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Ventro-Ventral Copulation by an Adult Male-Female Pair of Japanese Macaques at Arashiyama

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Ventro-ventral (VV) mountings during copulation are most dominant in humans. In contrast, nonhuman primates have a strong bias toward dorso-ventral mountings, and only apes have been known to show VV mountings during copulation between a pair of mature individuals. Reporting VV mountings during copulation in primates other than apes is critical to discussions regarding why VV mountings have been limited to apes among primates. Here, I report VV mounting in a mature male and female pair of provisioned Japanese macaques (*Macaca fuscata*). This is the first report of VV mountings during copulation by adult nonhuman primates without disabilities other than apes. The pair of monkeys performed VV mountings 13 times over a week. Following the mounting series, including VV mountings, the presence of a copulatory plug was confirmed around the female's vagina, indicating that the VV mountings were part of their copulatory behaviors. The male initiated all VV mountings, and the female was often uncooperative during these attempts. In all cases, the female was lying on her back, and the male was on top. The pair were in close contact and did not see each other's faces during VV mountings. This report suggests that eye contact between mates and morphological characteristics are the primary reasons for the evolution of VV mountings during copulation in apes.

Keywords
Macaca fuscata, copulatory posture, face-to-face, eye contact, morphological constraints

Introduction
Although dorso-ventral (DV) mounting is prevalent during copulation in nonhuman primates (Dixson, 2012), ventro-ventral (VV) mounting, wherein males and females face each other, is the most dominant in humans (Gebhard & Johnson, 1998; Kinsey et al., 1948). Among nonhuman primates, only apes other than chimpanzees (*Pan troglodytes*) have been reported exhibiting VV mountings during copulation between mature individuals (*Symphalangus syndactylus*: Koyama, 1971; *Hoolock leuconedys:* Pan, 2000; *Pongo pygmaeus*: Nadler, 1977; *Gorilla beringei*: Breuer & Ndoundou Hockemba, 2007; *Pan paniscus*: Kano, 1980; Thompson-Handler et al., 1984; summarized in Supplementary material 1). Only one exception has been recorded from the Japanese macaque (*Macaca fuscata*), where the male held the female up ventrally and copulated with her while standing on two legs (Hanby et al., 1971). However, in this case, the female had severe limb disabilities, which made copulation in the typical DV posture difficult. To the best of my knowledge, there have been no reports of VV mountings during copulation between mature individuals in primates other than the Hominoidea, except in this case.

Here, I report the first case of VV mountings during copulation by a pair of adult Japanese macaques without disabilities. The Japanese macaque is a seasonally breeding species that generally copulates with multiple partners from October to February (Takahata, 1980; Wolfe, 1978). Male Japanese macaques require multiple mountings during one mating encounter for ejaculation (Tokuda, 1961). After successful ejaculation, a sperm coagulum ("copulatory plug") can be seen around the vagina. Although VV mountings have been reported in various age-sex pairs in this species (Hanby & Brown, 1974; Leca et al., 2014b; Vasey & Reinhart, 2009), mature male-female pairs show only DV mountings during copulation (Wolfe, 1978).

Methods
I studied a semi-provisioned free-ranging group of Japanese macaques at Arashiyama Monkey Park Iwatayama (AMP), Kyoto, Japan. As provisioning and long-term research activities in AMP started in the 1950s (Huffman et al., 2012), the monkeys in this group were habituated to human observers. As of October 2020, there were 130 monkeys in this group and all members were individually identified by their physical features.

A mature male-female pair showed VV mountings during copulation. The male was Cooper-65-75-84-96 (Co96), a 24-year-old second-ranking monkey, and the female was Yun-76-81-91-03 (Yu03), a 17-year-old nulliparous monkey. Both monkeys did not have any injuries or disabilities during the study period. During the mating season, some of the females in this group were reproductively controlled using oral contraceptives (Shimizu, 2012). However, Yu03 was not under reproductive control in the study year.

From October 24, 2020, to November 8, 2020, I recorded the behavior of the target pair through focal sampling and video recording. On October 24, park staff observed the first and second cases of VV mounting.

