

- Stewart, R.N., and Dermen, H. (1970). Determination of number and mitotic activity of shoot apical initial cells by analysis of mericlinal chimeras. Am. J. Bot. 57, 816–826.
- 10. Barlow, P.W. (1976). The concept of the stem cell in the context of plant growth and development. In Stem Cells and Tissue

Homeostasis, B.I. Lord, C.S. Potten, and R.J. Cole, eds. (Cambridge: Cambridge University Press), pp. 87–113.

- Pineda-Krch, M., and Fagerström, T. (1999). On the potential for evolutionary change in meristematic cell lineages through intraorganismal selection. J. Evol. Biol. 12, 681–688.
- Fulcher, N., and Sablowski, R. (2009). Hypersensitivity to DNA damage in plant stem cell niches. Proc. Natl. Acad. Sci. USA 106, 20984–20988.

# **Aging: Lessons for Elderly People from Monkeys**

### **Catherine Crockford**

Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany Correspondence: crockford@eva.mpg.de http://dx.doi.org/10.1016/j.cub.2016.05.002

As life expectancy increases, health in the elderly is a growing issue. Health is linked to remaining socially active, but the elderly typically narrow their social networks. The social life of aging monkeys shows interesting parallels, indicating social patterns may be rooted in evolution.

Social isolation experienced by the elderly is an ever increasing problem in first world countries. This is a particular concern given that social isolation exacerbates the risk of physical and mental illness, dementia and death [1,2]. More than a fifth of over-65s are living alone [3] or participate in fewer than one social activity per month [4]. Such factors make individuals vulnerable to feeling socially isolated or low in selfworth, no longer sensing a role in society [5]. Given that people are living longer [2] and hence are living a greater proportion of their lives as elderly, it is unclear to what degree these patterns of social isolation should be considered a modern phenomenon and how much is an inevitable part of aging, associated with motivational, physical and cognitive decline

One way to address this problem is to examine the impact of aging on the social life of other primates. In this issue of *Current Biology*, Almeling *et al.* [6] report a new study on Barbary macaque monkeys in Rocamadour, France, which shows how aging affects social engagement patterns when the availability of social partners remains relatively unchanged. Strikingly, the authors find that, for Barbary macaques living in large social groups, older individuals' interest in *others*' social life does not decline whilst their interest in their non-social world does. Older males and females (Figure 1) remain just as interested in observing and 'commenting' on the social interactions of others as do younger individuals; however, individuals of both sexes show a marked decline in interest with age in novel physical objects placed around their home range [6].

Almeling et al. [6] also show that whilst elderly Barbary macaques reduce the number of individuals that they themselves groom, they continue to receive grooming from others at similar rates as young individuals. It is unclear why they reduce their own grooming, whether this is, for example, due to shifts in motivation, energy or physical ability. It is also unclear why others maintain interest in elders as grooming partners, even though they receive little grooming in return. One possible explanation is that the elders provide benefits other than grooming. Given that there is no strong evidence of obvious roles such as allo-parenting or grandparenting in Barbary macaques, Almeling et al. [6] posit, rather, that maintaining close social bonds may hold inherent value. Maintaining close social bonds in both human and non-human primates is known to provide compelling benefits in terms of stress-reduction as

well as gaining health, longevity and reproductive success [1,7,8]. Thus, younger macaques may continue to maintain their relationship to older ones, even in the absence of returned grooming.

Human studies show that relationships remain important for the elderly, although there is some shift in their priorities with age. Unlike for young people, who show preferences for expanded social networks, for the elderly, preferences for a few very close social partners predominate [9], often with individuals whom they have been close to for many years [10]. Whilst the possibility to maintain such relationships brings satisfaction [11], the paradox is that social networks that are too contracted can presumably leave people vulnerable to social isolation. Interestingly, the elderly Barbary macaques also experienced a narrowing of their social network, at least in terms of who they continued to groom, although it is not yet clear which social partners are preferred. A narrowing social network has been observed not only in elderly monkeys but also adult female baboons of all ages when exposed to social stressors. Baboons that were better able to focus their grooming on a few close social partners experienced a quicker return of stress hormones to baseline levels [11]. It



Cairns, J. (1975). Mutation selection and the natural history of cancer. Nature 255, 197–200.

### Current Biology Dispatches

is not yet clear whether a similar narrowing of social networks seen in elderly Barbary macaques incurs stress, health and longevity benefits, and whether such shifts reflect preferred patterns, as seems to be the case in humans [12]. Further work could ascertain inevitable trade-offs between social preferences and the physical, motivational and cognitive constraints of aging primates.

