

Does mirror enrichment improve primate well-being?

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Abstract

Primates are highly social animals and appropriate enrichment is required to ensure their psychological well-being. Mirrors are sometimes used as social or sensory environmental enrichment. In this paper we investigate the suitability of mirrors as enrichment for captive primates, by reviewing the literature on mirror implementation in captive primate environments. Mirror-directed responses are mainly social as the mirror self-image is often seen as a conspecific. Although positive exploration and affiliative behaviours are observed, negative aggressive behaviours towards the mirror are most frequently recorded, and abnormal behaviours in primates do not decrease in mirror-enriched environments. There appear to be differences in habituation rates to mirrors amongst primates. While habituation to enrichment is generally perceived to be undesirable, this criterion should not apply when mirrors elicit negative behaviours. Primates that show mirror self-recognition, which are mostly great apes, may be best suitable for mirror enrichment, as they do not perceive the mirror self-image as a threatening conspecific. Increasing the understanding of the reflective properties of a mirror might help primates to understand that the image in the mirror is not real. This could be attained by using small, mobile mirrors. We suggest that mirrors can make decent primate enrichment if the primate understands its reflective properties, which should be evaluated on an individual level. Appropriate use of mirrors as sensory enrichment can improve primate well-being and prevent suffering.

Keywords: abnormal behaviour, animal welfare, captivity, self-recognition, solitary, stress

Introduction

Although wild non-human primates (hereafter referred to as primates) are mainly restricted to tropical habitats, captive primates can be found all over the globe. In zoos they are a popular visitor attraction, and laboratories house primates for various experimental purposes. Humans have the obligation to ensure the well-being of these captive animals (Clark *et al* 1997). In this work we will refer to well-being as the psychological state of the animal, and welfare as comprising both well-being, the animals' physical health and the ethical issues involved in these topics (eg Clark *et al* 1997; Fraser *et al* 1997).

The captive environment often differs substantially from its wild counterpart, which can have negative consequences for animal well-being (Broom 1991; Morgan & Tromborg 2007). Laboratory environments — and to a lesser extent zoo environments — can restrict the natural behavioural repertoire of animals and thereby lead to abnormal behaviours (Mason 1991b; Hosey 2005). Abnormal behaviours comprise unusual performances that indicate that the animal's well-being is, or has been, sub-optimal (Broom 1991; Mason 1991a). Abnormal behaviours are observed in captive environments and rarely seen in the wild (Hosey 2005; Birkett & Newton-Fisher 2011, but see Grewal 1981).

The behaviours can signal psychological strain since they may be performed by the animal to cope with a stressful environment (Mason 1991a). Furthermore, self-injurious abnormal behaviours, such as hair-pulling, slapping or biting oneself, can be physically harmful for the animal. It appears that the prevalence and severity of abnormal behaviours rises with the deterioration of the animal's environment or life experiences (Lutz *et al* 2003; Hosey 2005; Olsson & Westlund 2007).

Primates are highly social animals and social companionship is as much a need in a primate's life as food (Dettmer & Fragaszy 2000). The absence of social companionship is particularly detrimental to the primate's well-being (Mason 1991a). Oxytocin and arginine vasopressin, two hormones associated with good well-being, were significantly lower in socially isolated common marmosets (*Callithrix jacchus*) than in social marmosets (Seltzer & Ziegler 2007). Social isolation generally causes a high number of abnormal behaviours in the animal (Olsson & Westlund 2007; Price & Stoinsky 2007), which can persist even after the captive conditions are improved (Mason 1991a,b; Olsson & Westlund 2007). Ridley and Baker (1982) argue that to decrease abnormal behaviours and increase well-being, one should rather stimulate social interactions than attempt to suppress the abnormal behaviours. In situations where social