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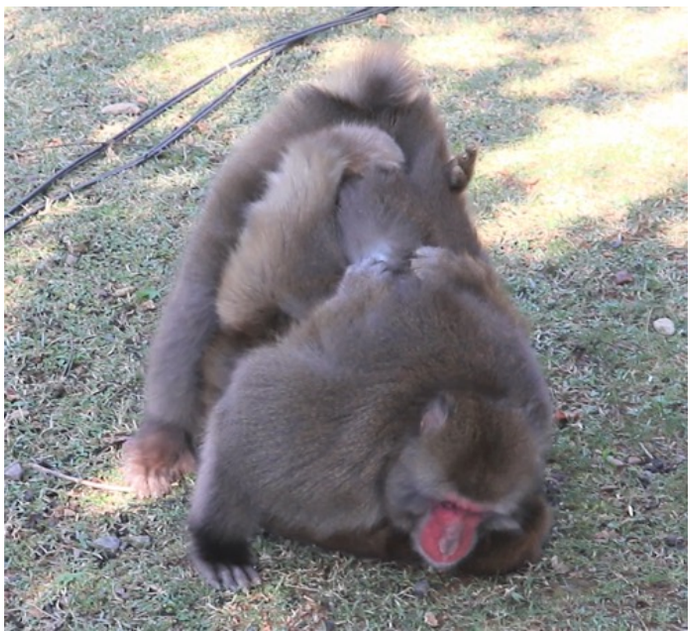

Figure 1. Ventro-ventral mounting between Co96 and Yu03. The top was Co96 (male), and the other was Yu03 (female). They were in close ventro-ventral contact and did not exhibit eye contact with each other.

After the second observed VV mounting, I started focal observation and continued following the pair until 16:00 (total 167.1 minutes), except when I lost sight of the targets. From October 25, observational sessions started when both targets were simultaneously in view. These sessions ended when the pair finished their mounting series with ejaculation or when I lost sight of one or both monkeys. I stopped observation during feeding shows in AMP. From October 27, no mounting between the targets was observed in some sessions. For this reason, from October 31, the observation was put on hold when mounting did not occur after >10 minutes of continuous observation. The total observation time was 586.4 minutes. Additionally, I recorded mounting postures when I observed Co96 mounting females other than Yu03 until February 7, 2021.

I defined "VV mountings" as follows: "the two participants embraced each other with their arms and legs, with chest-to-chest and belly-to-belly contact, facing each other in a standing, sitting, or lying position" (Gunst et al., 2013, p. 1234) and "DV mountings" as "the mounter grasping with his or her feet between the mountee's ankles and hips, and with his or her hands on the mountee's back" (Vasey et al., 2006, p. 120). When the mountings ended in the middle, I named them "incomplete."

Results

Overview

VV mountings by the pair were recorded 13 times (Figure 1). The first case was observed by park staff at 12:09 JST on October 24, 2020. It was unclear in what context the first VV mounting occurred. A total of 12 mountings were consecutively observed in this mounting series, with eight VV mountings (including the first observed VV mounting) and four DV mountings (Figure 2). The mounting series ended at 12:21 with a DV mounting, which seemed to be accompanied by ejaculation. A copulatory plug was confirmed around the female's vagina at 12:37. After this observation, VV mountings were observed twice on October 24 and once each on October 25, 28, and 30. After the mounting series on October 25 that included one VV mounting and ended with a DV mounting, a copulatory plug was observed around the female's vagina.

Although VV mountings were rarely observed after

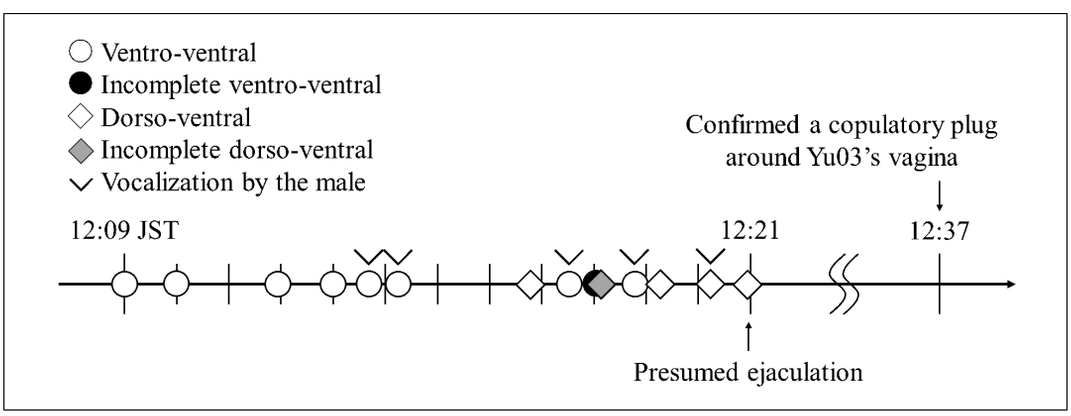

Figure 2. Mounting series including the VV mounting observed for the first time. In "incomplete" mountings, the mounting ended in the middle (see the methods).

