

Why Marmosets?

Over the past several years the common marmoset (*Callithrix jacchus*) has ascended from an established, albeit niche, model species in neuroscience to one with broad appeal that stands to expand and reshape the scientific landscape. Despite years of pioneering research involving marmosets (Dias et al., 1996; Roberts and Wallis, 2000; Bourne et al., 2002; Bendor and Wang, 2005; Wang et al., 2005; Solomon and Rosa, 2014), it was not until Sasaki et al. (2009) used marmosets to demonstrate the first germ-line transmission of exogenous genetic information in a nonhuman primate that this New World monkey entered the broader collective awareness of the neuroscientific community. The raw excitement was fueled, at least in part, by a confluence of events. While modern molecular techniques were revolutionizing the study of neural circuits in mice, there was reasonable expectations that the same methods could, in principle, be similarly effective at explicating questions of primate brain function. However, efforts to apply these molecular techniques to the rhesus monkey, the most commonly used primate model, had proven significantly less effective than in rodents (Geritis and Vanduffel, 2013; O'Shea et al., 2017). The marmoset offered the hope of bridging these technologies and their significant advantages to elucidate the intricacies of the primate brain.

Prospects for developing cutting-edge technologies to deliver exogenous genes to primates with a marmoset model remain considerable (Kaiser and Feng, 2015; Jennings et al., 2016; Okano et al., 2016a,b), particularly as these efforts are quickly beginning to bear fruit (Sasaki et al., 2009; Sadakane et al., 2015; Watakabe et al., 2015; MacDougall et al., 2016; Park et al., 2016; Santisakultarm et al., 2016; Sato et al., 2016). This line of work, however, is no longer the principle force driving the species' continued growth across the field. There is a maturing appreciation of this Neotropical primate's distinctive behavioral characteristics and the potential to leverage these qualities to expand the types of questions being asked

at the neurobiological level (Saito, 2015; Miller et al., 2016). The principal goal of this Special Issue is to both highlight the current state of work developing and implementing modern molecular technologies for marmosets and to underscore the significance of several areas of ongoing research where this New World primate offers exciting opportunities to advance the frontiers of primate neuroscience. Certainly this collection of manuscripts is not exhaustive, there are many other areas of research for which marmosets can serve as a valuable animal model.

WHY PRIMATES?

Before turning our attention to marmosets, it is important to consider the more general question of why neuroscience needs primate models of the brain at all. The significance of this question partly explains the recent interest in marmosets. Other species offer distinct advantages for applying the spectrum of modern molecular tools to the study of brain function and disease. Research on mice, for example, is able to apply the most cutting-edge genetic tools to the study of their brains with thousands of transgenic lines available to parse neural circuits with remarkable precision, while large proportions of the neurons can be identified and imaged in behaving *C. elegans* and zebrafish (Ahrens et al., 2013; Prevedel et al., 2014; Fosque et al., 2015; Nguyen et al., 2016). Describing the technical gap between the methods available to study the brains in these models and those of nonhuman primates as significant would be a gross understatement. Certainly if the goal of modern neuroscience was simply to understand any brain, then primates would be of limited value. There is, however, no single model of "the brain." As much as evolution is conservative, it enables idiosyncratic solutions to the challenges faced by each organism to adapt to its niche. This is, after all, one of the principle processes by which speciation occurs and the source of much of the diversity evident within and across taxonomic groups. Selection for a particular behavior will, by extension, include the neural circuits and mechanisms that support it. As a result,

behavioral differences evident across species are likewise reflected at the neural level. Any one model of the brain would effectively fail to capture the extent of diversity represented across animals, vertebrates, mammals, or even primates. Identifying the unique properties of primate neural circuits can be effectively investigated through the more distinctive and sophisticated elements of their natural behavioral repertoire.

