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National Centre for the Replacement, Refinement  
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# Primate sensory capabilities and communication signals: implications for care and use in the laboratory

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## Abstract

To understand non-human primates and to provide them with good welfare it is important to know how they perceive the world and communicate among themselves. Of all the animals used in the laboratory, the perceptual world of the non-human primates is assumed to be most similar to that of man, in particular because of our shared refined visual capabilities. However, there are important differences between the sensory capabilities of non-human primates when compared with man, and there are genera and some species differences too. This article summarises the sensory capabilities of the non-human primates commonly used in the laboratory, highlights important modes of communication, and identifies several implications of these for designing and refining experiments, housing and husbandry systems and enrichment strategies.

**Keywords:** animal welfare, communication signals, hearing, non-human primates, refinement, senses, smell, taste, touch, vision, vocalisations

## Vision

### Visual acuity and binocular vision

With the exception of the prosimians, vision is considered the dominant sensory modality for non-human primates (hereinafter primates). Monkeys,

apes and humans demonstrate high visual acuity (ability to distinguish between closely-spaced visual stimuli), surpassed only by large, diurnal raptors, such as eagles. Behavioural tests demonstrate maximum acuities between about 40 and 53 c/deg for macaques and squirrel monkeys and 50 and 77 c/deg for humans (1). Even small sized monkeys, such as the common marmoset, demonstrate acuities that surpass much larger-eyed animals like the horse. Forward-facing eyes with overlapping visual fields give excellent binocular vision and together these capabilities enable primates to detect potential predators or harmful situations in the complex 3-dimensional forest environment, and to judge depth and distance when moving at speed between trees and branches. They also enable the accurate hand-eye coordination required for, say, capturing fast moving insect prey or manipulating plant material.

### Visual stimulation

From the point of view of housing and husbandry in the laboratory, it is a common observation that primates are highly reactive to visual stimuli and will make considerable efforts to gain visual information about their surroundings. They show a constant high level of attention to conspecifics.

- Whenever possible, rooms housing primates should be provided with windows, since these

can provide visual stimulation and are a source of natural light (2) (Fig 1). Light intensity is important since it is positively correlated with activity (3,4), and affects fecundity in common marmosets (5).

- Doors and access corridors should also have windows, so that animals can see who is about to enter the room and when – this will prevent them being startled when staff appear unexpectedly.
- Mirrors can be used to allow primates to observe activity in other areas, such as an adjacent corridor, and so expand the animals' environment (6-8) – adjustable mirrors can be controlled by the animals (Fig 2).
- Where primates are housed in cages, two-tiers should not be used, so that all animals receive the same opportunities for visual stimulation and staff interaction, quantity and quality of light, and ability to retreat to a high perch above care staff (9-10).
- Motion in various forms, such as TV, video images or video games, can be used as visual stimulation for primates (11-13). However, note that TVs and video monitors are designed with humans in mind and, since primates differ in aspects of visual processing, such as visual acuity, colour vision and critical flicker-fusion threshold, other species may perceive video images differently to us (14).



**Figure 1.** *Windows are a valuable source of visual stimulation – animals at the UK Centre for Macaques spend a great deal of time looking out of the large bay windows.*



**Figure 2.** *Adjustable mirrors provide an element of control of the environment, and allow animals to observe themselves, conspecifics and staff.*

### Colour vision

Most primates have excellent colour vision that is quantitatively and qualitatively superior to that of other mammals (15-17). Colour vision is important for detecting and selecting ripe fruits from unripe and semi-ripe ones. However, fruit ripeness is not always indicated by colour or other external properties of the fruit so, in addition to visual inspection, primates will sniff, lick and touch individual fruits to assess their stage of maturity (18-19). Unfamiliar and experimentally modified foods tend to be assessed using smell, taste and touch, in addition to vision, and for longer than familiar food items (20).

