Eye gaze metrics reflect a shared motor representation for action observation and movement imagery

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RUNNING HEAD: Congruence between motor simulation states

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Abstract

Action observation (AO) and movement imagery (MI) have been reported to share

similar neural networks. This study investigated the congruency between AO and MI using

the eye gaze metrics, dwell time and fixation number. A simple reach-grasp-place arm

movement was observed and, in a second condition, imagined where the movement was

presented from the first person perspective (1PP) and the third person perspective (3PP).

Dwell time and number of fixations were calculated for whole scene and regions of interest

(ROIs). For whole scene, no significant differences were found in the number of fixations for

condition (AO, MI) or perspective. Dwell time, however, was significantly longer in AO than

MI. For ROIs, the number of fixations was significantly greater in 1PP than 3PP. The data

provide support for congruence between motor simulation states but also indicate some

functional differences.

Key words: action observation; imagery; simulation hypothesis; eye gaze; perspective.

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1. Introduction

Contemporary evidence from the neuroscience literature suggests that action observation (AO) and movement imagery (MI) share parts of a similar neural network (Grézes & Decety, 2001). Specifically, activation of motor cortex and ventral parts of premotor cortex have been reported during observation of an agent's actions (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995), as well as motor imagery (Gerardin et al., 2000). Considering that there is strong support for congruency between action execution and AO, and action execution and MI, there is limited research that demonstrates congruence between MI and AO. The simulation hypothesis (Jeannerod, 2001) suggests that intended action, MI and AO are driven by a similar, but not identical, activation of the motor system. The theory postulates that the simulation states access a shared motor representation for a given task. This mutual access suggests that the motor pathways associated with one simulated action may be enhanced via any of the other simulation states through a process of Hebbian learning (Hebb, 1949). Although the extent of the shared neural overlap is the subject of current debate (Vul, Harris, Winkielman, & Pahler, 2009), convincing evidence from brain imaging studies supports the existence of, at least a partial neural overlap between the simulation states (Decety, 1996).

The determination of the shared neural overlap in humans was preceded by the discovery of a particular subset of visuomotor neurons in area F5 of the premotor cortex in macaque monkeys (Rizzolatti et al., 1988). These neurons, referred to as 'mirror neurons' were found to discharge when the macaque either observed or performed a goal-directed motor act. Using functional magnetic resonance imaging (fMRI), Iacoboni et al. (Iacoboni et al., 1999) highlighted their anatomical location in humans and stated that they were homologous to those of the macaque. Further, using transcranial magnetic stimulation (TMS), Fadiga, Fogassi, Pavesi and Rizzolatti (1995) observed increased motor evoked potentials

(MEPs) in the human motor cortex during observation of goal-directed movements, they also concluded that an action-observation matching system was present in humans.

An indirect approach that offers an objective and dynamic marker of neural activity during MI is the study of gaze behaviour (Henderson, 2003). Recording eye movements provides an unobtrusive, sensitive, real-time behavioural index of on-going visual and cognitive processing (Liversedge & Findlay, 2000). Furthermore, both fixation location and duration characteristics are thought to be indicative of the perceptual strategy used for the action/behaviour in question. Specifically, foveal fixations indicate critical task-related cues, whereas fixation duration/dwell time reflects the information-processing demands of the task. It is suggested that if an image is a reinstatement of the perceptual process then it should include similar eye movements and be constructed in a similar manner (Hebb, 1968). Brandt and Stark (Brandt & Stark, 1997) demonstrated this phenomenon by comparing scanpaths during visual imagery and a previously viewed static scene. Although comparable eye movements were observed there was a 20% increase in fixation duration and smaller fixation patterns. These findings were later corroborated by Laeng and Teodorescu (Laeng & Teodorescu, 2002), who found visual scanpaths during perception to be highly correlated to those during imagery, of the same visual scene. These findings provide further support for the idea of congruence between AO and MI, with the manifestation of similar, but not identical, eye movement patterns being evidence of a shared neural network.