Primates are perhaps most readily distinguished from other mammals and vertebrates by the breadth of their cognitive capabilities and the sophisticated societies in which they frequently apply these skills (Hare et al., 2001, 2006; Cheney and Seyfarth, 2007; Rosati et al., 2010; Drayton and Santos, 2014; Seyfarth and Cheney, 2014; Martin and Santos, 2016; Miller et al., 2016; Platt et al., 2016; Toarmino et al., 2017). The social domain is not the only one in which primates excel, their cognitive prowess and flexibility is frequently on display in their capacity to solve problems in diverse contexts (McGrew, 1992; Tomasello and Call, 1997; Whiten et al., 1999). The point here is not that primates are the only species to exhibit a certain degree of cognitive complexity across these and other domains, as other Taxa also demonstrate similarly sophisticated cognitive capabilities (Rendell and Whitehead, 2001; Marino et al., 2007; Heinrich, 2011; Bugnyar, 2013), but that a more precise characterization of these behaviors and how they unfold over time is key to identifying the neural mechanisms distinct to primates. Like all species, a primate view of the world is distinctive, as it reflects solutions to unique challenges that faced the Order over its evolutionary history. These selective forces have shaped primates to rely heavily on vision and audition, for example, rather than the olfactory and tactile signaling more typical of many other mammals (Mitchell and Leopold, 2015; Miller et al., 2016). When faced with a challenge, the process of making a decision about how to proceed, as well as executing that sequence of behaviors, will arise from distinct calculations related to an assessment of available options and weighing the various solutions over both short and long time scales. This process has remarkable similarity across primates (Rosati and Santos, 2015), likely owing to the shared core neural circuits that underlie decision-making (Gold and Shadlen, 2007; Lee, 2010; Chang et al., 2013; Haroush and Williams, 2015; Platt et al., 2016). Furthermore, the increased size and sophistication of primate prefrontal cortex likely evolved to support the progressively more complex forms of cognitive computation evident in the behavioral repertoire (Goldman-Rakic, 1971; Krasnegor et al., 1997; Miller and

Cohen, 2001; Semendeferi et al., 2001; Chang et al., 2013). In fact, numerous studies evidence the pivotal role of prefrontal cortex in many of the more complex aspects of primate behavior and related neural function (Hickok and Poeppel, 2004; Cromer et al., 2010; Roy et al., 2010; Miller and Wallis, 2012; Mante et al., 2013). As a result of these and other idiosyncrasies, the behavioral strategy employed to overcome ecological and social challenges encountered by primates, and the supporting neural mechanisms, are likely to be distinct from many other taxa, even in situations when the final behavioral outcome may appear analogous. The significance of this pattern is not only pertinent to our assessment of healthy brains, but also for disease as well (Jennings et al., 2016). Perhaps not surprisingly due to differences across species in both neural function and broader physiology, at least some rodent models of human disease have limited effectiveness (Seok et al., 2013). As a result, our simian cousins remain vital to understanding the human brain in its healthy state and dysfunction.

MARMOSETS

The common marmoset is a New World primate endemic to northeastern Brazil. As primates, marmoset share the core neural architecture of our Order, including humans (Chaplin et al., 2013; Solomon and Rosa, 2014). Likewise, marmosets exhibit the spectrum of characteristic behavior and cognition that typify primates (Miller et al., 2016; Schiel and Souto, 2017). Unfortunately, the neural mechanisms that support many of these behaviors are relatively poorly understood. Certainly, substrates have been identified that likely play key roles in some of the more sophisticated primate behaviors, such as prefrontal cortex and the “face-patch” system, but our understanding of these areas is limited to traditional methods, such as extracellular single-unit recordings and neuroimaging. Cutting-edge molecular technologies applied to the study of mice over the past decade have clearly demonstrated that studies of neuronal systems at this level of resolution is imperative for a complete understanding of the neural circuits supporting behavior. The amenability of marmosets to modern genetic techniques, such as those discussed by Watakabe et al. (2017) and Silva (2017) in this Issue, make this species a likely powerful model organism in the next generation of neuroscience research. The significance of marmosets as a neuroscientific model, however, is not exclusive to these technologies. Marmosets afford opportunities to expand the footprint of

primate neuroscience research by taking advantage of the species' shared and unique behavioral and neurobiological characteristics. In this way, marmosets represent a complementary model to the more commonly studied rhesus monkey, opening doors to investigate properties of primate brain function that were not previously possible.

