prinz 2001; Salomon et al. 2009), demonstrating that self-authored movements are more distracting than more visually similar movements in the context of self-recognition.

General discussion

The present results show that when the avatar's movements were actively controlled by the participant's self-movements, reaction times were shorter and did not increase as the number of distractors in the search display increased. As only the movements of one avatar were spatially congruent and self-related, we refer to this absence of increased search duration as "self pop-out." Conversely, reaction times for avatar movements that were experimenter-generated, passive movements, of the participant were associated with increased reaction times when increasing the number of distractors. The latter data are thus compatible with a more serial search in the passive condition. Thus, the participants were less susceptible to social noise introduced by the addition of distractors (avatars) when they controlled the movements. This is to the best of our knowledge the first demonstration of the effects of active movement on SR in a full body setting and extends findings of agency enhancing SR (Tsakiris et al. 2005). These previous experiments investigated the effects of agency on a single stimulus, thus not addressing the possible competition arising from several concurrent moving humans for representation within the sensorimotor system, which is the case in social interactions. The current findings strengthen the suggested role of efferent information as a factor, which allows segregation of representations of self and other within the common coding framework.

Previous research on visual search has highlighted the processes underlying guided visual search for targets defined by unique features such as color, shape, or orientation among distractors. Evidence has shown that such targets can be processed automatically and pre-attentively and this even applies to targets defined by a more complex conjunction of several features (Wolfe 1994, 1998; e.g. Duncan and Humphreys 1989). However, all these previous target displays were different from the present experiment in that the target visually differed from the distractors (and this could be seen be the experimental subject, but also by any other onlooker). This was not the case in the present experiment, where the difference can only be detected by the experimental subject who was either actively or passively moving the target among differently moved distractor items. The difference between target and distractors was thus not visual, but visuo-motor-proprioceptive (active condition) or visuo-proprioceptive (passive condition) in nature, extending the domain of visual search to agency, self-related processing and visuo-motor conflicts (Tsakiris et al. 2005; Jeannerod 2004).

Our task required the subjects to find a target defined by a conjunction of crossmodal properties (matching visual and proprioceptive information), and thus, we would expect an inefficient search for such a complex target. Yet, if the defining feature of the target is perceptually available to the visual modality and can be boosted by top-down attentional mechanisms, this feature may enjoy enhanced saliency. The results of our experiment showed that only the active movement condition allows this increased saliency, suggesting that efferent information can be used to enhance visual perception. This extends previous findings showing a causal influence of action on visual perception, for example, showing effects of action intentions (Bekkering and Neggers 2002), task irrelevant movement (Salomon et al. 2011), and movement selection (van Elk et al. 2010) on perception.

While the SR advantage in the active condition can be attributed to agency-related efferent information, several alternative explanations may be considered. As in the active condition, subjects were required to initiate movements, it could be argued that they were more engaged in the task and therefore more attentive during this condition leading to faster RTs. Alternatively, one of the reviewers suggested that in the passive condition, participants were required to relax their arm to allow it to be moved by the experimenter, which may have also required additional attentional resources. However, our own data suggest that this is not the case. First, while there was a main effect with faster RTs in the active condition, this was driven by the interaction between the active condition and the larger set size, with a non-significant difference between active and passive RTs in the smaller set size of experiment 1 (Fig. 2). Thus, if RTs were modulated by stronger attentional engagement in the active condition, we would expect this to affect both set sizes. Second, difficulty ratings from participants showed that they did not perceive any differences in the difficulty of the active and passive conditions. This despite noting the differences in task difficulty related to the number of distractors (Fig. 3). Finally, while the relaxation of the hand in the passive condition could be suggested to require additional attentional resources, the active condition could also be considered a dual task as participants had to both complete the SR task and actively move their hand, compared to the passive condition in which they could focus their attention on the SR task alone. This was reflected in the free reports of several participants' (6/20) who specifically claimed that the passive condition was easier due to the dual task required in the active condition, while no participants reported allocating any attentional resources to the relaxation of the hand in the passive condition. Thus, we believe that the SR advantage in the active condition is not related to differences in attentional load between the active and passive conditions.