Further support for the concept has been provided by Spivey and Geng (Spivey & Geng, 2001), who recorded eye movements whilst participants listened to auditory scene descriptions whilst facing a blank screen. Participants were not aware that their eye movements were being recorded and were given no instruction to fixate on any particular area. Observers tended to make saccades in the same directions as the spatiotemporal dynamics of the described object. These findings support the theory that when people are

imaging complex events, they activate the same perceptual-motor mechanisms used during observation of the event. Comparable results have been reported in motion imagery (de'Sperati & Santandrea, 2005) and motor imagery (Heremans, Helsen, & Feys, 2008) tasks.

Heremans et al. (Heremans et al., 2008) examined the physical execution and visual motor imagery of a cyclical aiming task using eye movement registration. Their results showed that 89% of participants made task-related eye movements during imagery with the eyes open and 84% did so during imagery with eyes closed. Furthermore, both the number and amplitude of the eye movements during imagery closely resembled those of eye movements made during the physical execution of the task. These data suggest that the coupling between neural patterns for eye and hand movements remains intact when hand movements are either imagined or physically executed. In a follow up study (Heremans et al., in press), Heremans et al. reported that eye movements during MI assisted movement accuracy but did not affect the temporal parameters of the action. In partial support of these findings, Gueugneau et al. (Gueugneau, Crognier, & Papaxanthis, 2008) report that while the temporal congruency between action execution and MI is not affected by the presence, or absence, of eye movement, the presence of saccades has a facilitation effect on the movement duration in both action execution and MI. It would appear that eye movement data could be used as an objective technique to evaluate motor imagery ability and improve the effectiveness of an imagery intervention. In the current paper, we extended this previous work by examining whether the congruency in eye movement metrics reported between action execution and motor imagery (Heremans et al., 2008), exists between AO and MI of a reach-grasp-place movement.

To progress these ideas and concepts, this paper also reports an examination of visual perspective influences on AO and MI congruence. The influence of perspective on imagery

remains unclear (Morris, Spittle, & Watt, 2005), and it is an area that has remained relatively unexplored. Visual perspective typically describes the viewpoint of an action but can also include the agent of the behaviour being viewed, i.e. self or other. First person perspective (1PP) is associated with the agent (self or other) performing the action. In contrast, third person perspective (3PP) is associated with the agent, in this case other, rather than self or other, being observed when performing the action (Holmes & Calmels, 2008). While not identical, common areas of cortical activation have been reported in 1PP and 3PP (Ruby & Decety, 2001). Using positron emission tomography (PET), Ruby and Decety (Ruby & Decety, 2001) reported that neural function during mental imagery was differentiated by perspective. Using TMS, Fourkas et al. (Fourkas, Avenanti, Urgesi, & Aglioti, 2006) observed increases in MEPs during visual imagery of finger abduction from both a 1PP and a 3PP, with larger MEPs recorded in the 1PP. In contrast, when MI is employed for observational learning, the sports psychology literature suggests imagery from a 3PP is most effective (White & Hardy, 1995); novice athletes initially use imagery from a 3PP to make approximations of the desired movement, progressing to 1PP imagery when the basic skill is acquired.

The present paper had two aims. First, we examined the similarity of eye movements between AO and MI, with the specific aim of determining whether congruency, in this metric, exists between the simulation states. Second, we examine the effect of visual perspective on the congruency of eye movements between AO and MI. Based on previous research using eye movement metrics, it was predicted that there would be significant congruency between AO and MI (Gueugneau et al., 2008; Heremans et al., 2008; Heremans et al., in press). Due to the ambiguity of previous findings we made no predictions regarding the effect of visual perspective on the congruency of eye movements between the two conditions.

2. Materials and methods

2.1. Participants

A sample of twenty-six participants were recruited for the study, however, four participants were excluded from the analysis because of luminance errors, and 3 made no task related eye movements. These exclusion rates are consistent with previous studies (Heremans et al., 2009; Rodionov, Zislin, & Elidan, 2004). The nineteen remaining participants (age: 37.89 ± 9.5 years, ten females) all had normal or corrected to normal vision and were assessed using the Edinburgh Handedness Inventory; all participants were right handed (mean laterality index: 94.41 ± 8.41) (Oldfield, 1971). Participants were informed that the study aimed to investigate memory function in tasks of varying complexity. The local institutional ethics committee approved the study and participants provided written informed consent prior to the study.