Marmosets are both typical of primates and exhibit species-specific features. Studies of marmosets that focus on properties shared across primates offer opportunities to identify core principles of primate brain and behavior. For example, Nummela and colleagues in this Issue characterized the visual acuity of marmosets and show that it is comparable to larger primates, including rhesus monkeys and humans (Nummela et al., 2017). Notably, they report a preponderance of myopia amongst captive marmosets that may emerge from limited visual environments. Likewise, Walker and colleagues highlight the importance of marmosets as a comparative model of the motor system for explicating the mechanisms underlying voluntary control (Walker et al., 2017). Given that differences in motor behaviors are evident between some New and Old World primates, such a comparison is particularly valuable. Comparative studies of this nature can also take advantage of recent experiments showing that marmosets can be trained to perform at least some tasks traditionally used in primate research (Remington et al., 2012; Osmanski et al., 2013; Mitchell et al., 2014; Song et al., 2016). The use of marmosets as a comparative model of the primate brain is likely to be a cornerstone of future work, but taking advantage of the species' unique characteristics offers opportunities to expand the scope of primate brain research.

In this Issue, Schiel and Souto provide what is perhaps the most extensive review of marmoset natural history and behavioral ecology, highlighting many of the species' defining characteristics that make them particularly well-suited as a neuroscientific model of broader significance (Schiel and Souto, 2017). Remarkably, certain aspects of the marmoset behavioral repertoire parallel humans. Marmosets and humans, for example, are amongst only a handful of primates that pair-bond and cooperatively care for their young (Digby and Barreto, 1993; French, 1997; Solomon and French, 1997) suggesting similar prosocial tendencies (Burkart et al., 2009; Burkart and van Schaik, 2010). Furthermore, with the exception of chimpanzees (Whitten, 1998; Whiten et al., 2009), marmosets are the only nonhuman primate species to consistently exhibit imitation in their behavior (Bugnyar and Huber, 1997; Voelkl and Huber, 2000, 2007), a unique social learning mechanism critical to

human culture. As Eliades and Miller discuss in this Issue, marmosets are also highly voluble, engaging in near tonic levels of vocal communication (Eliades and Miller, 2017). This degree of social signaling again shares parallels to humans, while the discovery of the "face-patch" system in marmosets described by Silva in this Issue (Silva, 2017) underlines the significance of visual signaling common to all primates (Tsao et al., 2006, 2008; Hung et al., 2015a). Beyond the social dimensions of their behavioral repertoire, marmosets are proficient hunters, relying on their speed and precision to quickly grab fast moving insects that make up a large portion of their natural diet (Schiel et al., 2010). As discussed by Walker and colleagues in this issue, natural motor behaviors such as these make marmosets an exemplary model of voluntary motor control amongst primates (Walker et al., 2017). Likewise, marmoset visual behavior, while comparable to other primates in some dimensions, also exhibits distinct characteristics reflective of their unique evolutionary history (Mitchell et al., 2014, 2015; Mitchell and Leopold, 2015). Much of the value of marmosets as a neuroscientific model comes from leveraging these types of behavioral characteristics with a rapidly increasing set of techniques to examine the supporting neural processes.

Marmosets are relatively small for a primate, weighing only approximately 400 g. As a result, it has been possible to develop techniques to record the activity of single neurons in freely moving marmosets (Eliades and Wang, 2008a; Roy and Wang, 2012). This approach has opened the door to exploring the neural processes underlying natural behaviors in the primate repertoire, such as in vocal communication (Eliades and Wang, 2008b; Miller et al., 2015; Eliades and Miller, 2017), and can readily be applied to a broader range of behaviors, including foraging, visual perception, development, and social cognition (Santos and Hauser, 1999; Voelkl and Huber, 2000; Burkart and Heschl, 2007; Chow et al., 2015; Walker et al., 2017), among many other facets of the primate behavioral repertoire that emerge under more naturalistic conditions (Cavanaugh et al., 2015; Mustoe et al., 2015; Saito, 2015). The lissencephalic (smooth) cortex of marmosets is advantageous because nearly all cortical substrates are on the surface of the brain, just below the skull. This characteristic is particularly beneficial for several neural recording techniques, such as multielectrode arrays and laminar electrodes, functional neuroimaging (Silva et al., 2011; Hung et al., 2015b; Mundiano et al., 2016), as well as modern multi-photon imaging techniques (Sadakane et al., 2015; Santisakultarm et al., 2016). Recent pioneering work applying 2-Photon

Ca⁺ imaging in marmosets is discussed in detail by both Watakabe et al. (2017) and Silva (2017) in this Issue. Furthermore, adeno-associated viruses (AAV) express robustly in marmosets (Watakabe et al., 2015, 2017), providing opportunities to apply modern optogenetic and pharmacogenetic techniques to the study of primate brain circuitry (MacDougall et al., 2016).