Additionally, the current paradigm has several advantages: As both the subject movements and the distractor movements were presented on a virtual avatar, there were no morphological differences in the body representation to assist SR. Second, the inclusion of a veridical presentation of the participant's movements is contained in the display. This makes the SR decision a true objective match between the participants' movements and the targets' movements rather than a subjective judgment of the degree of compatibility as in paradigms using forced-choice options for deviated feedback. Moreover, the inclusion of several moving avatars on each trial makes the results relevant for discrimination of the self from others during social interactions. Finally, many studies on agency show that temporal cues are of paramount importance to recognizing our own movements (e.g. another person could perfectly mimic our movements spatially but not temporally) (Flach et al. 2004; Leube et al. 2003). No temporal cues were present in the present study, as all avatars' movements were temporally synchronized to the movements of our participants by the motion capture system. Finally, the virtual reality environment allowed us to the effect of agency using realistic full body representations (as in Kannape et al. 2010) rather than abstract stimuli (e.g. Farrer and Frith 2002) or specific images of limbs and other body parts (Salomon et al. 2009).

The current experiment tested SR from movement in a social context. As illustrated in the example of the dance troupe, we often rely on information regarding our actions to be able to recognize ourselves among other humans. In a social context, the brain must choose between several competing images to find the best match to its' own movements. The current theories suggesting shared cognitive representations between action perception and action control (Hommel et al. 2001) as well as their neural substrates (Gazzola and Keysers 2009) pose a difficulty in ascribing the authorship of action to oneself or another agent (de Vignemont and Fourneret 2004). Our results suggest that efferent information is central to self-recognition from motion. This is in line with the idea of forward models (predictive models of the future state of the system) being essential to our sense of agency (Blakemore et al. 2002; Wolpert and Kawato 1998a; Kannape and Blanke 2012) and affecting our self-representation.

Conflict of interest None

References

Bekkering H, Neggers SFW (2002) Visual search is modulated by action intentions. Psychol Sci 13(4):370

Bermúdez JL, Marcel AJ, Eilan N (1998) The body and the self. The MIT Press, Cambridge

Blakemore S, Smith J, Steel R, Johnstone E, Frith C (2000) The perception of self-produced sensory stimuli in patients with auditory hallucinations and passivity experiences: evidence for a breakdown in self-monitoring. Psychol Med 30(05):1131–1139

Blakemore S, Wolpert D, Frith C (2002) Abnormalities in the awareness of action. Trends Cogn Sci 6(6):237–242

Blanke O, Metzinger T (2009) Full-body illusions and minimal phenomenal selfhood. Trends Cogn Sci 13(1):7–13

Blanke O, Mohr C (2005) Out-of-body experience, heautoscopy, and autoscopic hallucination of neurological origin Implications for neurocognitive mechanisms of corporeal awareness and self-consciousness. Brain Res Rev 50(1):184–199

Brass M, Bekkering H, Wohlschläger A, Prinz W (2000) Compatibility between observed and executed finger movements: comparing symbolic, spatial, and imitative cues. Brain Cogn 44(2):124–143

Calvo-Merino B, Glaser D, Grezes J, Passingham R, Haggard P (2005) Action observation and acquired motor skills: an fMRI study with expert dancers. Cereb Cortex 15(8):1243

Casile A, Giese MA (2006) Nonvisual motor training influences biological motion perception. Curr Biol 16(1):69–74. doi:10.1016/j.cub.2005.10.071

Corbetta M, Miezin FM, Dobmeyer S, Shulman GL, Petersen SE (1990) Attentional modulation of neural processing of shape, color, and velocity in humans. Science 248(4962):1556

de Vignemont F, Fourneret P (2004) The sense of agency: a philosophical and empirical review of the "Who" system. Conscious Cogn 13(1):1–19. doi:10.1016/s1053-8100(03)00022-9

Duncan J, Humphreys GW (1989) Visual search and stimulus similarity. Psychol Rev 96(3):433

Engbert K, Wohlschläger A, Thomas R, Haggard P (2007) Agency, subjective time, and other minds. J Exp Psychol Hum Percept Perform 33(6):1261

Farrer C, Frith C (2002) Experiencing oneself vs another person as being the cause of an action: the neural correlates of the experience of agency. Neuroimage 15(3):596–603

Flach R, Knoblich G, Prinz W (2004) Recognizing one's own clapping: the role of temporal cues. Psychol Res 69(1):147–156

Franck N, Farrer C, Georgieff N, Marie-Cardine M, Daléry J, d'Amato T, Jeannerod M (2001) Defective recognition of one's own actions in patients with schizophrenia. Am J Psychiatry 158(3):454–459

Gazzola V, Keysers C (2009) The observation and execution of actions share motor and somatosensory voxels in all tested subjects: single-subject analyses of unsmoothed fMRI data. Cereb Cortex 19(6):1239–1255. doi:10.1093/cercor/bhn181