2.2. Apparatus

Eye movements were recorded using the Applied Science Laboratories (ASL) Mobile Eye system (Bedford, Massachusetts). The system uses a method known as 'dark pupil tracking', which uses the relationship between the pupil and a reflection from the cornea to calculate point of gaze in relation to an external scene camera. The system computes the relationship between the pupil and corneal to locate gaze within a scene at a sampling rate of 30Hz. The equipment has a system accuracy of 0.5 ° of visual angle, a resolution of 0.10 ° of visual angle, and a visual range of 50 ° horizontal and 40 ° vertical. An experimenter, located behind the participant to minimize distraction, controlled the equipment.

2.3. Task and design

Participants were sat in a black booth, facing an 81.3 cm LCD screen (Logik, L32DIGB20) at a distance of 87 cm away. The experiment involved performing a repeated (x 2) block, which was separated by a 60 s rest and a calibration check (see Figure 1). Each

block comprised four tasks (2 x AO and 2 x MI) and all tasks involved the same goal-directed action, manipulated by perspective (1PP or 3PP). In AO, participants viewed a 5 s video (repeated continuously five times) of a model returning a cup to its saucer. In MI, the screen was black and participants were requested to imagine the observed action for the same time as AO (i.e., 25 s). Each MI task was always preceded by the congruent AO task; temporal and spatial accuracy were emphasized. A 15 s rest (looking at a black screen) was given to a random sample (N = 9) of the participants following final calibration. Collection of eye movements during this time permitted comparison of eye movements performed during MI and those associated with associated with non-specific gaze. To maintain ecological validity the video clips were presented in colour, however the key gaze features (cup and saucer) were neutral, as colour has been reported to increases fixation duration (Henderson, 2003). The horizontal distance between initial and final cup position was 16.81 cm. Instructions were standardized and demonstrated to participants using visual aids prior to the experiment. During the experiment and preceding each task, instructions were presented on the screen. To support neural activity in the action/execution matching system, participants were specifically requested to "observe with intention of later imagining the action" (Buccino et al., 2004).

Insert Figure 1 here

2.4. Procedure

Prior to the experiment, the imagery ability of each participant was assessed by the Movement Imagery Questionnaire Revision (MIQ-RS; Gregg, Hall, & Butler, 2007) and the Vividness of Movement Imagery Questionnaire-2 (VMIQ-2; Roberts, Callow, Hardy, Markland, & Bringer, 2008). The MIQ-RS comprises fourteen items, twelve concerning

visual imagery and twelve probing kinaesthetic imagery. Ratings for each item on the MIQ-RS are made from a 7-point scale, where 1 = very hard to see/feel and 7 = very easy to see/feel. The VMIQ-2 comprises thirty-six items, twelve items for visual imagery 1PP, twelve for visual imagery 3PP, and twelve related to kinaesthetic imagery. Vividness was rated using a 5-point scale where 1 = a perfectly clear image and 5 = no image at all. As a marker of spatial imagery ability, participants also completed the Mental Rotation Test (MRT; (Vandenberg & Kuse, 1978). The MRT is a timed test consisting of twenty items, each presenting a 3-Dimensional target block object and four rotated choice objects. Two of the four choices figures were identical to the target block and two were similar. A point was allocated if both correct figures are identified.

The Mobile Eye system was fitted and calibrated to an 11-point grid, presented onscreen. A chin rest was used to restrict head movement and participants were requested to limit both head movements and speech during the experiment. Participants were randomly assigned into two counterbalanced starting conditions (AO, 1PP and AO, 3PP) and, subsequently, completed the experimental tasks. Following the experiment all participants were debriefed, fully.

2.6. Statistical Analysis

A fixation was defined as holding gaze in a location of 0.55 ° of visual angle for ≥ 100 ms (Vickers, 2007). A bespoke algorithm, developed in-house, using Microsoft Excel, permitted frame-by-frame identification of the fixation indices. Two gaze regions of interest (ROIs) were defined in the scene (initial and final cup position) and the number of fixations within these areas was used as a measure of spatial similarity between the groups. The ROIs were equal to the size of the object plus a tolerance (± 2.58 cm) to accommodate for drift, compressions, expansions (Laeng & Teodorescu, 2002) and individual gaze behaviour preference during AO. Data loss due to artefacts, mainly resulting from eyelid closures or

saccadic shifts to locations outside the registration area (off screen) made up < 10% of all frames analysed.