Colour vision is thought to be important for the detection of insect prey and predators, as well as fruit (21-27), and communicating with conspecifics. For example, adult male and female rhesus macaques undergo a hormonally-regulated reddening of facial and anogenital skin during the mating season. Experiments have shown that females exhibit preferences for red versus pale computer-manipulated male faces, and it is proposed that male colouration might provide a cue to male quality (28).

Old World monkeys and apes have trichromatic colour vision, similar to most humans. They have three different kinds of opsins (retinal protein pigments) that absorb light of green, blue and red wavelengths, which the brain processes to produce full-colour images. Most diurnal New World monkeys and prosimians, however, have polymorphic colour vision. In these primates, trichromatic vision is achieved through the presence of multiple alleles at a single X-chromosome-linked opsin locus, and therefore only heterozygous females can be trichromatic; homozygous females and males are all dichromatic, similar to colloquially 'colour blind' humans (15,29) (Fig 3). In the case of marmosets, tamarins, squirrel monkeys and capuchins there are six different visual phenotypes possible. The nocturnal owl monkeys are different, as one might expect; they are phenotypically monochromatic.



**Figure 3.** A red-bellied tamarin against foliage as might be seen by a trichromatic conspecific (heterozygous females) (left) and dichromatic conspecific (homozygous females and males) (right).

Dichromacy has been shown to be advantageous over trichromacy for detecting and selecting certain foods, but the range of visual phenotypes in New World monkeys and prosimians is likely to have broader implications for predator detection, social behaviour and group dynamics (23-27). It is, therefore, of importance to all behavioural scientists

studying these animals in the field and in captivity (30).

- For example, use of artificial visual stimuli (e.g. photographs, slides and computerised images) to study behaviour should be used with caution (31) – colours that trichromats see as yellows, browns, greens, and reds may be alike to dichromats (21).
- Similarly, when choosing targets for positive reinforcement training, colour should not be a cue that is used as it may not be as distinguishable to the primate's eye as to the human eye.

### Night vision

The cone photoreceptors that are responsible for the ability to see colour in vertebrates only function effectively when in bright light. Consequently, diurnal vertebrates, including primates, are more or less blind to colour in the dark of night. Whilst rod photoreceptors permit them to see at low light intensities (e.g. the faint light of the moon), colour differentiation is reduced.

- To enhance night vision and prevent primates from being startled, low level lighting should be provided for the changeover from light to dark (i.e. dawn and dusk periods) (32). This will also help prevent the serious injuries that can occur if animals are caught "mid-leap" when "on-off" lighting (i.e. without a dawn/dusk control) is turned off. Complete darkness should be provided for the night period as continued activity will occur when light, tiring the animals.

### Visual signals

Visual signals are an important component of primate behaviour, alone or in combination with vocalisations, scents or touching. Everything from the coat colour of an animal to spacing between individuals can play an important role in determining behavioural responses. For example, the females of many Old World species, including macaques, baboons and chimpanzees,

signal proceptive and receptive sexual behaviour with changes in the size, shape, turgidity and, often, colour of their perianal “sexual” skin (33) (Fig 4). The reason for sexual swellings is not fully understood, but they may be a mechanism by which females signal their receptivity and fertility, to incite male competition and ensure that they get a good-quality father for their offspring. The sexual swelling increases in size as the female approaches the time in her cycle when she is due to ovulate, reaching its peak when the egg is released and she is at her most fertile. Female macaques also communicate sexual interest by approaching, following, and initiating proximity with, males (34).



**Figure 4.** A female rhesus macaque foraging with red perianal skin visible.

Soliciting behaviour in tamarins, and also marmosets according to some researchers, involves rapid tongue-flicking, which is displayed more frequently during the peri-ovulatory period (35-36). Tongue-flicking is also seen during agonistic encounters. Intra-group and inter-group agonistic encounters in marmosets often involve the ‘tail raised present’ behaviour pattern (Fig 5).

