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Humans and Monkeys Distinguish Between Self-generated, Opposing, and Random Actions

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Abstract

The sense of self-agency results from monitoring the relationship between prior thoughts and action plans, sensorimotor information, and perceived outcomes. It is thought to be an important factor underlying self-recognition and self-awareness. Three experiments investigated the sense of self-agency in humans and rhesus macaques (*Macaca mulatta*). First, humans were asked to move a cursor with a joystick while several distractor cursors also moved onscreen. They were asked to identify either the cursor they were controlling or to identify a distractor using visual cues alone. Six rhesus macaques were then given a similar task in which they needed to identify a self-controlled cursor that was paired with several different types of distractors. Both groups were able to identify the self-controlled cursor, and monkeys performed best when the oppositely moving cursor was the distractor. A third experiment showed that humans, like macaques, use both perceptual and self-agency information to make decisions.

Keywords

Agency; Self-agency; Self-monitoring; Self-recognition; Voluntary action; Rhesus macaque

Introduction

Recognizing the self is thought to be a key factor in human consciousness. Yet we currently understand very little about how self-recognition evolved (Terrace and Metcalfe 2005). Two lines of research have traditionally addressed this problem. The first examines the human and nonhuman animal (hereafter, animal) ability to recognize themselves in a mirror. Young human children (Amsterdam 1972), chimpanzees (Gallup 1982), orangutans (Lethmate and Dürcker 1973), magpies (Prior et al. 2008) and dolphins (Reiss and Marino 2001) have shown the ability to recognize marks on their bodies that can only be seen through a mirror. Passing this mirror self-recognition test indicates that the subject has some understanding of its body, and therefore possibly some concept of self. However, it is difficult to determine from the test what type of cognition is involved (Cheney and Seyfarth 1990). Another problem is that many species thought to be cognitively sophisticated fail this test due to social tendencies, aversions that are probably unrelated to self-awareness, or even when these are controlled for some species may simply not regard the mark as an important alteration to their body (Macellini et al. 2010). Examples include parrots, despite their ability to use mirrors in a variety of tasks (Pepperberg et al. 1995) and many humans with autism, mental retardation, Alzheimer's disease, and schizophrenia (Gallup et al. 2002).

Perhaps the most notable failures come from rhesus macaques, who make threat gestures at mirrors (Suarez and Gallup 1986) that prevent them from passing, despite their ability to monitor and report on aspects of their visual experience (Covey and Stoerig 1995).

The second line of research investigates the ability to monitor and recognize mental states. This work usually involves subjects making judgments about their own memory or level of uncertainty in addition to primary task judgments. Young human children, chimpanzees, orangutans, a dolphin, and rhesus macaques have demonstrated this metacognitive ability. In fact, rhesus macaques have demonstrated metacognition in a wide variety of situations (Smith et al. 2012) including delayed matching-to-sample tasks, memory tasks where transcranial magnetic stimulation disrupted memory traces, serial-position memory tasks, token-economy tasks, same-different tasks, numerosity tasks, on the first trial of novel tasks, in information-seeking paradigms, and in the absence of trial-by-trial feedback cues. Demonstrating metacognition indicates that the subject has some ability to monitor its mental states, and therefore possibly some concept of self. However, here too it is difficult to determine exactly what type of cognition is involved. Metacognition might exist in animals as an implicit process that monitors mental states, as explicit self-awareness, or as something in between those extremes (Couchman et al. 2010). While neither line of research fully answers the problem of self-awareness, taken together they clearly indicate that some mental process – one that monitors both bodily and cognitive information and is associated with self-awareness – ought to be found in animals. Because such a process would lie in the midground between implicit self-monitoring and explicit self-awareness, understanding how humans and animals use it might shed light on the emergence of self-recognition.

One possible candidate for such a process is self-agency – the ability to recognize that some actions are generated by the self. Humans usually experience self-agency, and it is especially noticeable when the normal relationship between performance and perception is disrupted. They are often influenced by cognitions about causal inference that include prior expectations, consistency between expectations and outcomes, and hypotheses about other possible causes of an event (Wegner 2002). Humans also take advantages of sensorimotor and other perceptual cues (Couchman et al. 2012; Repp and Knoblich 2007). A classic example of this phenomenon occurs in multi-player video games, where one must continually identify their own actions in the presence of distracting, often similar, actions from others. Spence and Feng (2010) noted that such games increase visual attention and inhibition of distracting information. Similar cues help guide orchestral performances and other cooperative activities (Pacherie 2012). In self-agency tasks, one must use both the bodily/sensorimotor information tapped by the mirror self-recognition task and the self-monitoring tapped by metacognitive tasks to guide behavior, identify self-controlled events, and make decisions. For these reasons, self-agency is thought to be an important factor underlying self-awareness (Kircher and Leube 2003), and also a kind of metacognition (Metcalf and Greene 2007).