In elderly people, key theories to explain changing social patterns suggest that, linked to decline in physical and cognitive ability, is a change in goals and motivations, which in turn are influenced by a perception of a limitation of future time. According to Socioemotional Selectivity Theory [12], young people, who are more likely to feel time is open-ended, focus on goals related to knowledge acquisition. In contrast, the elderly, who are more likely to feel that time is constrained, shift their focus to optimising a sense of well-being, which is linked to focusing their social life onto a few, deeply satisfying relationships. The Barbary macaque study [6] in this issue, however, demonstrates that similar shifts in social networks occur even in animals that (presumably) lack a perception of future time constraints, highlighting the value of an evolutionary perspective in relation to the topic of aging.

Drawing parallels with humans. Almeling et al. [6] conclude that the social patterns they find may indicate evolutionary continuity with humans. It is also possible that examining the social life of aging primates might provide insights into how to tackle the growing problem of social isolation currently faced by this, and no doubt following, generations of elderly people. Given that social isolation appears not to be an evolutionarily natural state for the old, it is worth exploring what keeps aged primates valuable to the young and whether sophisticated modern society can parallel this. A key challenge may be ensuring that the old continue to have a valuable role to play within society [5]. One apparently successful and widely copied scheme is the Men's Sheds scheme. Men's Sheds originated in Australia to give purpose to elderly men, providing them with a homely, social space to fix different kinds of tools for



Figure 1. An old female and old male Barbary macaque. ©Andreas Ploss (left), ©Julia Fischer (right).

others' benefits [13], whether for others within the community or within third-world countries. Although evidence of success for interventions against social isolation in elderly is generally sparse [5,14], Men's Sheds shows successes in renewing a sense of purpose in life for participants.

Other intriguing guestions arise. Even though old primates are not such great participators in social life, they remain avid observers of others' social life. What holds their interest and why? The cognitive capacity involved in keeping track of one's own and others' social relationships is considered to be one of the evolutionary drivers of primates and humans' - big brains [7]. Perhaps not coincidentally, maintaining social interest and relationships may be one of the key factors in keeping both brain and body tissue healthy with age [15]. Socially isolated, compared with integrated, people have greater inflammation within their bodies, at equivalent levels to smokers or those who are obese [16]. General body inflammation is correlated with inflamed myelin, the sheaths that protect white matter neurons in the brain - those that connect different brain areas. Astonishingly, it was recently found that social network richness was also linked to white matter integrity [16]. Stress is thought to be a key factor causing inflammation [17]. Positive social interaction and social bonds have both been shown to reduce stress [1,18]. Thus, integrated mechanisms that could be keeping socially-engaged individuals physically and mentally healthy may start from the social interactions themselves.

#### REFERENCES

- 1. Holt-Lunstad, J., Smith, T.B., and Layton, J.B. (2010). Social relationships and mortality risk: a meta-analytic review. PLoS Med. 7, e1000316.
- 2. Dickens, A.P., Richards, S.H., Greaves, C.J., and Campbell, J.L. (2011). Interventions targeting social isolation in older people: a systematic review. BMC Pub. Health *11*, 1.
- West, L. A., Cole, S., Goodkind, D., and Wan, H. (2014). 65+ in the United States: 2010. US Department of commerce, economics and Statistics administration, US Census Bureau, pp. 131 (http://www.census.gov/content/ dam/Census/library/publications/2014/demo/ p23-212.pdf).
- Gilmour, H. (2012). Social participation and the health and well-being of Canadian seniors. Health Rep. 23, 1B.
- 5. Age UK. (2010). Loneliness and Isolation Evidence Review (London: Age UK).
- Almeling, L., Hammerschmidt, K., Sennhenn-Reulen, H., Freund, A.M., and Fischer, J. (2016). Motivational shifts in aging monkeys and the origins of social selectivity. Curr. Biol. 26, 1744–1749.
- 7. Silk, J.B. (2007). Social components of fitness in primate groups. Science *317*, 1347–1351.
- Schülke, O., Bhagavatula, J., Vigilant, L., and Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. Curr. Biol. 20, 2207–2210.
- Lang, F.R., and Carstensen, L.L. (1994). Close emotional relationships in late life: further support for proactive aging in the social domain. Psych. Aging 9, 315.
- Field, D., and Minkler, M. (1988). Continuity and change in social support between youngold and old-old or very-old age. J. Gerontol. 43, P100–P106.
- Wittig, R.M., Crockford, C., Lehmann, J., Whitten, P.L., Seyfarth, R.M., and Cheney, D.L. (2008). Focused grooming networks and stress alleviation in wild female baboons. Horm. Behav. 54, 170–177.
- Carstensen, L.L. (2006). The influence of a sense of time on human development. Science 312, 1913–1915.