The importance of marmosets as a model of human disease stems not only from their phylogenetic relatedness, but also distinct behavioral attributes and logistical benefits afforded by the species. In this Issue, for example, Hagan and colleagues emphasize how marmosets' rapid development combined with their characteristic primate visual cortex afford distinct advantages for understanding blind sight (Hagan et al., 2017). Likewise, Oikonomidis and colleagues in this Issue point to the various reasons why marmosets are an ideal model for a range of neuropsychiatric disorders, such as their suitability for behavioral testing paradigms developed to effectively examine specific cognitive dysfunction associated with disease in humans (Oikonomidis et al., 2017). Coupled with cutting-edge molecular tools that precisely manipulate and test the genetic mechanisms underlying human disease, marmosets are likely to be at the forefront of medical discoveries in the coming decades (Belmonte et al., 2015; Kaiser and Feng, 2015).

TOWARD A PRIMATE DEVELOPMENTAL NEUROBIOLOGY

Developmental neurobiology is amongst the most exciting fields in neuroscience. These studies provide unique insight into how complementary contributions of exogenous factors and internal constraints shape brain organization and function, as well the behaviors they support. It is over development that a species evolutionary roots and its divergent characteristics can most clearly be observed. By and large, these data are missing in primates. This is not due to a lack of interest, but rather significant logistical constraints have impeded progress towards these questions in more commonly used primate models, such as rhesus monkeys. For perhaps the first time, the potential for a rigorous primate developmental neurobiology can be realized with marmosets as a model system.

Combined with the extensive behavioral and neurobiological tool kit described above, characteristics of marmoset reproductive biology makes it possible to envision a comprehensive study of primate developmental neurobiology. Marmosets are prolific breeders by primate standards. Gestation is only

approximately 140 days and births typically comprise fraternal twins (Tardif et al., 2003; Schiel and Souto, 2017). Development is also relatively rapid, with individuals achieving adulthood in approximately 16–18 months of age (Yamamoto, 1993; Tardif et al., 2003). These attributes make the prospect of marmosets as a developmental neurobiological model not only possible, but likely and are discussed at length by Homman-Ludiye and Bourne in this Issue (Homman-Ludiye and Bourne, 2017). These authors make the compelling case for why a primate model is critical to understanding human brain development, as other prevalently used vertebrate species, such as mice, exhibit notably distinct ontogenetic processes, particularly in the neocortex. In addition to the untold potential of utilizing marmosets to investigate questions of functional neuroanatomical development at multiple levels of analysis, a key advantage of these Neotropical monkeys for developmental neurobiology pertains to the behavioral repertoire described above. Indeed, many of the manuscripts in this Special Issue review work in adult marmosets for which there is little to no developmental data available, but offer key frameworks to explicate the related ontogenetic processes that sculpt the adult brain and behavior. Turning our attention to questions of development, including how the epigenetic landscape both shapes and constrains the primate brain over ontogeny, represents an exciting avenue of future marmoset research.

REFERENCES

- Ahrens MB, Orger MB, Robson DN, Li JM, Keller PJ. 2013. Whole-brain functional imaging at cellular resolution using light-sheet microscopy. *Nat Methods* 10:413–420.
- Belmonte J, et al. 2015. Brains, genes and primates. *Neuron* 86:617–631.
- Bendor DA, Wang X. 2005. The neuronal representation of pitch in primate auditory cortex. *Nature* 436:1161–1165.
- Bourne JA, Tweedale R, Rosa MGP. 2002. Physiological responses of New World monkey V1 neurons to stimuli defined by coherent motion. *Cereb Cortex* 12:1132–1145.
- Bugnyar T. 2013. Social cognition in ravens. *Comp Cogn Behav Rev* 8:1–12.
- Bugnyar T, Huber L. 1997. Push or pull: An experimental study of imitation in marmosets. *Anim Behav* 54:817–831.
- Burkart JM, Heschl A. 2007. Understanding visual access in common marmosets (*Callithrix jacchus*): Perspective taking and other behaviour reading?. *Anim Behav* 73:457–469.