Differences in dwell time and number of fixations were compared using a 2 x 2 repeated measures ANOVA, with condition (AO, MI) and perspective (1PP, 3PP) as within-subject factors. Separate analyses were performed for both whole scene and pre-defined ROIs. Paired samples *t*-tests were conducted to compare eye movement data during MI and at rest, as well as *post hoc* analyses. The effect sizes were calculated using partial eta squared values (η_p^2) and Cohen's *d* as appropriate. The alpha level for significance was set at 0.05 with Bonferroni adjustment to control for Type 1 errors.

3. Results

3.1. Imagery Ability Assessment

Global means scores per assessment were 89.47 ± 20.57 (VMIQ-2), 75.89 ± 14.64 (MIQ-RS), and 9.32 ± 5.15 (MRT). These scores indicate imagery ability was above average in all participants. Mean scores for the individual sub-components of the assessments are shown in Table 1.

Insert Table 1 here

3.2. Eye movements

3.2.1. Dwell time

There was a significant main effect for condition, $F_{1,18} = 10.354$, p = 0.005, $\eta_P^2 = 0.365$. Participants made fixations of longer duration in the AO (282.11 ± 17.25 ms), compared to MI (220.68 ± 10.06 ms) condition (see Figure 2). There were no significant

differences for perspective, $F_{1,18}=0.001$, p=0.988, $\eta_P^2=0.001$, or the condition x perspective interaction, $F_{1,18}=0.705$, p=0.412, $\eta_P^2=0.038$.

Insert Figure 2 here

3.2.2. Number of fixations (whole scene)

There were no significant main effects for condition, $F_{1,18} = 2.964$, p = 0.102, $\eta_P^2 = 0.141$, perspective, $F_{1,18} = 0.009$, p = 0.925, $\eta_P^2 = 0.001$, or the condition x perspective interaction, $F_{1,18} = 0.037$, p = 0.849, $\eta_P^2 = 0.002$ (see Figure 3).

Insert Figure 3 here

3.2.3. Number of fixations (ROIs)

There was a significant main effect for condition, $F_{1,18} = 5.631$, p = 0.030, $\eta_P^2 = 0.249$, and perspective, $F_{1,18} = 8.480$, p = 0.010, $\eta_P^2 = 0.333$. Participants made a greater number of fixations in the AO (105.47 ± 5.03) compared to MI (83.44 ± 8.00) condition (see Figure 4); and in the 1PP (106.86 ± 7.11) compared to the 3PP (82.06 ± 5.65). There was a significant condition x perspective interaction, $F_{1,18} = 9.295$, p = 0.007, $\eta_P^2 = 0.353$. Post hoc analysis revealed that, in the AO condition, participants made a significantly greater number of fixations in the 1PP (128.83 ± 39.32) compared to 3PP (82.11 ± 29.05), t (17) = 3.645, p = 0.002, d = 1.351. However, there were no differences in the number of fixations during MI, t (17) = 0.315, p = 0.757, d = 0.074.

Insert Figure 4 here

3.2.4. Rest

The number of fixations were compared between rest (15 s baseline viewing), and imagery for a randomly selected subsection (n = 9) of participants' data. There were significant differences between the number of fixations in MI (25.33 \pm 6.42) and rest (8.33 \pm 1.29), t (15) = -3.192, p = 0.013, d = 3.67.

4. Discussion

The main aims of this study were to examine the similarity of eye movement metrics between AO and MI, with the specific aim of determining the existence of congruency between the simulation states. A secondary aim was to investigate the effect of visual perspective on the congruency of eye movements between AO and MI.

4.1. Dwell time

Contrary to our predictions, dwell time was significantly longer (24.96 %; d = 4.35) in AO compared to MI. Mental chronometry studies have reported a similarity between the gross time taken to complete an action and the time to imagine it (Decety, Jeannerod, & Prablanc, 1989). Similarly, Gueugneau et al. (Gueugneau et al., 2008) reported no significant difference in dwell time between action execution and MI of a cyclic pointing task. In contrast, the present study demonstrated that the temporal accuracy of eye movements during MI was significantly different to that during AO. Comparable results have been reported by Calmels and Fournier (Calmels & Fournier, 2001), who observed significantly shorter durations in MI compared to action execution in gymnasts. Differences in task design may