Old World primates use a diversity of facial expressions as well as gestures, athletic displays and body postures. In the macaques, most visual signals appear to revolve around issues of dominance and

submission (37). For example, an open mouth gesture is a threat, whereas lip-smacking is a submissive or greeting gesture. The seeming casual yawn that exposes the canine teeth is a sign of tension or a threat (“look at my teeth”). An open-mouth grin is a sign of anxiety or fear and a means of diffusing tension, whereas a stare is a threatening gesture (Figs 6 & 7).



**Figure 5.** The common marmoset on the left is exhibiting the ‘tail raised present’ behaviour pattern, with the tail semi-piloerected, raised and coiled, and the genitals exposed.



**Figure 6.** A young long-tailed macaque exhibits a partial ‘fear grimace’ or ‘fear grin’, in which the mouth is open and lips retracted revealing the teeth.



**Figure 7.** A female rhesus macaque defends her enclosure against an approaching human with a stare, retracted ears and open mouth.

Compared with the Old World monkeys, the New World monkeys have traditionally been considered to have poorly developed visual signals and to not form the fine facial expressions seen in Old World monkeys (38-40). They do, in fact, have a rich repertoire of visual signals, but these may be less discernable due to their small size (see 35-36 & 41-42 for reviews) (Fig 8).



**Figure 8.** A common marmoset staring with bared teeth and ear tufts flattened – these visual patterns can signify fear and submission.

Some signals are common to all primates, for example piloerection (39). Piloerection of all of the pelage makes the individual appear larger than it actually is, and is used in aggressive interactions and can signify alarm and fear (Fig 9).

- Visual signals are the easiest signals for humans to recognise and can provide information on a primate's emotional and physical (welfare) state, and his/her intended action in response to, and ability to cope with, a situation or interaction. All staff coming into contact with primates should receive training in recognising and understanding primate visual signals.
- Visual signals can also be used determine the relationships between individual primates which is useful when creating and monitoring social groups (43).
- Staff need to be aware of the importance of visual signals when group housing primates or when arranging single-housing caging – allow visual stimulation from conspecifics but provide some means of temporary visual seclusion (e.g. screens) for privacy and to allow the animals to have some control over their social interactions.



**Figure 9.** An adult male rhesus macaque male erects his fur in response to an approaching veterinarian.

Primates can learn socially through observation of their conspecifics or of other species, including humans (44-47).

- Behavioural scientists should be aware of this when designing learning paradigms and training programmes – for example, allowing animals to be observers during training sessions may enable them to be trained more rapidly (48).

Primates will react not only to the facial expressions, gestures and body postures of conspecifics but also to those of humans, as well as to negligible changes in human clothing.

- Staff members should be aware of the potential negative effects of their behaviour on primates and adapt their behaviour accordingly (e.g. by avoiding direct eye contact which can be perceived by the animals to be a threatening gesture).
- Staff can engage in activity that communicates positive, as well as avoids negative, messages to the animals – for example, use of species-specific affiliative signals, combined with food provisioning, has been reported to reduce abnormal behaviour in macaques (49).

## Smell

### Olfactory sensitivity

Primates have long been regarded as visual animals with a poorly developed sense of smell. However, using conditioning paradigms to investigate olfactory detection thresholds for various organic compounds it has been shown that both New and Old World primate species have well-developed olfactory sensitivity, which for some substances matches or even is better than that of the rat or the dog. For example, squirrel monkeys, spider monkeys and pig-tailed macaques can discriminate concentrations of carboxylic acids and aliphatic aldehydes, alcohols and esters below 1 ppm and in some cases even

below 1 ppb (50-57). Sensitivity for certain odours appears to reflect their biological relevance for the tested species.

- The importance of olfactory stimulation in captive environments for primates is often overlooked – many primate species are likely to benefit from being provided with enrichment items or foods with a variety of different scents (58-60) (e.g. capuchins like to rub their bodies with scented objects such as garlic bulbs).