Gusnard D, Akbudak E, Shulman G, Raichle M (2001) Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. Proc Natl Acad Sci USA 98(7):4259

Hommel B, Musseler J, Aschersleben G, Prinz W (2001) The theory of event coding (TEC): a framework for perception and action planning. Behav Brain Sci 24(5):849–877

Jacobs A, Shiffrar M (2005) Walking perception by walking observers. J Exp Psychol Hum Percept Perform 31(1):157

James W (1890) The principles of psychology. Dover Publications, New York

Jeannerod M (1999) The 25th Bartlett Lecture: to act or not to act: perspectives on the representation of actions. Q J Exp Psychol 52(1):1–29

Jeannerod M (2003) The mechanism of self-recognition in humans. Behav Brain Res 142(1–2):1–15

Jeannerod M (2004) Visual and action cues contribute to the self-other distinction. Nat Neurosci 7(5):422–423

Kannape O, Blanke O (2012) Agency, gait and self-consciousness. Int J Psycho 83(2):191–199

Kannape O, Schwabe L, Tadi T, Blanke O (2010) The limits of agency in walking humans. Neuropsychologia 48(6):1628–1636

Kilner J, Hamilton AFC, Blakemore SJ (2007) Interference effect of observed human movement on action is due to velocity profile of biological motion. Soc Neurosci 2(3–4):158–166

Knoblich G, Prinz W (2001) Recognition of self-generated actions from kinematic displays of drawing. J Exp Psychol Hum Percept Perform 27(2):456

Lenggenhager B, Tadi T, Metzinger T, Blanke O (2007) Video ergo sum: manipulating bodily self-consciousness. Science 317(5841):1096

Leube D, Knoblich G, Erb M, Grodd W, Bartels M, Kircher T (2003) The neural correlates of perceiving one's own movements. Neuroimage 20(4):2084–2090

Rizzolatti G, Craighero L (2004) The mirror-neuron system. Annu Rev Neurosci 27:169–192

Salomon R, Malach R, Lamy D (2009) Involvement of the intrinsic/default system in movement-related self recognition. PLoS One 4(10):e7527

Salomon R, Szpiro-Grinberg S, Lamy D (2011) Self-motion holds a special status in visual processing. PLoS One 6(10):e24347. doi:10.1371/journal.pone.0024347

Salomon R, van Elk M, Aspell JE, Blanke O (2012) I feel who I see: Visual body identity affects visual–tactile integration in peripersonal space. Conscious Cogn 21(3):1355–1364

Salomon R, Ruby-Levi D, Malach R (2013) Deconstructing the default: cortical subdivision of the default mode/intrinsic system during self-related processing. Hum Brain Mapp (in press)

Synofzik M, Vosgerau G, Newen A (2008) I move, therefore I am: a new theoretical framework to investigate agency and ownership. Conscious Cogn 17(2):411–424

Treisman AM, Gelade G (1980) A feature-integration theory of attention. Cogn Psychol 12(1):97–136

Tsakiris M, Haggard P, Franck N, Mainy N, Sirigu A (2005) A specific role for efferent information in self-recognition. Cognition 96(3):215–231

Tsakiris M, Longo MR, Haggard P (2010) Having a body versus moving your body: neural signatures of agency and body-ownership. Neuropsychologia 48(9):2740–2749

Uddin L, Iacoboni M, Lange C, Keenan J (2007) The self and social cognition: the role of cortical midline structures and mirror neurons. Trends Cogn Sci 11(4):153–157

van Elk M, van Schie HT, Neggers SFW, Bekkering H (2010) Neural and temporal dynamics underlying visual selection for action. J Neurophysiol 104(2):972

Wang Q, Cavanagh P, Green M (1994) Familiarity and pop-out in visual search. Atten Percept Psychophys 56(5):495–500

Wolfe JM (1994) Guided search 2.0: a revised model of visual search. Psychon Bull Rev 1(2):202–238

Wolfe JM (1998) Visual search. Attention 1:13–73

Wolpert D, Kawato M (1998a) Multiple paired forward and inverse models for motor control. Neural Netw 11(7–8):1317–1329

Wolpert DM, Kawato M (1998b) Multiple paired forward and inverse models for motor control. Neural Netw 11(7–8):1317–1329

Wolpert DM, Ghahramani Z, Jordan MI (1995) An internal model for sensorimotor integration. Science 269(5232):1880

Yantis S, Jonides J (1984) Abrupt visual onsets and selective attention: evidence from visual search. J Exp Psychol Hum Percept Perform 10(5):601–621