Table 1. Details of all cases of VV mountings.

Date	Top	Duration[1]	Before VV mountings			During VV mountings			
			Initiation[2]	Turning[3]	Running away[4]	Eye contact	Thrusting	Vocalization[5]	Insertion
10/24	♂	–	–	–	–	–	–	–	–
"	♂	6.5	♂	■	□	□	□	□	–
"	♂	9.8	♂	□	□	□	■	□	–
"	♂	–	–	–	□	□	■	□	□
"	♂	2.9	♂	□	■	□	□	■	□
"	♂	5.4	♂	■	□	□	□	■	–
"	♂	4.3	♂	■	□	□	□	■	–
"	♂	5.3	♂	■	□	□	□	■	–
"	♂	5.2	♂	□	□	□	□	□	□
"	♂	2.1	♂	□	□	□	□	□	–
10/25	♂	4.1	♂	■	□	□	■	□	–
10/28	♂	2.0	♂	□	□	□	□	□	–
10/30	♂	–	–	–	–	–	–	–	–

■…Observed, □…Not observed, –…Unclear
1. Duration from when the female's back on the ground to the end of VV contact (seconds)
2. Individual who approached and started contact
3. The female turned around the body to face the male initiating contact
4. The female ran away from the male approaching her
5. The male vocalized during VV mountings

October 24, the male sometimes approached the female to mount her ventro-ventrally. However, these attempts were mostly incomplete for the following reasons: the female refused to be pushed down by the male in 18 cases (Supplementary material 7), the male quit the mounting abruptly in two cases, and they lost their balance due to poor footing in three cases. Even though the female rejected these attempts many times, she often turned her body to face the male initiating the mountings. Furthermore, DV mountings were sometimes incomplete, mainly because the male quit the mounting in the middle.

Mountings by the pair were last recorded on October 30. Subsequently, I observed three mounting series by the male with two other females. In these cases, the male and a female exhibited DV mounting. Only once was the male observed attempting to perform VV mountings on an adult female other than Yu03, but the female rejected this attempt.

Yu03 gave birth on May 10, 2021. This was 198 days after the first mounting and 192 days after the last mounting by both sexes observed in 2020.

Detailed descriptions of VV mountings

(a) Before VV mountings

Table 1 presents the details of all observed cases of VV mountings. In all cases where the beginning of the mounting was clear, the male approached the female. At the beginning of the VV mounting, the male pushed her down from her front or side in all cases, and the female jumped on the male from the front in one case. In five cases, the female turned her body to face the male approaching her. In one case, the female ran away from the male in response to his approach, but the male caught her.

(b) During VV mountings

In all cases, the female was lying on her back, and the male was on top with his hand and feet on the ground. Their heads were positioned next to each other (Figure 1), and they did not show eye contact with each other in all cases (Table 1). The genital areas of both monkeys appeared to be in contact, except in one case where the pair showed a crossing posture with their ventral positions in contact. The female hugged him with her arms and legs, and her hands grabbed the fur on his back. Three cases included pelvic thrusting by the male, while they only kept in close contact with each other in the remaining cases. The male vocalized in four cases (Supplementary material 4, 5). In three cases where the genital areas were visible, the penis was not inserted into the vagina (Supplementary material 6).

(c) After VV mountings

The results are described in Supplementary material 2.

(d) Comparison with other mountings by Co96 and Yu03

Figure 3 shows the frequency of each mounting between the targets during the study period. Observational sessions wherein no mounting was observed were excluded from the overall data. The total observation time for the analysis was 463.8 minutes. The frequency of VV mounting was much lower than that of DV mounting. The frequency of incomplete VV mountings was over twice that of complete VV mountings. Additionally, the female frequently mounted the male (Supplementary material 4).