### Olfactory communication

As well as its more obvious role in food identification and selection (61-63) there is now evidence from a number of primate species for olfactory involvement in social behaviours, such as the establishment and maintenance of rank (64), defence of territory (65-66), identification of sexual partners (67), recognition of group members (68-69) and communication of reproductive status (70).

Communication through olfactory means is particularly important for New World monkeys and prosimians, many of which possess odour-producing skin glands and demonstrate conspicuous marking behaviours (71-72) (Fig 10). For example, in the squirrel monkey, hand washing with urine (73), nasal rubbing and sneezing (74), back rubbing (75) and anogenital inspection (76) all appear to be associated with olfactory communication. In addition to the main olfactory system (MOS), New World monkeys and prosimians possess an intact accessory olfactory system (AOS) (i.e. a structurally competent vomeronasal organ linked to a distinct primary processing centre – the accessory olfactory bulb), whereas this is near vestigial in Old World monkeys, apes and humans (77-78). In prosimians the OAS is involved in processing social information, such as dominance and sexual signalling (79), but its relative importance for the New World monkeys remains enigmatic.



**Figure 10.** *The common marmoset on the left is scent marking, rubbing its anogenital area on the wooden shelf.*

Preference tests have revealed that a wide variety of information is coded in the scent marks of marmosets and tamarins, including species, subspecies, sex, individuality, social status, hormonal status and timing of ovulation (see 68 & 80 for reviews). Marking appears to have several functions including the reproductive suppression of subordinate females, advertisement of individual “quality” (mate attraction), preparing males to assist in the delivery and care of newborn infants, and territorial defence. Odours are effective for up to 3 days after deposition.

- Objects should be provided which allow marmosets and tamarins to mark their environment (e.g. wooden perches and ladders).
- Because of their role in modulating reproductive physiology and regulating social interactions, it is important that familiar scents are not totally removed from the captive environments of these species during cleaning. Alternate cleaning and sanitation of enclosures and enrichment devices will help to retain scent and has beneficial effects on the psychological well-being of the animals by reducing over-stimulated scent-marking.
- Scent-marking behaviour has been reported to increase following stress in common marmosets and, therefore, may be a useful non-invasive behavioural measure of stress in this species, along with locomotion and self-scratching (81).

## Taste

Taste is one of the most important senses for efficient choice of foods in primates (63,82) and many primates consume a diverse diet (e.g. macaques may consume over 100 or more plant species in a year: 83-84). In general, primates show a positive response to sweet sugars (to maximise ingestion of beneficial substances) and an avoidance response to bitter plant compounds such as alkaloids and tannins (to minimise ingestion of substances most likely to be toxic) (85). Primates also show differential facial expressions in response to these stimuli (86), and these are present at an early stage of life. For example, newborn rhesus macaques exhibit ‘tongue exposure’ in response to bitter stimuli but not in response to water or sweet stimuli (87). Such expressions are potential cues for social communication about unpalatable food (88).

- Given the highly developed sense of smell and taste and generalist diet of most primate species, providing a variety of palatable food types and tastes is likely to be beneficial for their psychological well-being (89).

The taste of most fruits is characterised by a mixture of sensations termed sweet and sour by humans. Sourness is basically acidity and indicates the state of maturation of fruits, which often increase in pH as they ripen, as acids are converted to sugars. The food selection behaviour of primates suggests that they may use the relative salience of sweetness and sourness to assess palatability of potential food items. For example, using two-bottle preference tests, Laska et al. (56) found that squirrel monkeys, spider monkeys, pig-tailed macaques and olive baboons differ in their acceptance of physiological concentrations of sour-tasting citric acid. Whereas olive baboons showed the highest degree of sour-taste tolerance and actually preferred sweet-sour taste mixtures over sweet-tasting reference solutions,

squirrel monkeys showed the least degree of sour-taste tolerance and rejected sweet-sour taste mixtures, even when they contained considerably more sucrose than reference solutions. Additional tests demonstrated that the animals perceive both the sweetness and the sourness of the taste mixtures and make a trade-off between the attractive and aversive properties of the two taste qualities.