housing is not feasible for experimental or logistical reasons, mirrors are sometimes used as social enrichment to simulate a conspecific, which is thought to reduce the negative effects of isolation (eg Bayne 1989; Piller *et al* 1999; McAfee *et al* 2002; Sherwin 2004; Dalle Zotte *et al* 2009). Mirrors can also be regarded as sensory enrichment as they can expand the animals' visual field, thereby providing a visually stimulating environment (Lambeth & Bloomsmith 1992; Brent & Stone 1996; Lutz & Novak 2005; Wells 2009). For example, a mirror gives primates visual access to its own face and other parts of the body, but also to parts of the environment that otherwise cannot be seen. Additionally, mirrors can be used to monitor other individuals or humans without a direct gaze, which is a threat behaviour in many monkey species. Providing monkeys with an enhanced ability to scan the environment may contribute to their well-being by increasing predictability. In animals other than primates, mirrors have been demonstrated suitable environmental enrichment (hereafter referred to simply as 'enrichment'). Rabbits (*Oryctolagus cuniculus*), for example, preferred a cage with mirrored walls over a cage without mirrored walls (Dalle Zotte *et al* 2009). Similarly, Java sparrows (*Padda oryzivora*) showed a preference for a situation in which they could see themselves in a mirror over a situation without such opportunity (Watanabe 2002). Lutz and Novak (2005) defined enrichment, aimed at improving animal welfare, as 'any change to the cage environment that would appear to be positive from our human perspective'. However, not all enrichment attempts improve the animals' well-being and physical health (Lutz & Novak 2005; Skibieli *et al* 2007; British and Irish Association of Zoos and Aquariums [BIAZA] 2014). For the welfare of the animal, only 'beneficial enrichment' (Würbel & Garner 2007) should be used.

This work provides a review of the literature in which primates are confronted with mirrors, either for enrichment or experimental purposes, to assess the suitability of mirrors as enrichment for captive primates. Following Novak and Suomi's (1988) assessment of enrichment, we look at: (i) positive and negative behavioural reactions after implementation of the mirror; (ii) indicators of stress upon confrontation with the mirror; and (iii) habituation to the mirror. Additionally, we provide a summary of studies on mirror self-recognition in various primate species to fully assess the suitability of mirrors as enrichment. We conclude with suggestions on how primate well-being could be improved by the appropriate use of mirror-enrichment.

Behavioural responses to mirrors

Positive behaviour

Enrichment should lead to an increase in positive behaviour and either no change of, or a decrease in, negative behaviour (Lutz & Novak 2005; Boissy *et al* 2007; Tarou & Bashaw 2007; Würbel & Garner 2007). Behavioural indicators of good welfare include play behaviour, affiliative behaviour and exploration (Boissy *et al* 2007). Both increases and decreases in positive behaviour are observed in primates

confronted with mirrors. Young stump-tailed macaques (*Macaca arctoides*) frequently directed play and exploration behaviour towards their mirror self-image (Anderson 1983). Additionally, pygmy marmosets (*Cebuella pygmaea*) are observed to interact with their mirror self-image, and follow their own reflection in the mirror (Eglash & Snowdon 1983). Self-exploration behaviour is frequently observed in great apes, and in a lesser degree in gibbons, when the mirror is used to view and manipulate body parts which otherwise are out of sight (chimpanzees [*Pan troglodytes*]: Gallup 1970; Suarez & Gallup 1981; Swartz & Evans 1991; Lambeth & Bloomsmith 1992, orangutans [*Pongo pygmaeus*]: Suarez & Gallup 1981, bonobos [*Pan paniscus*]: Westergaard & Hyatt 1994; Walraven *et al* 1995; Inoue-Nakamura 1997, gorillas [*Gorilla gorilla*]: Patterson & Cohn 2006; Posada & Colell 2007, and gibbons [*Hylobates lar*]: Hyatt 1998; [*H. lar*; *H. gabriellae*; *H. leucogenys*]: Ujhelyi *et al* 2000). Contrary to these apes, most animal species react to the mirror as if they are confronted with a conspecific, which we will hereafter refer to as *misidentification* of the mirror self-image. Primates that do not recognise themselves but misidentify their mirror self-image may direct positive social behaviours to the mirror. Anderson and Chamove (1986) found that solitary, mirror-reared stump-tailed macaques did not substantially differ in showing affiliative behaviour compared to peer-reared macaques. Nonetheless, the latter macaques showed more play behaviour, and especially more social play, than the solitary-reared macaques in a mirror-enriched room. The overall social responsiveness of peer-reared macaques was also higher than for the mirror-reared macaques. Furthermore, a decrease in positive behaviour due to mirror enrichment was observed by Lambeth and Bloomsmith (1992), who reported that affiliative behaviour among chimpanzee group members decreased when a mirror provided visual access to a neighbouring group of conspecifics. Thus, mirrors do not increase positive behaviour in all situations, and they appear to be unable to fully replace social companionship for primates.