Discussion

This is the first report of VV mountings during copulation by a pair of adult primates without disabilities other than apes. A mature male and female pair of Japanese macaques engaged in VV mounting multiple times. After multiple mountings, including VV mountings, a copulatory plug was confirmed around the female's vagina, indicating that the VV mountings in this pair were not simply "embracing" (Nakagawa et al., 2015) but were part of their copulatory behavior. The female gave birth in 2021. However, the infant's biological father might not have been the male because the gestation period of provisioned Japanese

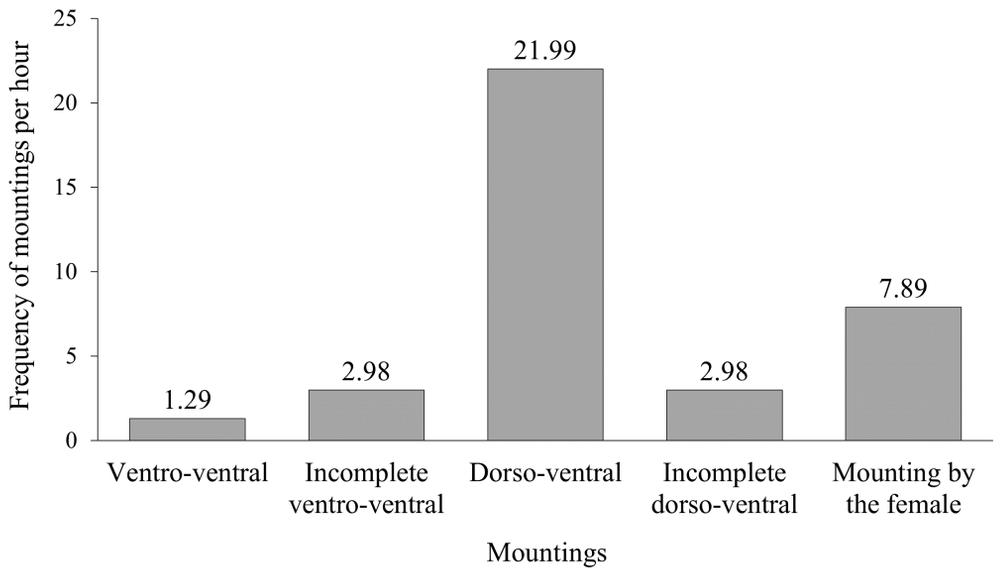

Figure 3. Frequency of each mounting between Co96 and Yu03 during focal observation. Of 13 cases of VV mountings, 10 cases were recorded during focal observation.

macaques is 161–188 days (Nigi, 1976), and the number of days between the case day and the delivery day (192–198) was not within this range.

VV mountings during copulation by Japanese macaques had some similarities and differences to VV mountings by apes (Supplementary material 1, 3); the female responses to VV mountings are particularly noteworthy. The male initiated VV mountings in all cases. When the male attempted to mount ventro-ventrally, the female frequently rejected him. Even in one case of VV mounting, the female tried to run away from the male approaching her. Although the female turned her body to face the male before VV mountings in some cases, which would have made VV mountings easier, it is unlikely that the female accepted VV mountings because similar behaviors were also observed when the female rejected the attempts by the male. Contrary to Japanese macaques, females actively invite males into VV mountings in apes (Breuer & Ndoundou Hockemba, 2007; Thompson-Handler et al., 1984), except in "sexual coercion" (Nadler, 1977), one of the common mating strategies by male orangutans (MacKinnon, 1974). The reason for this interspecific difference is unclear; however, it is possible either that this particular female was unfamiliar with VV mountings or that VV mountings and the behavior of the male pushing down the female imposed a great burden on her.

VV mountings may be associated with immaturity in sexual behaviors in this species (Gunst et al., 2013). However, both sexes in this study were fully mature adults, and the female gave birth in the next birth season. Therefore, it was unlikely that the sexual behaviors of both sexes were immature. Additionally, as both the male and the female were not under reproductive controls in the study year, the contraceptive management in AMP did not affect the VV mountings. Furthermore, provisioning is unlikely to have had an effect as there are no similar reports from other long-term provisioned groups of Japanese macaques.

Co96 was 24 years old and thus an elderly male (Koyama et al., 1975; Sugiyama, 1976). Wolfe (1978) reported an unusual copulatory behavior in an old male Japanese macaque where the male put his hands on the female's shoulder and rubbed his genitals on her perineum. These findings suggest that old age is associated with unusual copulatory behaviors by male Japanese macaques. However, this explanation is contrary to the fact that Co96 showed typical DV mountings when he mounted a female other than Yu03. Detailed information regarding copulatory behaviors of old male Japanese macaques is limited and is necessary before examining this possibility.