Current Biology Dispatches

- Cordier, R., and Wilson, N.J. (2014). Community-based Men's Sheds: promoting male health, wellbeing and social inclusion in an international context. Health Promot. Int. 29, 483–493.
- Cattan, M., White, M., Bond, J., and Learmouth, A. (2005). Preventing social isolation and loneliness among older people: a systematic review of health promotion interventions. Ageing Soc. 25, 41–67.
- Fratiglioni, L., Wang, H.X., Ericsson, K., Maytan, M., and Winblad, B. (2000). Influence of social network on occurrence of dementia: a community-based longitudinal study. Lancet 355, 1315–1319.
- Molesworth, T., Sheu, L.K., Cohen, S., Gianaros, P.J., and Verstynen, T.D. (2015). Social network diversity and white matter microstructural integrity in humans. Soc. Cog. Affect. Neurosci. 10, 1169–1176.
- Slavich, G.M., and Cole, S.W. (2013). The emerging field of human social genomics. Clin. Psych. Sci. 1, 331–348.
- Young, C., Majolo, B., Heistermann, M., Schülke, O., and Ostner, J. (2014). Responses to social and environmental stress are attenuated by strong male bonds in wild macaques. Proc. Natl. Acad. Sci. USA 111, 18195–18200.

# Face Recognition: Canonical Mechanisms at Multiple Timescales

#### Martin A. Giese

Section for Computational Sensomotorics, Department of Cognitive Neurology, Centre for Integrative Neuroscience & Hertie Institute for Clinical Brain Research, University of Tübingen, D-72076 Tübingen, Germany Correspondence: martin.giese@uni-tuebingen.de http://dx.doi.org/10.1016/j.cub.2016.05.045

Adaptation is ubiquitous in the nervous system, and many possible computational roles have been

Adaptation is ubiquitous in the nervous system, and many possible computational roles have been discussed. A new functional imaging study suggests that, in face recognition, the learning of 'norm faces' and adaptation resulting in perceptual after-effects depend on the same mechanism. Adaptation is a fundamental property the opposite direction. More recent work V2 in the macaque cortex) in terms of

of neurons, and many possible computational roles of adaptation in cortical processing have been discussed (for example [1]). Adaptation affects the perception of simple visual features, such as color or local motion, as well as higher visual processes, for example the recognition of faces [2,3]. It has been proposed that adaptation might be crucial for the statistically optimal neural encoding of stimuli [3,4]. According to a popular theory, faces might be represented in terms of their deviation from a 'norm face' representation, which is learned by averaging over many previously perceived faces. On the basis of a functional imaging study, Mattar et al. [5] propose in this issue of Current Biology that high-level adaptation effects for faces and the learning of norm faces might rely on the same underlying mechanism.

Historically, adaptation in vision has been studied extensively with respect to elementary stimulus properties, such as color or motion. A well-known example is the motion after-effect (the 'waterfall illusion'), a misperception where a static background is perceived as moving after extended exposure to motion in the opposite direction. More recent work has demonstrated that higher visual functions, such as face recognition, are also affected by adaptation [2,3,6].

In psychology, faces are often characterized as points in abstract perceptual spaces or face spaces [7]. The dimensions of such spaces are usually identified with features that change with facial identity or expression. Such a perceptual space is illustrated in Figure 1: it contains Asian and Caucasian faces (C1,C2;A1,A2), and its center is defined by an 'average' or 'norm face' (N), which is typically derived by averaging the features of a large number of typical face pictures. According to a popular hypothesis ([8,9], but see [10]) faces might be encoded in terms of their position relative to this norm face in the perceptual space (norm-referenced or norm-based encoding). In Figure 1, the face C1 would thus be encoded by the length and the direction of the green arrow.

The right panel of Figure 1 shows a hypothetical neural circuit for the realization of norm-referenced encoding [11]. The circuit receives its input from lower-level shape-selective cortical areas (for example, corresponding to areas V4 or V2 in the macaque cortex) in terms of a feature vector s, whose components signal the presence of specific shape features. The circuit consists of two modules (hypothetical classes of neurons). One of them, the 'norm neurons', just computes a moving average of all previous stimuli, resulting in an estimate  $\mathbf{r}_t$  of the average input feature vector over the previous stimulus history. If the time scale of this computation is long enough to average over a large number of previous stimulus presentations,  $\mathbf{r}_t$  is effectively an estimator of the expectation value of the input vector  $\mathbf{s}_t$  over time. Typically, this vector corresponds closely to the feature vector of the norm face, since (by definition) this face is characterized by 'average' features.

The second module of the hypothetical circuit consists of 'face identity neurons' whose activity depends on the length and direction of the difference vector  $\mathbf{d}_t = \mathbf{s}_t - \mathbf{r}_t$ . This difference feature vector corresponds to the green arrow in the face space. The inset below the face identity neurons shows schematically the tuning curves of real face-selective neurons that have been measured in macaque area IT [12]. The response rate