Negative behaviour

Mirrors can also increase negative behaviours in primates. In this work, negative behaviours include aggressive and submissive behaviours, which are also commonly described in primate ethograms and behavioural repertoires (eg Stevenson & Poole 1976; Dolhinow 1978; Arnold & Barton 2001; Bezerra *et al* 2011). Abnormal behaviours tend to become established after a long period of negative experiences, and although they can be triggered by aversive stimuli, they do not necessarily follow directly after (Mason 1991b). We therefore classify abnormal behaviour as a behavioural marker of distress rather than negative behaviour here. The effect of mirrors on distress in primates will be discussed in the next section. Aggression is the most likely observable behaviour indicating anger or fear (eg Averill 1983; Davidson *et al* 2000), which are generally classified as negative emotions (Averill 1983). One exception to this statement may be found in the 'excited' feeling of shared anger that group members experience when acting aggressively toward a shared enemy

(‘Excitatory anger’; see Potter-Effron & Potter-Effron 2006). When an increase in aggressive behaviour is observed in the presence of a mirror compared to mirror absence, this most likely implies that the mirror elicits negative emotions which reduce the animals’ well-being. Increases in aggressive behaviour towards the mirror are quite frequently observed in a number of primate species: chimpanzees (Lambeth & Bloomsmith 1992), stump-tailed macaques (Anderson 1983; Straumann & Anderson 1991), lion-tailed macaques (*Macaca silenus*) (Clarke *et al* 1995) and tufted and white-headed capuchin monkeys (*Cebus apella* and *C. capucinus*) (Anderson & Roeder 1989; Marchal & Anderson 1993). Clarke *et al* (1995) additionally recorded an increase in submissive behaviour in long-tailed macaques (*Macaca fascicularis*), which may signify fear (Gilbert & Allan 1994; O’Connor *et al* 2002). Apart from the chimpanzees, the primates in the above described studies acted as if they misidentified their mirror self-image as a threatening conspecific. We will later discuss the potential cause and implications for the discrepancy between self-identifying great apes and other primates that misidentify the image. This disturbing experience of misidentification likely has a negative influence on the animals’ well-being. The aggression of the chimpanzees in Lambeth and Bloomsmith’s (1992) study was not directed at their self-images but at a group of conspecifics, to which they had visual access to via the mirror. Although one could argue that the intergroup aggression in the chimpanzees might increase intra-group social bonding (eg Slater *et al* 2009) and thereby increase well-being, the apes showed a decrease in affiliative behaviour upon mirror confrontation. This finding provides little support for the argument that mirror-presence increases well-being.

All in all, mirrors frequently contravene with the premises of beneficial enrichment. Although great apes often show exploration behaviour and little negative behaviour when confronted with their self-image, primates which misidentify their reflection show more negative than positive mirror-directed behaviours (see also Table 1).

Some authors argue that enrichment should facilitate and stimulate more natural, or species-specific, behaviours (eg Carlstead & Shepherdson 1994; Dawkins 2004; Honess & Marin 2006b; Skibieli *et al* 2007; Würbel & Garner 2007; Wells 2009). Allowing an animal to exhibit its natural behavioural repertoire can increase the animal’s well-being, and its chance of survival when reintroduced into the wild (Rabin 2003; Shepherdson 1998, cited in Skibieli *et al* 2007). Mirrors that simulate conspecifics can facilitate natural social behaviour in socially isolated primates which misidentify their mirror self-image for another individual. However, this can also cause negative behaviour and distress in the animal. And while primates may be confronted with their self-image when peering at a water surface, this is seldom as smooth as the surface of a mirror. Moreover, when a wild primate is startled by its self-image, a touch of the water’s surface disrupts the reflection, but with a fixed mirror the inability to remove the stressor could be a welfare issue.

Table 1 A summary of behavioural responses of primates upon confrontation with a mirror.

Positive behaviour	Negative behaviour
+ Chimpanzees ^{1,2,3,4}	– Chimpanzees ⁴
+ Orangutans ²	+ Tufted capuchin monkeys ¹¹
+ Bonobos ^{5,6,7}	+ Stump-tailed macaques ^{10,12}
+ Pygmy marmosets ⁸	+ White-headed capuchin monkeys ¹³
+ Stump-tailed macaques ^{9,10}	+ Crab-eating macaques ¹⁴
– Chimpanzees ⁴	+ Lion-tailed macaques ¹⁴

Responses can be positive (affiliative, play, exploration) or negative (aggression, submission) and increasing (+) or decreasing (-).