In addition to the cognitive processes, we also have some understanding of the neural processes involved in self-agency. The posterior medial frontal cortex (Ridderinkhof et al. 2004) helps monitor performance and mediates goal-directed behavior, and has direct and indirect projections to motor areas (Matsumoto and Tanaka 2004) that may bring

sensorimotor information into conscious awareness. Several studies have suggested that the prefrontal cortex also plays a role in monitoring motor processing and actions (Averbeck et al. 2002; Luu et al. 2000). One recent study showed that electrical stimulation to the inferior parietal regions produce intentions to act, and at higher levels of stimulation the belief that one has acted even when no motor movements took place (Desmurget et al. 2009). Similar stimulation to the premotor cortex produced movements without awareness, suggesting that the parietal cortex also plays a role in self-monitoring and judging whether some actions are self-generated. Also, PET investigations suggest that the cerebellum receives a copy of motor commands and compares them to observed sensory consequences (Blakemore et al. 2001), which could account for the cognitive process of comparing perceived outcomes to intended performance.

It is therefore crucial to understand how this ability emerged evolutionarily and to what degree humans and animals understand self-agency. Early research has shown that chimpanzees (Kaneko and Tomonaga 2011), humans, and rhesus macaques (Couchman 2012) may have some understanding of self-agency. These tasks used visual discriminations in which participants manipulated a trackball or joystick to move an onscreen computer cursor toward a goal while a distractor cursor also moved onscreen. Participants were able to identify the self-controlled cursor at greater than chance levels, suggesting that they could indeed distinguish between the two types of movements (self- and other-generated). These tasks established that investigations into the evolution of self-agency are possible, but left open one possible alternative explanation: Animals might identify the correct cursor through purely visual cues associated with a “normal” cursor (e.g., it always moves directly toward a designated endpoint). This would be an interesting inference and a cognitive decision, but might not incorporate self-agency information. A similar shortcoming is that these studies focused on self vs. other information, but did not examine important subtypes of other-generated information such as random and opposing actions. Visual explanations would place all types of movements on equal ground; self-agency explanations would predict differences in judgments between self, opposing, and random movements because they would each result in different feelings of self-agency.

Experiment 1: Human Self-controlled vs. Random

Figure 1 shows the general setup for all experiments. Participants were presented with an array of randomly colored letters that would move in pre-defined algorithms based on joystick movements. One cursor was self-controlled, in the sense that participant movements were completely isomorphic with cursor movements. One distractor cursor was completely directionally reversed so that it moved exactly opposite the participants' movements. Another distractor was left-right reversed so that it moved normally in the vertical direction but oppositely in the horizontal. The final distractor moved randomly, in the sense that it only moved when the joystick was pressed but its directionality did not correlate with the participant's movements. A pilot experiment confirmed that, visually, the randomly moving cursor was the most distinct because its movement path was qualitatively different from the others. All distractors covered approximately the same distance onscreen, moved for the same amount of time and were identical in every other respect.

Note that, strictly speaking, all cursor movements depended on the actions of the participant. Thus, rather than force a complete self vs. other situation, these experiments explored the relative level of self-agency produced by different types of cursors and the ability to monitor and respond to that feeling.

Methods

Participants—Twenty humans from the University at Buffalo participated in the study as part of an Introductory Psychology course requirement. Their mean age was approximately 18.5 years and they were approximately 35% female. All had normal or corrected-to-normal vision.

Apparatus—Humans used a game pad, functionally equivalent to a joystick, to control the cursor. Computer software detected 8 directional movements (up, up right, right, down right, down, down left, left, up left) and translated them into onscreen movements. This resulted in the functional ability to move the cursor in any direction. The cursor was steered by the game pad at a fixed speed, and continued to move so long as any pressure was exerted on it.