Dixson (2012) proposed three reasons explaining why VV mounting during copulation is limited to apes among primates. The first is that the higher cognitive abilities characteristic of apes promote diverse copulatory behaviors (Nadler, 1975). This possibility cannot be examined only by the current case. However, considering that Japanese macaques exhibit VV mountings in non-conceptive sexual activities (Leca et al., 2014b; Vasey & Reinhart, 2009; Wolfe, 1978), factors other than their cognitive abilities are likely to be associated with VV mountings in this species, such as age (Gunst et al., 2013; Hanby & Brown, 1974; Leca et al., 2015), size difference (Leca et al., 2014b), or group "traditions" (Leca et al., 2014a; Vasey & Reinhart, 2009).

Secondly, VV mounting can facilitate eye contact between partners (Dixson, 2012). In primates, such communication can promote successful copulatory behaviors (Savage-Rumbaugh & Wilkerson, 1978; Zanoli et al., 2021) that would increase reproductive success. Compared to other mountings, VV mounting would greatly facilitate this communication, and many studies have reported eye contact during VV mountings in apes (Breuer & Ndoundou Hockemba, 2007; Nadler, 1988; Thompson-Handler et al., 1984). In Japanese macaques, a female often looks back at a male's face during DV mountings (Wolfe, 1984). However, during the VV mountings in the current study, neither monkey looked at the other's face. This result indicates that VV mountings do not promote, or even decrease eye contact between copulating males and females in Japanese macaques.

The third reason is that morphological specialization for suspensory positions facilitates VV mountings during copulation when hanging on a tree, as reported in gibbons and orangutans (Pan, 2000; Rijksen, 1978), and this might have been inherited by more terrestrial species such as gorillas, bonobos, and humans (Dixson, 2009; 2012). The fact that the penis was not inserted during VV mountings in some cases of this study supports this suggestion. This hypothesis is more conducive to the second potential reason for this behavior: eye contact. The trunk is often vertical during brachiation in apes (Leutenegger, 1974). The morphological features of apes are adapted to such vertical positions which allow individuals on the top to have an upright upper body and to make eye contact with their partner during VV mountings. Unlike apes (Hess, 1973; Nadler, 1977; Savage-Rumbaugh & Wilkerson, 1978), the male in the current case did not have his upper body upright during VV mountings (Figure 1). Morphological constraints in Japanese macaques would have made it difficult or even impossible to do so and to make eye contact during VV mountings. DV mountings would allow monkeys to be more vigilant to surrounding dangers than VV mountings (Baker & Bellis, 1995). Therefore, VV mountings could not contribute to eye contact, and DV mountings might be more adaptive than VV mountings for Japanese macaques. This explanation may be significant when examining why VV mountings during copulation are limited to apes.

VV mountings can reduce the physical burden on the mountee compared with DV mountings when the difference in body size between individuals is considerable. Leca et al. (2014b) and Yamagiwa (1987), who reported male homosexual behavior in Japanese macaques and mountain gorillas, respectively, offered this suggestion. However, in the current case, the body size difference between Co96 and Yu03 was not particularly large compared with that in other mating pairs. Additionally, the pair performed DV mountings much more frequently than VV mountings during copulation (Figure 3). Therefore, reducing physical burden cannot adequately explain the VV mountings observed in this study. This hypothesis would also be rejected for VV mountings in apes because the size difference between sexes in this lineage is not particularly large compared to other primate lineages (Plavcan, 2001).

The current case provides critical information when comparing VV mountings during copulation in apes. Morphological specialization to suspensory positions in apes may facilitate VV mountings, and these mountings can promote eye contact during copulation, which is a crucial form of communication used to increase reproductive success. The primary reason why primates other than apes do not perform VV mountings may be that their morphological constraints make maintaining eye contact with their mates during VV mountings difficult. Future studies need to investigate this possibility, for example, by compiling similar reports of VV mountings in Japanese macaques and apes or using morphological simulation to examine whether primates other than apes can make eye contact during VV mountings.

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Author contribution

The author developed the study concept and design, collected and analyzed data, and wrote the manuscript.

Ethical statement

This study was conformed to the Guidelines for Field Research established by the Ethics Committee of the Primate Research Institute, Kyoto University. This study was approved by Arashiyama Monkey Park Iwatayama.

Supplementary material

Electronic supplementary materials are available online.

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