- Burkart JM, van Schaik CP. 2010. Cognitive consequences of cooperative breeding in primates?. *Anim Cogn* 13:1–19.
- Burkart JM, Hrdy SB, van Schaik CP. 2009. Cooperative breeding and human cognitive evolution. *Evol Anthropol* 18:175–186.
- Cavanaugh J, Huffman MC, Harnisch AM, French JA. 2015. Marmosets treated with oxytocin are more socially attractive to their long-term mate. *Front Behav Neurosci* 9:251.
- Chang SW, Garipey JF, Platt ML. 2013. Neuronal reference frames for social decisions in primate frontal cortex. *Nat Neurosci* 16:243–250.
- Chaplin T, Yu H, Soares J, Gattass R, Rosa MGP. 2013. A conserved pattern of differential expansion of cortical areas in simian primates. *J Neurosci* 18:15120–15125.
- Cheney DL, Seyfarth RM. 2007. *Baboon Metaphysics: The Evolution of a Social Mind*. Chicago: University of Chicago Press.
- Chow C, Mitchell J, Miller CT. 2015. Vocal turn-taking in a nonhuman primate is learned during ontogeny. *Proc R Soc B* 282:210150069.
- Cromer J, Roy J, Miller E. 2010. Representation of multiple, independent categories in the primate prefrontal cortex. *Neuron* 796–807.
- Dias R, Robbins TW, Roberts AC. 1996. Dissociation in prefrontal cortex of affective and attentional shifts. *Nature* 380:69–72.
- Digby LJ, Barreto CE. 1993. Social organization in a wild population of *Callithrix jacchus*: Part 1: Group composition and dynamics. *Folia Primatol* 61:123–134.
- Drayton LA, Santos LR. 2014. A decade of theory of mind research on Cayo Santiago: Insights into rhesus macaque social cognition. *Am J Primatol* 78:106–116.
- Eliades SJ, Wang X. 2008a. Chronic multi-electrode neural recording in free-roaming monkeys. *J Neurosci Methods* 172:201–214.
- Eliades SJ, Wang X. 2008b. Neural substrates of vocalization feedback monitoring in primate auditory cortex. *Nature* 453:1102–1106.
- Eliades SJ, Miller CT. 2017. Marmoset vocal communication: Neurobiology and behavior. *Dev Neurobiol* (in press).
- Fosque BF, Sun Y, Dana H, Yang C, Ohyama T, Tadross MR, Patel R, et al. 2015. Labelling of active neural circuits in vivo with designed calcium indicators. *Science* 347:755–760.
- French JA. 1997. Proximate regulation of singular breeding in callitrichid primates. In: Solomon N, French JA, editors. *Cooperative Breeding in Mammals*. Cambridge, UK: Cambridge University Press, pp 34–75.
- Geritis A, Vanduffel W. 2013. Optogenetics in primates: A shining future?. *Trends Genet* 29:403–411.
- Gold JI, Shadlen MN. 2007. The neural basis of decision making. *Ann Rev Neurosci* 30:535–574.
- Goldman-Rakic PS. 1971. Functional development of the prefrontal cortex in early life and the problem of neuronal plasticity. *Exp Neurol* 32:366–387.
- Hagan MA, Rosa MGP, Lui LL. 2017. Neural plasticity following lesions of the primate occipital lobe: The marmoset as an animal model for studies of Blindsight. *Dev Neurobiol* (in press).
- Hare B, Call J, Tomasello M. 2001. Do chimpanzees know what conspecifics know. *Anim Behav* 61:139–151.
- Hare B, Call J, Tomasello M. 2006. Chimpanzees deceive a human competitor by hiding. *Cognition* 101:495–514.
- Haroush K, Williams ZM. 2015. Neuronal prediction of opponent's behavior during cooperative social interchange in primates. *Cell* 160:13–11.
- Heinrich B. 2011. Conflict, cooperation and cognition in the common raven. *Adv Study Behav* 43:189–238.
- Hickok G, Poeppel D. 2004. Dorsal and ventral streams: A framework for understanding aspects of the functional anatomy of language. *Cognition* 92:67–99.
- Homman-Ludiye J, Bourne JA. 2017. The marmoset: An emerging model to unravel the evolution and development of primate neocortex. *Dev Neurobiol* (in press).
- Hung CC, Yen CC, Ciuchta JL, Papoti D, Bock NA, Leopold DA, Silva AC. 2015a. Functional mapping of face-selective regions in the extrastriate visual cortex of the marmoset. *J Neurosci* 35:1160–1172.
- Hung CC, Yen CC, Ciuchta JL, Papoti D, Bock NA, Leopold DA, Silva AC. 2015b. Functional MRI of visual responses in the awake, behaving marmoset. *Neuroimage* 120:1–11.
- Jennings GC, Landman R, Zhou Y, Sharma J, Hyman J, Movschoon JA, Qiu Z, et al. 2016. Opportunities and challenges in modeling human brain disorders in transgenic primates. *Nat Neurosci* 19:1123–1130.
- Kaiser T, Feng G. 2015. Modeling psychiatric disorders for developing effective treatments. *Nat Med* 21:979–988.
- Krasnegor NA, Lyon GR, Goldman-Rakic PS. 1997. *Development of the Prefrontal Cortex: Evolution, Neurobiology, and Behavior*. Baltimore: Paul H. Brookes Publishing Co.
- Lee D. 2010. Neuroethology of decision making. In: Platt M, Ghazanfar AA, editors. *Primate Neuroethology*. New York, NY: Oxford University Press, pp 550–569.
- MacDougall M, Nummela SU, Coop S, Disney AA, Mitchell JF, Miller CT. 2016. Optogenetic photostimulation of neural circuits in awake marmosets. *J Neurophys* 116:1286–1294.
- Mante V, Sussillo D, Shenoy K, Newsome WT. 2013. Context-dependent computation by recurrent dynamics in prefrontal cortex. *Nature* 503:78–84.
- Marino L, Connor RC, Fordyce RE, Herman LM, Hof PR, Lefebvre L, Lusseau D, et al. 2007. Cetaceans have complex brains for complex cognition. *PLoS ONE* 5:e139.
- Martin A, Santos LR. 2016. What cognitive representations support primate theory of mind?. *Trends Cogn Sci* 20:375–382.
- McGrew WC. 1992. *Chimpanzee Material Culture*. Cambridge, UK: Cambridge University Press.
- Miller EK, Cohen JD. 2001. An integrative theory of prefrontal cortex function. *Ann Rev Neurosci* 24:167–202.
- Miller EK, Wallis JD. 2012. The prefrontal cortex and executive brain functions. In: Squire L, Berg D, Bloom FE, du Lac S, Ghosh A, Spitzer N, editors. *Fundamental*