Procedure—Participants were told that they would need to identify both a self-controlled and randomly moving cursor. They saw a screen like the one shown in the first panel of Figure 1 and made any movements they chose for two seconds. Pilot experiments showed that they performed similarly if given four seconds and/or only two cursors at a time, but they were near ceiling levels of accuracy in those situations. The four letters moved onscreen according to the algorithms described above, sometimes overlapping each other. The task presented 8 blocks of 8 trials each, with two conditions randomly distributed in each block: (i) *Identify Self-controlled*: After the cursor movements, participants were told: “Please choose the letter that YOU were controlling” when the third panel of Figure 1 appeared and were rewarded only for choosing the self-controlled cursor; and (ii) *Identify Random*: After the cursor movements, participants were told: “Please choose the letter that was moving RANDOMLY” when the third panel of Figure 1 appeared and were rewarded only for choosing the randomly moving cursor. Because these instructions came after the movements on each trial, participants needed to move the joystick in a way that allowed them to identify both cursor types. The task thus directly pitted self-agency against purely visual identification of a specific movement style using a within-subjects design. There was also no goal to the cursor movements, except to move in a way that helped make the final judgment, and no onscreen landmarks that could be used as visual discrimination cues. Humans were rewarded with 1 point for making a correct selection, and given a 20s timeout for errors.

Results—The proportion of cursors selected in each condition are shown in Figure 2. Humans were able to identify and select the correct cursor at greater than 25% chance levels for the *Identify Self-controlled* condition, Pearson’s $\chi^2(3, N = 20) = 267.8, p < 0.001$, and the *Identify Random* condition, $\chi^2(3, N = 20) = 75.6, p < 0.001$. However, a repeated-measures ANOVA revealed that there were significantly more correct selections made in the *Identify Self-controlled* condition, $F(1, 19) = 5.46, p < 0.05$, suggesting that humans were better at identifying the cursor that was associated with feelings of self-agency.

In a debriefing after the experiment, half of participants reported looking for the self-controlled cursor first, and half the randomly moving cursor, suggesting that no aspect of the task instructions biased them to one type of cursor. Still, when asked which cursor was easier to identify, 16 participants, a significant number based on a two-tailed binomial sign test ($p = 0.012$), reported that the self-controlled cursor was easier to identify. This suggests that it was indeed more salient. Self-agency information probably gave an advantage to the self-controlled cursor, despite its visual similarity to the oppositely moving and left-right reversed cursors and the unique visual distinctiveness of the randomly moving cursor.

Experiment 2: Monkeys

Rhesus macaques were then given a similar task in which they freely moved their cursor and were asked to distinguish it from several types of distractors. Unlike Couchman (2012) and Kanako and Tomonaga (2011), there was no goal to their movements other than to identify their cursor, and each trial showed the self-controlled cursor paired with one type of distractor.

Methods

Participants—Six male rhesus macaques were recruited from the Language Research Center, Georgia State University. See Couchman (2012) for full details of their training procedures.

Apparatus—Monkeys were tested using the Language Research Center's Computerized Test System—LRC-CTS (see Washburn and Rumbaugh 1992)—comprising a Compaq DeskPro computer, a gamepad similar to humans in Experiment 1 but with a joystick mounted on it for better grip, a color monitor, and a pellet dispenser. Monkeys could manipulate the joystick through the mesh of their home cages, and the movements were read by computer software as described in Experiment 1. The system could deliver a 94-mg fruit-flavored chow pellet (Bioserve, Frenchtown, NJ) using a dispenser interfaced to the computer.

Procedure—Monkeys followed the same procedure as humans in the *Identify Self-controlled* condition, again using a within-subjects design, except that there were no written instructions and each trial presented one randomly selected distractor cursor and the self-controlled cursor. There were thus three conditions: (i) *With Opposite*, (ii) *With Left-Right*, and (iii) *With Random*. This was done to determine the effects of the different types of distractors on self-agency judgments. Data shown come from 400 such trials, during which time only selections of the self-controlled cursor were rewarded and all monkeys were individually significantly above chance at selecting it. Monkeys used the test apparatus and reward structure of Couchman (2012), and could move the cursors for four seconds. Correct selections resulted in a reward of 1 food pellet; incorrect selections resulted in a 20s timeout. All monkeys had been trained on their testing apparatus (Washburn and Rumbaugh 1992) and had extensive experience with joysticks.

Results—Figure 3 shows that monkeys were able to select the self-controlled cursor at greater than chance levels in the conditions *With Opposite*, $\chi^2(3, N = 6) = 511.2, p < 0.001$,

With Left-Right, $\chi^2(3, N = 6) = 290.9$, $p < 0.001$, and *With Random*, $\chi^2(3, N = 6) = 332.8$, $p < 0.001$. This suggests that the monkeys were clearly able to access the sensorimotor and perceptual information that results in self-agency in humans and allowed humans to select their cursor in Experiment 1.