explain the contrasting findings. The complexity of the task was greater in this study, and that of Calmels and Fournier (2001), compared to Gueugneau et al. (2008) and Decety et al. Specifically, in this study, the externally timed reach-grasp-place movement involved horizontal, vertical and vergence responses of the eyes compared to a simple pointing movement in the horizontal plane. Therefore the longer dwell time in AO, compared to MI, may be associated with the difference in cognitive demands of the task. Specifically, the participants in the AO condition may be gathering perceptual information and planning their strategy in order to reproduce the action in the MI condition. Conversely, in the MI condition, the participants may be 'acting out' the previously planned action, which theoretically may require fewer cognitive resources. Laeng and Teodorescu (Laeng & Teodorescu, 2002) suggest a similar analysis; during perception of visual scenes, occulomotor commands are stored along with a visual representation of the action to be used as a spatial index of the movement. Researchers in other disciplines have also demonstrated longer dwell times to be related to the amount of cognitive processing required for task execution (Causer, Bennett, Holmes, Janelle, & Williams, 2010; Williams, Singer, & Frehlich, 2002). Furthermore, it is suggested that in perception, cognitive demand is dictated by 'bottom up' processes, which cause the eyes to respond to movement, and 'top down' processes, which drive the eyes to new locations (Mast & Kosslyn, 2002). This suggestion is supported by PET studies (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991), where attending to form, motion or colour has been demonstrated to increase neural activity. An increase in cognitive activity during AO, influenced by higher stimulus complexity and reflected through an increase in pupil size, has also been reported (Mataric & Pomplun, 1998). Thus, during AO, the cognitive demand of the participants may have been influenced by both the vagaries of the stimulus, as well as determination of their own search strategy.

These main cognitive factors may be the main contribution to recent studies identifying differences between conditions (Macuga & Frey, 2011).

4.2. Number of fixations (whole scene)

Despite disparities in dwell time, the number of fixations in the whole scene was not significantly different between AO and MI (d=0.51). Whilst similarities in eye movements have been reported between imagery and action execution (Heremans et al., 2008), auditory object descriptions (Spivey & Geng, 2001), mental rotation (Rodionov et al., 2004) and motion perception (de'Sperati & Santandrea, 2005), the current study highlights the congruency between MI and AO. It is suggested that during AO of motion, eye movements are generated as the action is encoded in portions over time (Kosslyn, 1994). During imagery of the same action, the location of the eye determines the index of the next image to be generated. The data would, therefore, appear to demonstrate strict congruence between the simulation states for this metric. Confirmation that the fixations were related to the MI and not artefacts is provided through the comparison of number of fixations during MI and rest. Significantly fewer (32.9 %; d=3.67) fixations were observed in rest. Similar reductions have been reported in previous studies (Heremans et al., 2008).

4.3. Number of fixations (ROIs)

The simulation hypothesis (Jeannerod, 2001) suggests that MI and AO access a shared motor representation. This implies that imagined action and AO should take place in the same mental space. To compare the spatial accuracy of the movement between AO and MI the number of fixations to pre-defined ROIs were compared. Significantly more fixations occurred in the ROIs (30.7 %; d = 3.30) in AO compared to MI. The disparity in number of fixations to the ROIs supports the idea of an incomplete neural overlap between the simulation states (Decety, 1996) and is comparable to the work of others (Brandt & Stark, 1997). The data show support to the idea that the 'bottom up', stimulus driven mechanisms

employed during AO are not necessarily used in MI tasks (Kosslyn & Thompson, 2000) and demonstrate that only some of the processes are shared by the simulation states.

Further analysis of the data indicated that, whilst similarity existed in fixation location between AO and MI, there was inter-subject variability in fixation location during AO. Specifically, participants appeared to perform, in the main, either saccadic or smooth pursuit-like movement between the ROIs. de'Sperati and Santandrea (de'Sperati & Santandrea, 2005) have suggested that during MI of smooth pursuit, small 'staircases' (fixations linked by short saccades) occur in an attempt to replicate the tracking motion. Evidence of such movement was observed for some participants in this study. It has been suggested that, during perception, smooth pursuit is stimulated by the velocity of the target and saccades stimulated by target position (Rashbass, 1961). Given that both temporal and spatial task accuracy were emphasized prior to AO, it is possible that some participants may have chosen to focus on one of the aspects only. Indeed, the observed data suggests that participants who demonstrated small 'staircases' of eye movements were temporally more accurate than those who did not (i.e., they performed 5 repetitions of the arm movement rather than 6).

