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Self-agency in rhesus monkeys

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Rhesus monkeys (*Macaca mulatta*) have shown the ability to monitor their own mental states, but fail the mirror self-recognition test. In humans, the sense of self-agency is closely related to self-awareness, and results from monitoring the relationship between intentional, sensorimotor and perceptual information. Humans and rhesus monkeys were trained to move a computer icon with a joystick while a distractor icon partially matched their movements. Both humans and monkeys were able to monitor and identify the icon they were controlling, suggesting they have some understanding of self-agency.

Keywords: self-agency; self-awareness; rhesus monkeys

1. INTRODUCTION

Self-awareness—the sense that one is an individual separate from the environment—has traditionally been measured by the mirror self-recognition test [1,2]. Chimpanzees (*Pan troglodytes*) [3], orangutans (*Pongo pygmaeus*) [4], 18–24 month-old children [5] and dolphins (*Tursiops truncatus*) [6] appear to recognize themselves in mirrors and notice foreign marks that can only be seen via the mirror. Of the many species that fail the mirror self-recognition task, rhesus monkeys (*Macaca mulatta*) are particularly interesting because their failures are probably not owing to cognitive factors, but rather social tendencies to make threat gestures towards any monkey image [7,8].

Similarly, when given the option, as a reward, to see a previously recorded video of themselves, a familiar monkey, an unfamiliar monkey or a blank screen, monkeys strongly preferred the blank screen. However, when they did choose a video, they tended to choose a video of themselves [9].

Though they apparently lack mirror self-recognition, findings in comparative metacognition suggest that rhesus monkeys might have some other form of self-awareness. Like apes [10] and a dolphin [11], rhesus monkeys can monitor their mental states and use cognitive information about memory strength and feelings of uncertainty to selectively decline difficult trials or engage in information-gathering strategies [12]. They show this ability in abstract situations, including same–different [13] and numerosity tasks [14], on the first trial of novel tasks [15], during metamemory judgements [16,17] when transcranial magnetic stimulation disrupts memory traces [18], in information-seeking paradigms [19], and in the absence of trial-by-trial feedback cues and other environmental factors [20]. In all of these tasks, rhesus monkeys know what they know and what they do not know, suggesting that they have some awareness of their own mental states.

These two conflicting lines of evidence require a resolution. Rhesus monkeys apparently lack the form of self-awareness measured by the traditional test, but do show some awareness of their own mental states. Cognitive access to mental states is probably an important aspect of self-awareness, because thoughts are inherently self-generated and separate from the environment. Thus, it is difficult to imagine an individual that understands it has thoughts, and can use mental information to make responses that are not entirely dictated by the environment, but does not understand that it is an individual separate from the environment. If an individual understands it has thoughts, it seems that it should also understand that it has a body and control over some actions.

In fact, investigations into self-agency—the sense that some actions are self-generated—suggest that awareness and sense of control over one's body results from monitoring the relationship between thoughts and expectations that occur prior to an event [21], sensorimotor cues [22] and perceived outcomes. These experiments often ask subjects to distinguish between actions that are self-generated or partially altered. Comparing cognitive expectations, sensorimotor information and perceptual outcomes is a special kind of metacognitive judgement [23] that gives rise to the sense of self-agency, and contributes to our sense of self-awareness.

Thus, one potential way to resolve the conflicting results in mirror self-recognition and uncertainty-monitoring is to create a task in which subjects are asked to identify their own self-generated actions. Such a task would tap the cognitive and sensorimotor cues involved in self-monitoring, self-agency and self-awareness, while eliminating distracting self-images. The current task asks humans and monkeys, for the first time, to distinguish between self-controlled and partially directionally reversed (distractor) cursors that are equally perceptually salient. If monkeys have any sense of self-agency, they ought to be able to distinguish self-generated from partially altered actions.

Furthermore, because the task does not rely on any optional responses (e.g. glances, body touches and uncertainty responses), at least one other prediction and measure of performance can be made. Because the distractor cursor on each trial partially, but not exactly, matches expectations, humans and monkeys ought to choose it more often than cursors for which no such cues are available.