In the *With Opposite* condition, there was a significant effect of cursor type on endorsements, $F(3, 23) = 26.2$, $p < 0.001$, and Tukey's HSD tests ($\alpha < 0.05$) showed that selections of the self-controlled cursor were greater than selections of all distractors, while the oppositely moving cursor was selected more often than the other two choices. Note that although monkeys did not see the other two cursor types onscreen, they were pre-determined by the computer program, assigned a letter and color, and presented on the choice screen; that they were chosen at equal levels suggests that there was no relationship between the color, letter, and cursor type that biased the animals in any way. In the *With Left-Right* condition there was a similar significant effect, $F(3, 23) = 39.7$, $p < 0.001$, and Tukey's HSD tests ($\alpha < 0.05$) showed that selections of the self-controlled cursor were greater than selections of all distractors, while the left-right reversed cursor was selected more often than the other two choices. This was also the case in the *With Random* condition, $F(3, 23) = 32.8$, $p < 0.001$, and Tukey's HSD tests ($\alpha < 0.05$) showed that selections of the self-controlled cursor were greater than selections of all distractors, while the randomly moving cursor was selected more often than the other two choices.

Like humans, the monkeys appeared to use both perceptual and self-agency cues, with self-agency adding extra salience to some cursors. The Tukey HSD tests show that the main distractor in each condition was often chosen. This result by itself would seem to indicate that they were heavily influenced by perceptual cues and, as in previous experiments, had only some understanding of self-agency. But, further analysis of these errors showed that monkeys selected the left-right reversed cursor at above chance levels in the *With Left-Right* condition, $\chi^2(3, N = 6) = 17.3$ $p < 0.001$, and the randomly moving cursor at above chance levels in the *With Random* condition, $\chi^2(3, N = 6) = 12.9$ $p < 0.01$. They did not, however, choose the oppositely moving cursor at greater than chance levels in the *With Opposite* condition. This suggests they found the *With Opposite* condition easiest, despite the perfect negative correlation between the distractor and the self-controlled cursor.

Discussion—These results are curious because the randomly moving cursor shared no correlation with the self-controlled, and was most visually distinct. From a purely perceptual hypothesis, should it not be the easiest to avoid? Previous research (Couchman 2012; Kaneko and Tomonaga 2011) has shown that even when animals demonstrate self-agency they are heavily dependent on perceptual cues.

There are two possible causes of this result: Monkeys may have felt a weaker sense of self-agency that made the oppositely moving cursor a less salient distractor. However, it seems bizarre to think that an oppositely moving cursor, whose movements were completely dictated by self-movements, elicited a less strong feeling of agency than a randomly moving cursor. A second possibility is that the randomly moving cursor was actually *more* difficult to avoid, precisely because it was most visually distinct and thus most likely to capture attention. The third possibility is that they felt a stronger sense self-agency associated with

the oppositely moving cursor due to the perfect negative correlation and, because they were primarily relying on self-agency information, used that information to identify and ignore it. In any case, perceptual cues are probably a very important factor, even though self-agency information is also used.

Experiment 3: Human Distractor Types Test

Experiment 3 sought to test whether humans also found opposite actions to be more salient or easier to identify.

Method

Participants—Forty humans from the University at Buffalo participated in the study as part of an Introductory Psychology course requirement. Their mean age was approximately 18.5 and they were approximately 55% female. All had normal or corrected-to-normal vision.

Procedure—To determine the effect of the oppositely moving cursors on self-agency, humans were given a task similar to Experiment 1, with two new conditions: (i) *Pick Opposite*: Half of the participants were told to always choose the cursor moving exactly opposite their movements, and were rewarded only for choosing the oppositely moving cursor (ii) *Pick Distractor*: The other half were told to always pick any cursor they were not controlling, and were rewarded for picking either the oppositely moving, left-right reversed, or randomly moving cursor. They were rewarded as described in Experiment 1.

Results—The *Pick Opposite* condition, shown in Figure 4, established that humans could indeed identify the oppositely moving cursor, $\chi^2(3, N = 20) = 650.3, p < 0.001$.

In the *Pick Distractor* condition, only the oppositely moving cursor was selected at greater than 25% chance levels, $\chi^2(3, N = 20) = 329.4, p < 0.001$. In this condition, despite their selections being fully correct and rewarded, participants were actually below chance levels at selecting the left-right reversed and randomly moving cursors. In fact, results for all these selections did not differ from those in the *Pick Opposite* condition. This result is highly surprising from a visual discrimination perspective, but fits perfectly with the results from Experiment 2. Like monkeys, humans found the oppositely moving distractor most salient and selected it most even though the other distractors yielded equal reward.