Further species differences have been found in responsiveness to carbohydrates. Squirrel monkeys, spider monkeys and olive baboons prefer sucrose, over polycose or maltose, which is similar to the order of relative sweetness in humans. Pig-tailed macaques, however, display a high sensitivity to polycose and show a vivid predilection for this polysaccharide and its disaccharide constituent maltose, which suggests that this species, unlike other primates, but like rodents, may have specialised taste receptors for starch (90).

- Genera and species preferences need to be considered in providing gustatory variety.

Although the salt concentration of most primate natural foods is below the taste threshold, primates are sensitive to salts (91) and have been found to discriminate concentrations of sodium chloride as low as 1 mM (spider monkeys), 20 mM (pig-tailed macaques), 50 mM (olive baboons) and 200 mM (squirrel monkeys) (47). The detection threshold for humans is around 6-15 mM (92).

In addition to the four conventional taste qualities (bitter, sweet, sour and salty), electrophysiological work with macaques has also demonstrated neurons responsive to glutamate, responsible for the taste umami (savouriness), and tannic acid, which produces the taste of astringency and is of biological importance to arboreal primates (93-94).

## Hearing

### Auditory sensitivity and sound localisation

All primate species tested so far are able to hear frequencies below 125 Hz, meaning they have comparatively good low frequency hearing in common with the majority of mammals (95). The low frequency sensitivity of Old World monkeys is similar to that of humans, but they hear approximately an octave higher than humans do. The hearing of New World monkeys and prosimians is further shifted toward higher frequencies compared with Old World monkeys and humans – this is likely because high frequencies are more useful to small species than to large species for sound localisation (detecting the direction a sound is coming from) (95).

The acuity of sound localisation is known for only three primates. Humans, macaques and squirrel monkeys are relatively good sound localisers (macaques and squirrel monkeys have a minimum audible angle of around 5°, roughly similar to other mammals such as cats, pigs and opossums). This is in keeping with the pattern among mammals, in which species with narrow fields of best vision, such as a retinal fovea only 1-2° wide, are better sound localisers than those with broad fields of vision. This is likely because orientating the eyes for visual scrutiny requires more precise directional (sound) information when the field of best vision is very narrow (95). In contrast, species with broad visual streaks, such as horses or rabbits, require very little acuity to bring sound within their field of best vision.

### Ultrasound

At 60 dB SPL the highest audible frequency for the human is around 20 kHz, whereas for the common marmoset it is around 30 kHz, and for the squirrel monkey, rhesus macaque and long-tailed macaque it is around 42 kHz (<http://psychology.utoledo.edu/lch>).

Frequencies above the nominal upper limit of human hearing are termed 'ultrasonic'.

- The effects of laboratory sound at ultrasonic frequencies (e.g. from sources such as dripping taps, trolley wheels and computer monitors) might be a welfare problem. It is important therefore that any analysis of noise level should include ultrasonic frequencies (96).

### **Auditory stimulation and noise**

Naturalistic sounds and music and have been used as auditory stimulation for primates and can apparently have beneficial effects in terms of reducing aberrant behaviour and decreasing arousal (97-99). Auditory stimulation is apparently most beneficial when the animals have some control over it (100).

Under certain conditions, auditory stimulation can be aversive and turn into noise. Loud or unexpected noise has been reported to cause abnormal behaviour and physiological effects in primates (101-104).

- For most species, satisfactory sound levels will be the same as those recommended for staff.
- Restful background sound, such as music or radio programmes, can be used to screen out sudden loud noises but it should not be provided permanently, should be kept at human conversational level and should only exceed 65 dBA for short periods (32).
- Noise producing equipment should be sited as far away from the animals as possible. Power hoses are very noisy and aversive to many primates – dry cleaning should be used where possible, and the animals moved to a separate area before power hoses are used.
- Enclosures for primates are commonly constructed of metal which is noisy – materials such as wood, laminates and glass have been

used successfully to provide a quieter environment (32,105).