¹ Gallup 1970; ² Suarez & Gallup 1981; ³ Swartz & Evans 1991;

⁴ Lambeth & Bloomsmith 1992; ⁵ Westergaard & Hyatt 1994;

⁶ Walraven *et al* 1995; ⁷ Inoue-Nakamura 1997; ⁸ Eglash & Snowdon 1983; ⁹ Anderson & Chamove 1986; ¹⁰ Anderson 1983; ¹¹ Anderson & Roeder 1989; ¹² Straumann & Anderson 1991; ¹³ Marchal & Anderson 1993; ¹⁴ Clarke *et al* 1995.

Stress responses to mirrors

As opposed to negative behaviour, distress is not a direct response to the mirror but develops over time. Stress is generally described as an individual’s biological response to a threat to its homeostasis (Moberg 2000). This reaction can be measured physiologically, by examining blood pressure, heart rate or cortisol levels, or behaviourally, through observation of stereotypical, abnormal, or displacement activities (see Troisi 2002) (Honess & Marin 2006a). Stress is not necessarily harmful, but when the animal is unable to cope with the stressor and return to homeostasis, stress can become *distress*, which is detrimental to the animal’s welfare (Moberg 2000; National Research Council 2008). Mirrors that are used as enrichment should reduce and not increase distress levels. In theory, mirrors could improve the welfare of socially isolated animals by providing a simulated social situation if the mirror self-image is perceived to be a conspecific. However, social introductions are known to be extremely stressful to primates (Clarke *et al* 1995) as the dominance hierarchy has to be determined (Tamashiro *et al* 2005). Moreover, a mirror reflection could be a stressor if the mirror self-image is perceived as a threat, or as a conspecific that does not react in a socially appropriate way. Mirrors may also simulate inappropriate social groups and overcrowding, which too are sources of distress in animals in captivity (Morgan & Tromborg 2007).

Assessing the incidence of stereotypies and abnormal behaviours is a frequently used method to assess primate welfare, and it is often applied in evaluating the effectiveness of enrichment. For example, Bayne *et al* (1992) found that rhesus macaques (*Macaca mulatta*) showed a decrease in abnormal behaviour when their cage was enriched, but this increased in rate again upon removal of the enrichment devices. A similar stereotypy-reducing effect was observed when mirrors were used as stable enrichment for horses (*Equus ferus caballus*) (McAfee *et al* 2002; Mills &

Table 2 A summary of studies that found mirror self-recognition (MSR) in the described primate species by using the mark test or mirror self-recognition (MSE) only.

	Mark test	MSE only
Chimpanzee	<i>Pan troglodytes</i>	Gallup 1970
		Gallup <i>et al</i> 1971
		Suarez & Gallup 1981
		Povinelli <i>et al</i> 1997
Orangutan	<i>Pongo pygmaeus</i>	Suarez & Gallup 1981
Bonobo	<i>Pan paniscus</i>	Westergaard & Hyatt 1994
		Walraven <i>et al</i> 1995
		Inoue-Nakamura 1997
Gorilla*	<i>Gorilla gorilla</i>	Patterson & Cohn 2006 Posada & Colell 2007
Gibbon**	<i>Hylobates lar</i>	Hyatt 1998
	<i>H. gabriellae</i>	Ujhelyi <i>et al</i> 2000
	<i>H. leucogenys</i>	Ujhelyi <i>et al</i> 2000
Other primates***	<i>Macaca mulatta</i>	Chang <i>et al</i> 2015 Rajala <i>et al</i> 2010

* But see Suarez & Gallup 1981; Ledbetter & Basen 1982; Shillito *et al* 1999; Zaragoza *et al* 2011.

** But see Suddendorf & Collier-Baker 2009.

*** But see Anderson & Gallup 2011.

Davenport 2002). Rabbits, too, performed less displacement behaviour when their cage was enriched with a mirrored wall (Edgar & Seaman 2010). Finally, isolated heifers (*Bos taurus*) had a lower heart rate when a mirror was present (Piller *et al* 1999). Yet, for primates, this effect is not commonly observed. Lambeth and Bloomsmith (1992) found no decrease in abnormal behaviours in chimpanzees, most likely since the chimpanzees appeared to recognise themselves which inhibits the social effect, and mirror enrichment did not protect stump-tailed macaques from developing the typical isolation-related abnormal behaviours observed in solitary primates (Anderson & Chamove 1986). Moreover, Harris and Edwards (2004) observed African green monkeys (*Chlorocebus sabaues*) performing certain stereotypies only in front of a mirror.