General Discussion

Experiment 1 established that humans could identify both a self-controlled and randomly moving cursor and the self-controlled cursor was easier to identify. This was probably because it was associated with stronger feelings of self-agency. Experiment 2 showed that rhesus macaques were able to identify a self-controlled cursor in a similar situation, and were also more strongly influenced by factors associated with self-agency than by visual perception alone. Results from all 3 experiments suggest that in complex visually overlapping environments, humans and monkeys rely on self-agency information to distinguish their actions from other actions. They also make distinctions between opposing

and uncorrelated random actions, suggesting that they may be able to understand and discriminate between different types of movements using both perceptual cues and self-agency information. This is particularly interesting for rhesus macaques because, in addition to failing mirror self-recognition tasks, they also fail Theory of Mind tasks that tap into the understanding of others' intentions (Tomasello and Call 1997). Though they may have no access to the intentions of others, and in the current task there are no such intentions, they do seem to be able to discriminate between different types of actions that fall on a continuum between self- and other-generated.

These results do not fully rule out the possibility that humans and monkeys were relying on some visual cues to accomplish the task. In fact, given that the link between performance and perception is important in the experience of self-agency, it is likely that these cues played some role. The results do suggest that humans and monkeys process self-agency information differently than visual information alone and that self-agency information has priority in some cases. The results also dovetail with recent findings that monkeys prefer situations in which rewards are determined by self-generated actions rather than external factors, even when the timing and frequency of the rewards equal (Jensen et al. 2013). Self-agency seems to be an important factor that influences general cognitive processes.

The findings reported here fit well with previous self-agency research in humans. It has long been known that during speech and musical performances, sensory information that is similar to expectations, but not identical or random (Couchman et al. 2012), is disruptive because it confuses the perception-action system mediated in part by the cerebellum. It is possible that a mental process that could acutely distinguish between these types of situations would be evolutionarily selected for. One demonstration of such a mechanism is the principle behind the famous result that one cannot tickle oneself (Blakemore et al. 2001) – because expectations match perceived outcomes – but delayed or other-generated stimulation can result in the tickle sensation. Humans and monkeys in the reported experiments might be relying on similar neural mechanisms. The oppositely moving cursor might be easier to “tune out” precisely because it carries with it self-agency information that, in this task, could be confusing or result in error. Assuming that humans and monkeys were relying on self-agency information to process the task, it makes sense that they would be more capable of distinguishing between self-generated and opposite movements because more resources would be allocated to the neural mechanisms governing self-agency and less to neural mechanisms focused on uncorrelated actions.

Though it is intuitively obvious that randomly generated actions are not one's own, there are many situations in which it might also be important to distinguish self-generated, opposing, and similar actions. Both cooperative (Plotnik et al. 2011) and competitive (Hare et al. 2000) tasks that require sophisticated forms of cognition would benefit from self vs. opposing vs. similar distinctions. For example, two animals that are each trying to pull a piece of food away from the other would benefit if they could focus on oppositely-generated actions or their own intentions partially distorted by external forces. It is plausible that animals might have developed a specialized ability to regulate this activity that recruits metacognitions of intentions and expectations, inferential information, sensorimotor information, and might result in a sense of self-agency similar to that which is experienced by humans. Further

research into the factors influencing what causes an animal to feel that something is self-controlled, self-controlled but disrupted, other-controlled, or external, could help explain the evolution of abilities like theory of mind and cooperation that might benefit from self-agency information.

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Figure 1.

An illustration of the task given to humans and monkeys. The cursors, which were randomly selected colored letters, start out in randomly selected positions on the screen (first panel). Movement of a joystick resulted in the self-controlled and distractor cursor final positions, one example of which is shown in the second panel. The third panel shows the choice screen, in which participants used a red cursor to make a selection.

Figure 2. Proportion selected for all types of cursors for the *Identify Self-controlled* and *Identify Random* conditions. Error bars indicate standard error.

Figure 3.

Proportion selected for monkeys for all types of cursors for the *With Opposite*, *With left-Right*, and *With Random* conditions. Rewarded cursor types are shown in dark grey. Error bars indicate 95% confidence intervals.

Figure 4.

Proportion selected for all types of cursors for the *Pick Opposite* and *Pick Distractor* conditions. Rewarded cursor types are shown in dark grey. Error bars indicate standard error.