2. MATERIAL AND METHODS

Forty humans and four male rhesus monkeys were trained to use a joystick to move a computer icon around an onscreen obstacle towards a large dot, and then use a small cursor to select the icon they had just been controlling. Humans received points (shown onscreen) for each correct answer; monkeys received food pellets. Both species experienced 20 s penalty timeouts for errors. After achieving 80 per cent choices correct, they were moved to the testing phase where they did the same task in the presence of a distractor cursor. The distractor was either left–right or up–down directionally reversed so that it always exactly mirrored the controlled cursor. Figure 1 depicts this situation. The distractor was always on the screen exactly as long as the controlled cursor, covered the same amount of screen area, moved towards the same goal, and shared

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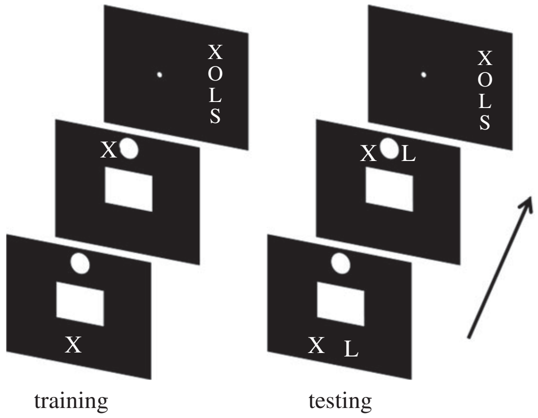

Figure 1. *Training*. An illustration of the training task. Participants were in control of a cursor—in this example, the 'X'—and moved it around the large rectangle towards the large circle. The second panel shows the cursor arriving at the circle, which triggered the next panel. Participants used the cursor, shown in the third panel, to select the icon they controlled. *Testing*. An illustration of the testing task. The task was exactly the same as training, except that a distractor cursor of a different shape and colour mirrored the controlled cursor's movement. In this example, the 'X' could be either the controlled or distractor cursor; in either case, the distractor is left–right reversed. The position, letter and colour of the cursors, as well as the position of the large circle, changed from trial to trial (see electronic supplementary material for full details).

all other perceptual properties of the controlled cursor. The only difference was that the distractor was reversed in either the horizontal or vertical plane.

3. RESULTS

Figure 2*a* shows that humans $\chi^2(3) = 5833$, $n = 40$, $p < 0.001$, and monkeys $\chi^2(3) = 3502$, $n = 4$, $p < 0.001$, were able to select the self-controlled cursor significantly more often than chance would predict. Monkeys Hank $\chi^2(3) = 3585$, $n = 1$, $p < 0.001$, Gale $\chi^2(3) = 346$, $n = 1$, $p < 0.001$, Lou $\chi^2(3) = 326$, $n = 1$, $p < 0.001$ and Murph $\chi^2(3) = 138$, $n = 1$, $p < 0.001$, each demonstrated individual performances that were above chance. Individual humans were all significantly above chance as well. This suggests that humans and monkeys had the ability to monitor their own actions and identify the cursor they were controlling. This is the first demonstration that monkeys can recognize their own self-generated actions. Debriefings of human subjects found that most (67.5%) freely reported feelings of self-control when describing their strategy for completing the task; no human reported any strategy that did not involve self-control.

As predicted, when humans and monkeys did make errors, they tended to select the distractor cursor more often than the other cursors that were not onscreen while the controlled cursor was being moved (figure 2*b*). Humans $\chi^2(1) = 44$, $n = 40$, $p < 0.001$, monkeys $\chi^2(1) = 498$, $n = 4$, $p < 0.001$ and individual monkeys Hank $\chi^2(1) = 260$, $n = 1$, $p < 0.001$, Gale $\chi^2(1) = 97$, $n = 1$, $p < 0.001$, Lou $\chi^2(1) = 100$, $n = 1$, $p < 0.001$ and Murph $\chi^2(1) = 82$, $n = 1$, $p < 0.001$ all selected the distractor cursor more often. Individual analysis of each human revealed similar trends. Both species probably relied on sensorimotor- or kinesthetic-visual matching [24] and were thus sometimes confused by the relationship between their actions and those of the distractor.