### **Vocalisations**

Vocalisations are an important mode of communication for most primate species, especially where visual contact is precluded (e.g. dense forest environments). Repertoires of vocalisations are relatively distinct between species and consist of a wide array of acoustic signals that can be defined by their frequency, intensity, spectral composition and duration. Examples of sounds produced by primates include the high-pitched, bird-like whirrs, chirps and twitters of the marmosets and tamarins (36,42) and the grunts, barks, coos, geckers and screams of the macaques (106-107). Vocalisations of various primate species, including cotton-top tamarins and rhesus macaques, can be listened to on the Primate Info Net website (<http://pin.primate.wisc.edu/av/vocals/>).

Using both field playback experiments and psychophysical methods, ethologists are beginning to understand how primates themselves perceive their species-specific vocalisations. For example, field experiments on rhesus monkeys have tested the ability of females to distinguish kin from non-kin using the 'coo' vocalisation (108). On the basis of the latency and duration of head orientating responses toward the sound source, females respond quicker and for longer to the coos of their kin than to those of non-kin or distantly related kin. Cotton-top tamarins, common marmosets and squirrel monkeys, like rhesus macaques, can identify individuals using only the acoustic cues of their calls (109-110). In fact, in primates, differences in acoustic structure not only encode different call categories, but they also potentially encode information about individual, species, sex and group identity (108,111-115), motivational state (106,116), body size and reproductive status (117-118).

Some of the functions of vocalisations in primates are to attract the attention of group members and to maintain a certain level of awareness among group members. For example, infants of many species produce isolation calls after becoming separated from their care-givers (e.g. isolation phee in marmosets, isolation peep in squirrel monkeys). Calling reflects the infant's emotional state, and attracts care-givers and induces them to retrieve the caller. Primates can also make non-vocal sounds, such as cage banging, to express their emotions.

- Animal care staff can use vocalisations and non vocal-sounds produced by primates to evaluate their welfare (119).

Both New and Old World monkeys produce contact calls, allowing individuals to keep track of the general whereabouts of group members and thereby maintain intra-group cohesiveness and permit co-operative ventures, such as vigilance or transferring an infant (120-121). Many primates also produce long or loud calls, which are louder in amplitude and longer in duration than those used in resting contact (122-124). These calls have a variety of functions, depending on the species, including territorial defence, to promote cohesion, to reunite separated group members and to attract mates (125-127).

When palatable food is found, some species give food calls which are thought to recruit group members to the vicinity of the caller, probably for their anti-predatory vigilance benefit (128). Chimpanzees and rhesus macaques apparently have the largest repertoire of food-specific calls, with several distinct food-vocalisations being recognised (129-131). Moreover, some primate species reportedly recognise the food calls of non-primate forest frugivores and use them to navigate toward fruiting trees (132-133).

Marmosets produce mobbing (tsik) calls in response to seeing predators. Laboratory studies with common marmosets have shown that producing tsik calls, and hearing the tsik calls of familiar conspecifics, may lower their physiological stress levels (134).

- These findings indicate that it may be possible to reduce the amount of stress an animal experiences during stressful procedures by strategic playback of the calls of conspecifics.

Calls of some primate species have been found to refer to external phenomena, an attribute which has been variously labelled 'symbolic', 'representational', 'semantic' and 'referential' by different authors. The first concrete evidence came from vervet monkeys which give different alarm calls depending on the type of predator at hand (135-138). However, this attribute is not restricted to Old World monkeys. At least two species of tamarin, for example, have different functionally referential alarm calls for terrestrial, aerial and snake predators (139).

Learning does appear to play a role in the usage and comprehension of calls. For example, the appropriate response to, and hence the correct classification of alarm and long-distance contact calls emerges at around 6 months of age in vervet monkeys and chacma baboons (140).