4.4. Perspective

There were no significant differences in dwell time or number of fixations in the whole scene between 1PP and 3PP. However, participants made significantly more fixations in ROIs in the 1PP compared to 3PP. There was also a significant interaction effect between simulation condition and perspective. Specifically, during AO significant more fixations were exhibited in 1PP compared to 3PP, whereas, there were no significant differences between perspectives in the MI condition.

As there were no significant differences in the overall number of fixations, participants may have made fixations in different areas of the scene, depending upon the perspective employed. In the 3PP, participants were free to observe the hand, cup, saucer and

model's face. However, in the 1PP, the model's face was omitted from view. Given the innate desire to establish joint social attention (Emery, 2000), it is possible that the reduction in the number of fixations in the 3PP was due to the participants fixating on the model's face (an area not included in the task-specific ROIs). Indeed, reflexive eye gaze shifts in an observer, mirroring those of the observed, are not uncommon (Laube, Kamphuis, Dicke, & Thier, 2011) and might, therefore, be predicted to be different across perspective conditions. Moreover, some participants (n = 5) reported, at debrief, consciously meeting the eyes of the model at the end of each action in the 3PP, and waiting for his [the actor] eyes to move downwards to initiate the next repeat.

Whilst an equal number of fixations was not expected, based on a hypothesis of incomplete neural overlap (Macuga & Frey, 2011), the difference was larger than anticipated. Some researchers (Brandt & Stark, 1997) have reported observing similar, but not identical, fixation patterns during visual imagery, whilst others report highly accurate movement patterns (Heremans et al., 2008). For example, Heremans et al. (Heremans et al., in press), recently reported that the quality of MI was optimized when assisted with the same visual cues as used in action execution. Such accurate movement patterns observed between the action execution and MI may have been achieved through the equivalence between tasks. This concept of supporting MI in this way is common in the sport psychology literature (Holmes & Collins, 2001).

There is evidence to suggest that AO has a positive effect on rehabilitation of motor deficits after stroke (Ertelt et al., 2007). It is believed that the increased activation of the action-execution matching system facilitates reactivation of motor representations related to the observed actions in addition to providing motivational support to patients. Furthermore, it is suggested that imagery perspective effectiveness shifts from a 1PP to a 3PP following stroke, and aging (Ewan, Smith, & Holmes, 2010). Therefore, by examining the congruency

between 1PP and 3PP we may be able to determine the potential effectiveness of AO and MI in rehabilitative settings. Future research should focus on examining the role of perspective on AO and MI, specifically the role of priming in the effectiveness of MI.

5. Conclusions

The current paper extends previous work by identifying new markers of eye movement congruency between the simulation states of AO and MI. Furthermore, although previous studies have established some level of eye movement congruency between the simulations states, they have mainly focused on behaviours that suppress information processing, such as saccadic eye movements (Heremans et al., 2008). Through the analysis of fixation data, behaviour can be decomposed into a sequence of information processing stages (Just & Carpenter, 1976), the duration of which can be measured directly. This duration is considered to represent the time needed to encode or process the characteristics of the presented stimuli (Causer, Holmes, Smith, & Williams, 2011). In the current paper, we measured fixation duration (dwell time), which permitted comparison of information processing and mental operations between AO and MI. It is suggested that the extended dwell times in AO, compared to MI, may represent the difference in processing/encoding time required in each task. The findings have implications for mental imagery practice, especially in rehabilitative environments.

List of captions

- Table 1. Descriptive statistics for the subcomponents of the VMIQ-2, MIQ-r and MRT.
- Figure 1. Schematic overview of the experimental protocol.
- Figure 2. a) Mean (+ SD) dwell time between AO and MI.
- Figure 3. Mean (\pm SD) number of fixations made within the whole scene.
- Figure 4. Mean (\pm SD) number of fixations made within the ROIs.

References

Brandt, S. A., & Stark, L. W. (1997). Spontaneous eye movements during visual imagery reflect the content of the visual scene. *Journal of Cognitive Neuroscience*, *9*(1), 27-38.