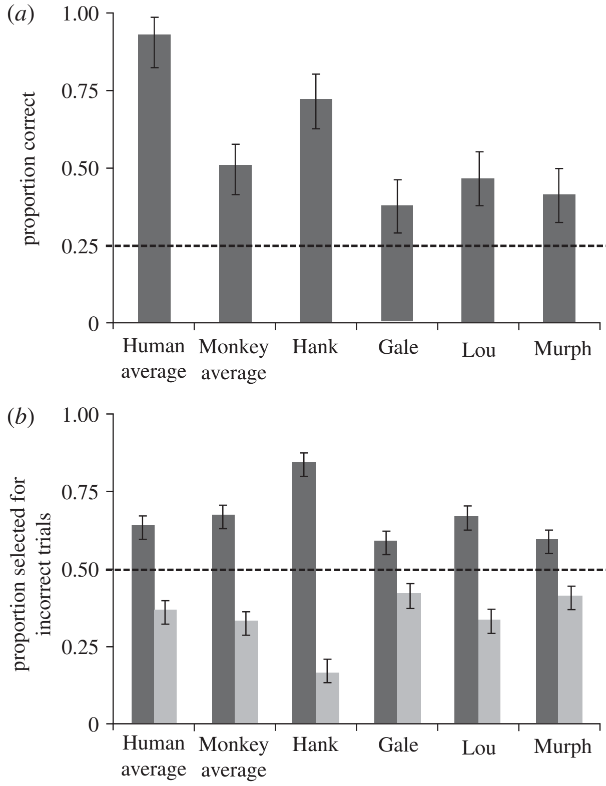

Figure 2. (*a*) Proportion of correct selections of the self-controlled cursor for humans and monkeys in the testing phase (figure 1, right). Individual averages for monkeys are also shown. (*b*) Proportion of incorrect selections of the distractor cursor and to the other cursors that were not onscreen while the subjects moved the controlled cursor. Because the two other cursors did not share any relationship from trial to trial, they are collapsed into a single column for humans and monkeys. As such, chance responding proportion is predicted to be the much stricter 0.50. Error bars indicate standard error; the dashed line shows performance predicted by chance. Dark grey bars, distracter; light grey bars, other.

4. DISCUSSION

Humans and four rhesus monkeys were able to identify their own actions, probably by monitoring the relationship between intentions, sensorimotor cues and perceived consequences. This process, in humans, gives rise to the sense of self-agency, and is closely related to self-awareness. Given that rhesus monkeys are capable of metacognition [12], and that self-agency judgements have been linked to metacognition [23], it is possible to conclude that rhesus monkeys probably have some sense of self-agency.

The current results are the first demonstration that rhesus monkeys have some understanding of self-agency. A great deal of further investigation is required to determine the extent and the nature of this ability. Do rhesus monkeys' failures on the mirror self-awareness test suggest that self-agency and self-awareness are two dissociable effects? Or does the current task simply eliminate a social bias and thereby allow monkeys' self-awareness to be measured? Did the monkeys' joystick training aid them, or would less experienced monkeys (or perhaps touchscreen-trained monkeys) perform equally well? It is possible that joystick experience taught the monkeys some non-agency-related tactic. Or, joystick use itself might require or benefit from some sense of self-agency. Future research must investigate these questions, as well as the role of executive processes in action monitoring and self-identification, the effect of temporal as well as directional distortions, and the ability of other species—both mirror self-recognizers and non-self-recognizers—to complete the task.

Because this is the first such demonstration of self-agency in a species that has not passed the mirror self-recognition test, the results may shed light on apparent self-awareness deficits in humans. Mirror self-recognition is developmentally delayed in autistic children, and absent in many mentally retarded, Alzheimer's, and schizophrenic subjects [25]. It is not entirely clear why this deficit occurs [26]; like rhesus monkeys, these groups may simply have biases against mirrors. If they attempted to distinguish self-generated actions from partially altered actions in the reported paradigm, we could potentially see whether the breakdown in their mirror self-recognition is due to an inability to process intentional, perceptual, sensorimotor or conscious self-monitoring information.

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