- Primates can readily distinguish between quiet, calm and loud, forceful human voice tones and words, which can be useful for training.

## **Touch**

### **Tactile stimulation**

In common with other vertebrates, primates have numerous kinds of sense capsules in their epithelial and connective tissues that are responsive to sensations such as touch, heat, cold, pressure and pain. Primates make behavioural choices based on these sensations, for example, marmosets prefer to

use wooden and plastic nest boxes as opposed to metal ones, which may be related to comfort and temperature (141), and will respond to soft materials (e.g. fleece) by rubbing their bodies against them.

- In outdoor enclosures the sense of touch is stimulated by environmental factors such as the sun, rain, and wind. In indoor enclosures, tactile stimulation can be provided by the materials composing the cage and items placed in the cage (e.g. wooden furniture, soft materials, browse, toys and food), as well as conspecifics (142). Note that marmosets and tamarins have claw-like tegulae and need textured substrates which they can grip onto (e.g. wood and mesh).
- Marmosets enjoy basking in warm sunlight – where it is not possible to include outdoor runs or windows, areas of additional heat/lighting can be provided indoors (e.g. heat lamps).

Several species of macaque are good swimmers and enjoy access to water. Where swimming pools are provided as environmental enrichment in the laboratory (Fig 11), these animals show high motivation to manipulate the water surface, immerse themselves, dive, swim and play (including underwater), even in the absence of submerged food rewards (e.g. raisins, nuts, banana chips) (143-145) ([www.nc3rs.org.uk/primatehousing](http://www.nc3rs.org.uk/primatehousing)).

- Consider providing macaques with swimming pools as sensory enrichment, on a period basis to maintain novelty. Advantages of this enrichment technique are that it is based on a natural behavioural inclination, encourages play rather than food-orientated enrichment, provides exercise, keeps both animals and their enclosure clean, and can facilitate thermoregulation in hot weather.



**Figure 11.** Long-tailed (*cynomolgus*) macaques using a custom-made polypropylene swimming pool built to fit within their enclosure.

### Manual dexterity

The fingers and hands of monkeys, apes and humans are highly sensitive and dexterous, allowing precise, delicate and diversified manipulation of objects. For example, Old World monkeys and apes have been observed to palpate fruits, such as figs (146-148). It has been proposed that the animals are using textural cues to assess nutritional value since elastic modulus, a key property of fruits that governs the ease of non-destructive examination using the fingers, is a strong predictor of sugar content for some fruits that colour is not (148). Assessment by palpation saves handling time as compared with bringing individual fruits to the mouth for evaluation. That said, primates do use their mouths to explore objects.

- Whole food manipulation may be an important part of the feeding repertoire of primates. To increase foraging time and provide sensory stimulation, offer foods that the animals must process before eating (e.g. whole fruits, nuts in their shells, etc.) (149).

Some primates, such as capuchins and saddle-backed tamarins, are extractive foragers, using their hands to obtain foods (e.g. insects and small vertebrates) that are hidden in tree holes, rotting

wood, termite nests, the base of palm fronds, bromeliads and embedded under bark (150). Several primates (e.g. capuchins, macaques and chimpanzees) also use tools to obtain food, in the wild and in captivity, which requires fine sensory and motor control (143,151-153).

- A variety of foraging devices to simulate extractive foraging behaviour, or manipulanda that require manipulation of moving parts, are commercially available or can be cheaply and easily made in house (154). These can be used to provide tactile stimulation for the animals and require them to work for their food, but their use should be monitored to ensure that animals are benefiting from them (142).
- A floor substrate, such as woodchip or straw, will provide tactile stimulation when foraging for scattered food (155).

#### **Tactile contact with conspecifics**

Tactile contact is very important for primates, especially early in life (156-157). Many species rest in contact (huddling) and this is probably a means of maintaining social cohesion in groups as well as reducing heat loss. This behaviour may be associated with pleasant sensations during infancy, since infant primates cling to their mothers (Fig 12).