Buccino, G., Vogt, S., Ritz, A., Fink, G. R., Zilles, K., Freund, H., et al. (2004). Neural circuits underlying imitation learning of hand actions: an event-related fMRI study. *Neuron*, 42, 323-334.

Calmels, C., & Fournier, J. F. (2001). Duration of physical and mental execution of gymnastic routines. *The Sport Psychologist*, *15*, 142-150.

Causer, J., Bennett, S. J., Holmes, P. S., Janelle, C. M., & Williams, A. M. (2010). Quiet eye duration and gun motion in elite shotgun shooting. *Medicine & Science in Sports & Exercise*, 42(8), 1599-1608.

Causer, J., Holmes, P. S., Smith, N. C., & Williams, A. M. (2011). Anxiety, movement kinematics, and visual attention in elite-level performers. *Emotion*, 11(3), 595-602.

Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L., & Petersen, S. E. (1991). Selective and divided attention during visual discriminations of shape, color, and speed - functional anatomy by positron emission tomography. *Journal of Neuroscience*, *11*, 2383-2402.

de'Sperati, C., & Santandrea, E. (2005). Smooth pursuit-like eye movements during mental extrapolation of motion: the facilitatory effect of drowsiness. *Cognitive Brain Research*, 25, 328-338.

Decety, J. (1996). Do imagined and executed actions share the same neural substrate? *Cognitive Brain Research*, *3*, 87-93.

Decety, J., Jeannerod, M., & Prablanc, C. (1989). The timing of mentally represented actions. *Behavioural Brain Research*, 34, 35-42. Emery, N. J. (2000). The eyes have it: the neuroethology, function and evolution of social gazes. *Neuroscience and Behavioural Review*, 24, 581-604.

Ertelt, D., Small, S., Solodkin, A., Dettmers, C., McNamara, A., Binkofski, F., et al. (2007). Action observation has a positive impact on rehabilitation of motor deficits after stroke. *NeuroImage*, *36*, 164-173.

Ewan, L. M., Smith, N. C., & Holmes, P. S. (2010). Disruption to the apects of imagery vividness after stroke. *Journal of Mental Imagery*, *34*(3), 3-14.

Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: a magnetic stimulation study. *Journal of Neurophysiology*, 73(6), 2608-2611.

Fourkas, A. D., Avenanti, A., Urgesi, C., & Aglioti, S. M. (2006). Corticospinal facilitation during first and third person imagery. *Experimental Brain Research*, *168*(2), 143-151.

Gerardin, E., Sirigu, A., Lehericy, S., Poline, J. B., Gaymard, B., Marsault, C., et al. (2000). Partially overlapping neural networks for real and imagined hand movements. *Cerebral Cortex*, *10*, 1093-1104.

Gregg, M., Hall, C., & Butler, A. (2007). *The MIQ-RS: A suitable option for examining movement imagery ability*. Retrieved June 21 from

http://www.ehpl.uwo.ca/Publication%20PDFs/eCAM%20MIQ-RS.pdf.

Grézes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta- analysis. *Human Brain Mapping*, 12, 1-19.

Gueugneau, N., Crognier, L., & Papaxanthis, C. (2008). The influence of eye movements on the temporal features of executed and imagined arm movements. *Brain Research*, 1187, 95-102.

Hebb, D. O. (1949). The Organization of Behavior. NY: Wiley & Sons.

Hebb, D. O. (1968). Concerning imagery. Psychological Review, 75, 466-477.

Henderson, J. M. (2003). Human gaze control during real-world scene perception. *TRENDS* in Cognitive Sciences, 7, 498-504.

Heremans, E., Helsen, W. F., De Poel, H. J., Alaerts, K., Meyns, P., & Feys, P. (2009). Facilitation of motor imagery through movement-related cueing. *Brain Research*, 1278, 50-58.

Heremans, E., Helsen, W. F., & Feys, P. (2008). The eyes as a mirror of our thoughts: quantification of motor imagery through eye movement registration. *Behavioural Brain Research*, 187, 351-360.

Heremans, E., Smits-Engelsman, B., Caeyenberghs, K., Vercruysse, S., Nieuwboer, A., Feys, P., et al. (in press). Keeping an eye on imagery: the role of eye movements during motor imagery training. *Neuroscience*.