- Neuroscience, 4th ed. New York: Academic Press, pp 1069–1089.
- Miller CT, Thomas AW, Nummela S, de la Mothe LA. 2015. Responses of primate frontal cortex neurons during natural vocal communication. *J Neurophys* 114:1158–1171.
- Miller CT, Freiwald W, Leopold DA, Mitchell JF, Silva AC, Wang X. 2016. Marmosets: A neuroscientific model of human social behavior. *Neuron* 90:219–233.
- Mitchell JF, Leopold DA. 2015. The marmoset monkey as a model for visual neuroscience. *Neurosci Res* 93:20–46.
- Mitchell J, Reynolds J, Miller CT. 2014. Active vision in marmosets: A model for visual neuroscience. *J Neurosci* 34:1183–1194.
- Mitchell J, Priebe N, Miller CT. 2015. Motion dependence of smooth eye movements in the marmoset. *J Neurophys* 113:3954–3960.
- Mundiano IC, Flecknell PA, Bourne JA. 2016. MRI-guided stereotaxic brain surgery in the infant and adult common marmoset. *Nat Protoc* 11:1299–1308.
- Mustoe AC, Cavanaugh J, Harnisch AM, Thompson BE, French JA. 2015. Do marmosets care to share? Oxytocin treatment reduces prosocial behavior towards strangers. *Horm Behav* 71:83–90.
- Nguyen JP, Shipley FB, Linder AN, Plummer GS, Liu M, Setru SU, Shaevitz JW, et al. 2016. Whole-brain calcium imaging with cellular resolution in freely-behaving *Caenorhabditis elegans*. *pnas* 113:E1074–E1081.
- Nummela SU, Coop SH, Cloherty SL, Boisvert CJ, Leblanc M, Mitchell JF. 2017. Psychophysical measurement of marmoset acuity and myopia. *Dev Neurobiol* (in press).
- O’Shea DJ, Trautmann E, Chandrasekaran C, Stavisky S, Kao JC, Sahani M, et al. 2017. The need for calcium imaging in nonhuman primates: New motor neuroscience and brain-machine interfaces. *Exp Neurol* (in press).
- Oikonomidis L, Santangelo A, Shiba Y, Clark H, Robbins TW, Roberts AC. 2017. A dimensional approach to modelling symptoms of neuropsychiatric disorders in the marmoset monkey. *Dev Neurobiol* (in press).
- Okano H, Miyawaki A, Kasai K. 2016a. Brain/MINDS: Brain mapping project in Japan. *Philos Trans R Soc Lond B: Biol Sci* 370:20140310.
- Okano H, Sasaki E, Yamamori T, Iriki A, Shimogori T, Yamaguchi Y, Kasai K, et al. 2016b. Brain/MINDS: A Japanese national brain project for marmoset neuroscience. *Neuron* 92:582–590.
- Osmanski MS, Song X, Wang X. 2013. The role of harmonic resolvability in pitch perception in a vocal non-human primate, the common marmoset (*Callithrix jacchus*). *J Neurosci* 33:9161–9168.
- Park JE, Zhang XF, Choi S, Okahara J, Sasaki E, Silva AC. 2016. Generation of transgenic marmosets expressing genetically encoded calcium indicators. *Sci Rep* 6:34931.
- Platt ML, Seyfarth RM, Cheney DL. 2016. Adaptations for social cognition in the primate brain. *Philos Trans R Soc Lond* 371:20150096.