Concluding, mirrors do not appear to offer beneficial enrichment for primates, perhaps because the mirror provides less satisfactory social stimulation for primates than it would for less socially intimate animals. Additionally, some primates seem to comprehend that the reflection in the mirror is not the same as a real conspecific (eg Eglash & Snowdon 1983; Harris & Edwards 2004; De Waal *et al* 2005) which may further reduce the socially facilitating impact of a mirror and hence its stress-allevi-

ating effect in socially isolated primates. On the other hand, primates may be able to habituate to stressors, including mirrors (Honest & Marin 2006a). Habituation, however, is in conflict with one of the success indicators of enrichment and will be discussed in the following section.

Habituation

It is generally agreed that enrichment should cognitively stimulate the animal (Lutz & Novak 2005; Skibieli *et al* 2007; Tarou & Bashaw 2007). Habituation to enrichment is therefore generally undesirable. The rate of habituation to mirrors seems to vary between and even within primate species. In chimpanzees, mirror usage increased or remained stable in the study of Lambeth and Bloomsmith (1992), while Brent and Stone (1996) reported a steep decrease of interest within less than two days. The latter authors argue that this discrepancy was due to characteristics of the mirror: while their study used a quite cloudy mirror with a flat surface, Lambeth and Bloomsmith (1992) used a convex mirror which could have been more interesting. Similar contrasting findings are observed in monkeys. While African green monkeys did not habituate to small mobile mirrors even one year after implementation (Harris & Edwards 2004), mirror-directed behaviours in stump-tailed macaques (Anderson & Chamove 1986), lion-tailed macaques, and crab-eating macaques (Clarke *et al* 1995) significantly decreased over time.

Regarding the primates' well-being, the question is not what causes these inter- and intraspecific differences in habituation, but rather whether a mirror's suitability as enrichment should be rated by habituation levels. Harris and Edwards (2004) and Lambeth and Bloomsmith (1992) argue that mirrors are an effective enrichment device as the primates showed low rates of habituation even after a considerable period of time. Yet, as noted earlier, the chimpanzees in Lambeth and Bloomsmith's (1992) study showed more negative behaviour towards the mirror and Harris and Edwards' (2004) African green monkeys incorporated the mirrors in stereotypic behaviours. Furthermore, Clarke *et al* (1995) reported that the rate of affiliative mirror-directed behaviours declined over time in both lion-tailed and crab-eating macaques, while the frequency of submissive behaviours did not decline in the latter.

Thus, counteracting habituation by providing animals cognitively challenging enrichment can increase well-being, but only under the condition that the animal possesses the skills to effectively deal with the challenge (Meehan & Mench 2007). When the primate is not able to 'solve' the puzzle of the mirror (ie it misidentifies its mirror self-image), the mirror may overstimulate the animal which leads to a decrease in well-being (Hosey *et al* 2009).

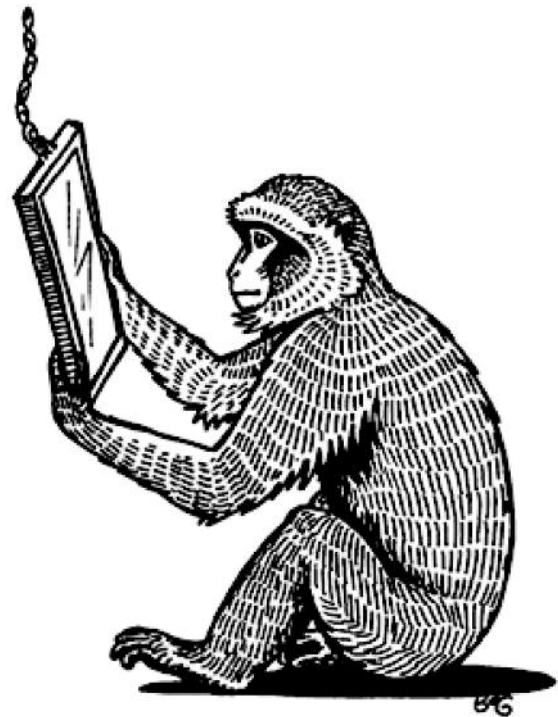
Mirror self-recognition

Perhaps the suitability of mirrors as enrichment depends on the primate's ability to comprehend the reflective properties of the mirror. One might argue that negative behaviour and distress will not occur if the primate is aware of the fact that its mirror self-image is him, and not a conspecific. The literature on mirrors used for self-recognition in primates is