Holmes, P. S., & Calmels, C. (2008). A neuroscientific review of imagery and observation use in sport. *Journal of Motor Behavior*, 40, 433-455.

Holmes, P. S., & Collins, D. (2001). The PETTLEP approach to motor imagery: a functional equivalence model for sport psychologists. *Journal of Applied Sport Psychology*, *13*, 60-81.

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, 286, 2526-2528.

Jeannerod, M. (2001). Neural simulation of action: a unifying mechanism for motor cognition. *NeuroImage*, *14*, 103-109.

Just, M. A., & Carpenter, P. A. (1976). Eye fixations and cognitive processes. *Cognitive Psychology*, 8, 441-480.

Kosslyn, S. M. (1994). Image and brain: the resolution of the imagery debate. Cambridge, MA: The MIT Press.

Kosslyn, S. M., & Thompson, W.L. (2000). Shared mechanisms in visual imagery and visual perception: insights from cognitive neuroscience. In M. S. Gazzaniga (Ed.), *The New Cognitive Neurosciences*). Cambridge, MA: The MIT Press.

Laeng, B., & Teodorescu, D. (2002). Eye scan paths during visual imagery re-enact those of perception of the same visual scene. *Cognitive Science*, 26, 207-231.

Laube, I., Kamphuis, S., Dicke, P., & Thier, P. (2011). Cortical processing of head- and eye-gaze cues guiding joint social attention. *Neuroimage*, *54*, 1643-1653.

Liversedge, S. P., & Findlay, J. M. (2000). Saccadic eye movements and cognition. *TRENDS* in Cognitive Sciences, 4, 6-14.

Macuga, K. L., & Frey, S. H. (2011). Neural representations involved in observed, imagined, and imitated actions are dissociable and hierarchically organized. *Neuroimage*.

Mast, F. W., & Kosslyn, S. M. (2002). Eye movements during visual mental imagery. TRENDS in Cognitive Sciences, 6, 271-272.

Mataric, M. J., & Pomplun, M. (1998). Fixation behaviour in observation and imitation of human movement. *Cognitive Brain Research*, 7, 191-202.

Morris, T., Spittle, M., & Watt, A. P. (2005). *Imagery in sport*. Champaign, IL: Human Kinetics.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh Inventory. *Neuropsychologia*, 9, 97-113.

Rashbass, C. (1961). The relationship between saccadic and smooth tracking eye movements. *Journal of Physiology*, 159, 326-338.

Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G., & Matelli, M. (1988). Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Experimental Brain Research*, 71, 491-507.

Roberts, R., Callow, N., Hardy, L., Markland, D., & Bringer, J. (2008). Movement imagery ability: development and assessment of a revised version of the vividness of movement imagery questionnaire. *Journal of Sport and Exercise Psychology*, 30, 200-221.

Rodionov, V., Zislin, J., & Elidan, J. (2004). Imagination of body rotation can induce eye movements. *Acta Oto-Laryngologica*, *124*, 684-689.

Ruby, P., & Decety, J. (2001). Effect of subjective perspective taking during simulation of action: a PET investigation of agency. *Nature Neuroscience*, *4*, 546-550.

Spivey, M. J., & Geng, J. J. (2001). Oculomotor mechanisms activated by imagery and memory: eye movements to absent objects. *Psychological Research*, 65, 235-241.

Vandenberg, S. G., & Kuse, A. R. (1978). Mental rotations, a group test of three dimensional visualization. *Perceptual and Motor Skills*, 47, 599-601.

Vickers, J. N. (2007). *Perception, Cognition and Decision Training: The Quiet Eye in Action*. US: Human Kinetics.

Vul, E., Harris, C., Winkielman, P., & Pahler, H. (2009). Puzzlingly high correlations in fMRI studies of emotion, personality, and social cognition. *Perspectives on Psychological Science*, 4(3), 274-290.

White, A., & Hardy, L. (1995). Use of different imagery perspectives on the learning and performance of different motor skills. *British Journal of Psychology*, 86, 169-180.

Williams, A. M., Singer, R. N., & Frehlich, S. G. (2002). Quiet eye duration, expertise, and task complexity in near and far aiming tasks. *Journal of Motor Behavior*, *34*(2), 197-207.