- If primates cannot be permanently group-housed, tactile contact should be allowed with conspecifics (e.g. through grooming bars).
- In contrast to contact with conspecifics, tactile and social contact with staff can be aversive for primates that have not been adequately habituated and socialised to humans, especially prey species like marmosets and tamarins. Care should be taken to ensure adequate attention is paid to these learning processes during the early life of the animals, because positive interactions between staff and animals are known to improve health and welfare and increase ability of the

animals to cope with stress (49,158-159) (Figs 13 & 14).



**Figure 12.** If primates are frightened, they usually seek physical contact with companions. The macaque on the right is exhibiting a 'fear-grin/grimace'.



**Figure 13.** Hand feeding young primates is a means of habituating the animals to human contact.



**Figure 14.** Common marmosets enjoying relaxed human contact with staff.

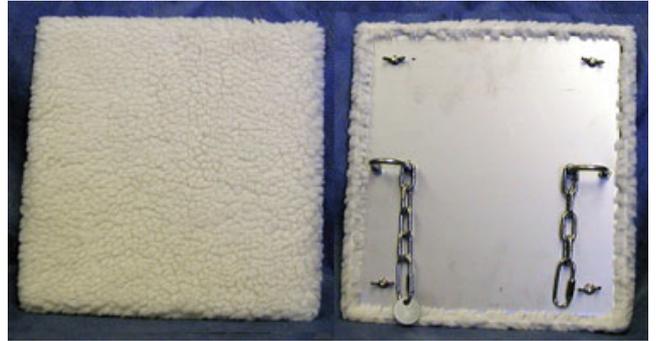
### Grooming

Grooming is an important affiliative behaviour among primate societies, reflecting the psychological well-being of individual animals and any grouping of them as well. Primate species spend up to 20% of each day engaged in this activity (160). Grooming relationships are extremely valuable in helping primates to cope with the stresses and strains of group life, and individual animals will make great efforts to maintain these relationships in the face of other demands on their time. For example, when food is scarce and animals are forced to spend longer foraging, baboons will sacrifice their resting time in order to keep up their grooming commitments (161).

- It is essential that habitats for captive primates be designed to facilitate grooming and huddling by providing suitable space for housing with compatible social companions and a sufficient number of resting surfaces for animals to occupy simultaneously. Wide flat surfaces are preferred grooming sites for tamarins and other primates (162).
- Singly-housed animals can be provided with fleece grooming/foraging boards to address their motivation for social grooming (Fig 15) – these

have been found to significantly reduce abnormal behaviours, such as hair pulling, in macaques (163-165).

- For animals well socialised to humans, grooming from staff members can be used as an alternative to food-based rewards for positive reinforcement training (166).



**Figure 15.** Fleece grooming/foraging board from Bio-Serv.

Grooming helps to relieve the stress that builds up as a consequence of competition within social groups. This is important because high levels of stress reduce a female's fertility (by blocking the action of reproductive hormones). Grooming counteracts this effect by stimulating the release of opium-like substances that suppress the production of stress hormones and neutralise their effects (167). Grooming also plays an important utilitarian role in cleaning the hair free of parasites and detritus (168) and in some species (e.g. macaques) is used as an appeasement gesture to reassure individuals that an animal has no aggressive intentions (169-170). In macaques, higher-ranking individuals are reported to receive more and longer-lasting grooming sessions from low-ranking individuals than vice versa (107,171). In both the field and in captivity, male marmosets groom females significantly more than vice versa (42).

- The direction of grooming can be used to ascertain the hierarchy in a group of macaques and bonds between individuals, which can be useful for animal management.

- A change in the pattern of grooming (e.g. decreased self-grooming leading to an unkempt coat, or increased grooming attention from conspecifics leading to hair loss) may be indicative of a welfare problem – staff members should be aware of this and seek expert advice if they have concerns.

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