more abundant than the effect of mirrors on primate well-being. Mirror self-recognition (MSR) is measured by observing self-directing behaviours in subjects while they look into the mirror (mirror self-exploration: MSE). Primates capable of MSR initially show positive or negative social responses to the mirror, which decrease over days and is replaced by MSE, such as grooming body areas that are visually inaccessible without the mirror (eg Gallup 1970; Swartz & Evans 1991). Gallup (1970) tested MSR in primates using the *mark test*, in which a spot which has no olfactory or tactile cues is painted on the face of an anaesthetised primate. If the primate later inspects the mark using the mirror, then it is said it possesses MSR. Although the mark test has become the standard method for measuring MSR in non-human animals (De Waal *et al* 2005), MSE can be accepted as evidence of MSR as well since the mark test is argued to be vulnerable to false negatives (De Veer & Van den Bos 1999; Heschl & Burkart 2006). More research into MSR in primates followed after Gallup's findings in the 1970s (Table 2). A paucity of studies failed to find MSR in a number of primate species that are not great apes. Despite some cases of primates other than great apes showing MSR (eg Rajala *et al* 2010; Chang *et al* 2015), the vast majority and more than half of the studied (great) ape subjects did not appear to recognise themselves in the mirror (Suddendorf & Collier-Baker 2009). The reasons for both inter- and intraspecies variability in MSR are still poorly understood (De Veer & Van den Bos 1999).

The absence of MSR does not necessarily imply that the primate misidentifies its mirror self-image as being another individual. De Waal *et al* (2005) argued that although some primates, including primates other than great apes, may not recognise their reflection as themselves, they do seem to understand the 'monkey in the mirror' is not a conspecific. A mobile mirror in which the characteristics of the reflection are influenced by the subject's manipulation of the mirror could aid primates in understanding that the image in the mirror is not a living animal (Figure 1). Indeed, little social behaviour is observed in some primates other than great apes when confronted with small mobile mirrors. The African green monkeys in Harris and Edwards' (2004) study showed no overt social responses to a small, hanging mirror, and little social behaviour was recorded in Rajala *et al* (2010), who used similar mirrors. In contrast, the properties of a large, fixed mirror may be difficult for a primate to comprehend, as the world in there appears so real. Indeed, Marchal and Anderson (1993) recorded a greater number of threats towards large mirrors compared to small. In summary, primates which show MSR may be best suitable to provide mirror-enrichment to, as they do not regard their mirror self-image as a threat. Nevertheless, the implementation of a small, mobile mirror could aid primates which initially misidentify their reflection to explore and eventually understand the reflective properties of a mirror. We hence suggest that mirrors should only be used as sensory enrichment, and not to simulate a social situation. The suitability of mirrors as enrichment should perhaps be assessed on a case-by-case basis.

Figure 1



A small mobile mirror could help primates understand a mirror's reflective properties. Illustration by B de Groot.

Animal welfare implications and conclusion

Mirrors are frequently used as primate enrichment. From this literature review we propose that mirrors can make suitable sensory enrichment for primates which understand the reflective properties of the mirror, since the negative influences outweigh the positive ones when the primate misidentifies its mirror self-image (ie it perceives its reflection as being a conspecific). While positive behaviours in the presence of a mirror are frequently observed in great apes, most mirror-directed behaviours in other primates which misidentify their mirror self-image are aggressive or submissive. Mirrors cannot replace social companionship and mirrors do not reduce the incidence of abnormal or stereotypic behaviours, perhaps due to the intimate nature of social contact in primates. Lack of habituation to mirrors may result from an inability to understand that the world in the mirror is not real. Although little habituation to enrichment is normally seen as positive, this is not the case when the mirror results in prolonged negative behaviour. Mirror self-recognition is only reliably found and replicated in great apes. Although not all individuals of great ape species are able to recognise their mirror self-image, they do seem to understand that their reflection is not a conspecific. This makes great apes the best candidates for the use of mirrors as sensory enrichment, but not as a remedy for social isolation. To determine whether mirrors are suitable enrichment, we suggest that it is necessary to examine whether the primate understands the mirror's reflective properties, by closely monitoring reactions to the mirror at an individual level.

Primates should initially be provided with a small, mobile mirror since this enables exploration and may aid in understanding that the reflection in the mirror is not another primate. Individuals should be monitored for negative social behaviours or stress. If a decrease in positive behaviours is observed, and negative behaviours are absent, the mirror could be relocated to increase interest. Mirrors can make appropriate sensory primate enrichment, improve the primate's well-being and prevent unintentional suffering. Lastly, we would like to stress the need for more research into the effect of mirror enrichment on primates, as most information on the topic is anecdotal rather than experimental.

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