- Prevedel R, Yoon Y, Hoffman M, Pak N, Wetzstein G, Kato S, Schrodell T, et al. 2014. Simultaneous whole-animal 3D imaging of neuronal activity using light-field microscopy. *Nat Methods* 11:727–730.
- Remington E, Osmanski M, Wang X. 2012. An operant conditioning method for studying auditory behaviors in marmoset monkeys. *PLoS ONE* 7:e47895.
- Rendell LE, Whitehead H. 2001. Culture in whales and dolphins. *Behav Brain Sci* 24:309–324.
- Roberts AC, Wallis JD. 2000. Inhibitory control and affective processing in the prefrontal cortex: Neuropsychological studies in the marmoset. *Cereb Cortex* 10:252–262.
- Rosati A, Santos LR. 2015. The evolutionary roots of human decision-making. *Ann Rev Psych* 66:321–347.
- Rosati A, Santos L, Hare B. 2010. Primate social cognition: Thirty years after Premack and Woodruff. In: Platt M, Ghazanfar AA, editors. *Primate Neuroethology*. Oxford, UK: Oxford University Press, pp 117–142.
- Roy S, Wang X. 2012. Wireless multi-channel single unit recording in freely moving and vocalizing primates. *J Neurosci Methods* 203:28–40.
- Roy JE, Riesenhuber M, Poggio T, Miller EK. 2010. Prefrontal cortex activity during flexible categorization. *J Neurosci* 30:8519–8528.
- Sadakane O, Masamizu Y, Watakabe A, Terada S, Ohtsuka M, Takaji M, Mizukami H, et al. 2015. Long-term two-photon calcium imaging of neuronal populations with subcellular resolution in adult non-human primates. *Cell Rep* 13:1989–1999.
- Saito A. 2015. The marmoset as a model for the study of primate parental behavior. *Neurosci Res* 93:99–109.
- Santisakultarn TP, Kresbergen CJ, Bandy DK, Ide DC, Choi S, Silva AC. 2016. Two-photon imaging of cerebral hemodynamics and neural activity in awake and anesthetized marmosets. *J Neurosci Methods* 271:55–64.
- Santos LR, Hauser MD. 1999. How monkeys see the eyes: Cotton-top tamarins’ reaction to changes in visual attention and action. *Anim Cogn* 2:131–139.
- Sasaki E, et al. 2009. Generation of transgenic non-human primates with germline transmission. *Nature* 459:523–527.
- Sato K, et al. 2016. Generation of a nonhuman primate model of severe combined immunodeficiency using highly efficient genome editing. *Cell Stem Cell* 19:127–138.
- Schiel N, Souto A. 2017. The common marmoset: An overview of its natural history, ecology and behavior. *Dev Neurobiol* (in press).
- Schiel N, Souto A, Huber L, Bezerra BM. 2010. Hunting strategies in wild common marmosets are prey and age dependent. *Am J Primatol* 71:1–8.
- Semendeferi K, Armstrong E, Schleicher A, Zilles K, Van Hoesen G. 2001. Prefrontal cortex in humans and apes: A comparative study of area 10. *Am J Phys Anthropol* 114:224–241.
- Seok J, et al. 2013. Genomic responses in mouse models poorly mimic human inflammatory diseases. *pnas* 110:3507–3512.
- Seyfarth RM, Cheney DL. 2014. Evolution of language from social cognition. *Curr Opin Neurobiol* 28:5–9.

- Silva AC. 2017. Anatomical and functional neuroimaging in awake, behaving marmosets. *Dev Neurobiol* (in press).
- Silva AC, Liu JV, Hirano Y, Leoni RF, Merkle H, Mackel JG, Zhang XF, et al. 2011. Longitudinal functional magnetic resonance imaging in animal models. *Methods Mol Biol* 711:281–302.
- Solomon N, French JA. 1997. The study of mammalian cooperative breeding. In: Solomon N, French JA, editors. *Cooperative Breeding in Mammals*. Cambridge, UK: Cambridge University Press, pp 1–10.
- Solomon SG, Rosa MGP. 2014. A simpler primate brain: The visual system of the marmoset monkey. *Front Neural Circuits* 8:1–24.
- Song X, Osmanski MS, Guo Y, Wang X. 2016. Complex pitch perception mechanisms are shared by humans and a New World monkey. *pnas* 113:781–786.
- Tardif SD, Smucny DA, Abbott DH, Mansfield K, Schultz-Darken N, Yamamoto ME. 2003. Reproduction in captive common marmosets (*Callithrix jacchus*). *Comp Med* 53: 364–368.
- Toarmino C, Wong L, Miller CT. 2017. Audience affects decision-making in a marmoset communication network. *Biol Lett* 13:20160934.
- Tomasello M, Call J. 1997. *Primate Cognition*. Oxford: Oxford University Press.
- Tsao DY, Freiwald WA, Tootell RB, Livingstone MS. 2006. A cortical region consisting entirely of face-selective cells. *Science* 311:670–674.
- Tsao DY, Moeller S, Freiwald W. 2008. Comparing face patch systems in macaques and humans. *Pnas* 105:19514–19519.
- Voelkl B, Huber L. 2000. True imitation in marmosets. *Anim Behav* 60:195–202.
- Voelkl B, Huber L. 2007. Imitation as faithful copying of a novel technique in marmoset monkeys. *PLoS ONE* 2: e611.
- Walker J, MacLean J, Hatsopoulos NG. 2017. The marmoset as a model system for studying voluntary motor control. *Dev Neurobiol* In Press.
- Wang X, Lu T, Snider RK, Liang L. 2005. Sustained firing in auditory cortex evoked by preferred stimuli. *Nature* 435:341–346.
- Watakabe A, Ohtsuka M, Kinoshita M, Takaji M, Isa K, Mizukami H, Ozawa K, et al. 2015. Comparative analyses of adeno-associated viral vector serotypes 1,2,5,8, and 9 in marmoset, mouse and macaque cerebral cortex. *Neurosci Res* 93:144–157.
- Watakabe A, Sadakane O, Hata K, Ohtsuka M, Takaji M, Yamamori T. 2017. Application of viral vectors to the study of neural connectivities and neural circuits in the marmoset brain. *Dev Neurobiol* (in press).
- Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, et al. 1999. Cultures in chimpanzees. *Nature* 399:682–685.
- Whiten A, McGuigan N, Marshall-Pescini S, Hopper LM. 2009. Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philos Trans R Soc Lond, B* 364:2417–2428.
- Whitten A. 1998. Imitation of sequential structure of actions by chimpanzees. *J Comp Psych* 112:270–281.
- Yamamoto M. 1993. From dependence to sexual maturity: The behavioural ontogeny of Callitrichidae. In: Rylands AB, editor. *Marmosets and Tamarins: Systematics, Behavior and Ecology*. London: Oxford University Press, pp 235–254.

Cory T. Miller

*Cortical Systems and Behavior Laboratory
Neurosciences Graduate Program
University of California
San Diego, California
(corymiller@ucsd.edu)*