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Review

Behavioral neuroscience, exploration, and K.C. Montgomery's legacy

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ABSTRACT

Exploration is a key animal and human behavior. Kay C. Montgomery (1921–1956) has made an important contribution to behavioral neuroscience of exploration, as well as motivation and learning. His works have many important applications to current experimental models of stress, fear and memory, continuing to influence research in this field. This paper, dedicated to the 85th anniversary of Montgomery's birth, and 50 years since his tragic death, summarizes Montgomery's contribution to behavioral neuroscience, and discusses its current importance for further progress in this field. It is aimed at neuroscientists with strong interests in both theory of animal exploration and motivation, and the history of behavioral neuroscience.

Exploration is a fundamental feature of activity in animals and humans (Adlerstein and Fehrer, 1955; Berlyne, 1950, 1954; Bindra and Spinner, 1958; Cryan and Holmes, 2005; Halliday, 1966; Hull, 1943; Kalueff et al., 2006; Kim et al., 2005; Kliethermes and Crabbe, 2006). Among many prominent scientists working in this field, Kay C. Montgomery (1921–1956) (Montgomery, 1951a,b,c, 1952,b) has his own special place. As this year marks the 85th anniversary of Montgomery's birth, and 50 years since his tragic death, it is now timely to acknowledge his contribution to behavioral neuroscience (Fig. 1).

Kay Cameron Montgomery was born in Greensbury, Pennsylvania, in 1921. He spent several years studying at the University of Florida, Murray State Teacher's college, Alabama Polytechnic, and the University of North Carolina before being drafted into the military during WW II, serving as a weather officer and becoming committed to learning new information. Montgomery spent 4 years at the University of Chicago, where he obtained his BS (1946) and PhD, only 3 years later (1949), in Psychology. In 1949 Montgomery accepted a position as instructor in Psychology at Harvard University, and a year later moved to Cornell University.

In 1953, he was offered an assistant professorship in psychology at Yale University, where he spent the last 3 years of his life. During these years, Montgomery was remembered as a very intense, extremely hard-working scientist who published extensively in a new area of exploratory behavior, challenging basic assumptions of drive reduction theory, in a department that had championed that approach from Clark Hull (1943) to Neal Miller (Bower and Miller, 1960; Miller, 1957; Zimbardo and Miller, 1958). Although only an untenured Assistant Professor, he was put in charge of reorganizing the large introductory psychology course to emphasize its scientific and historical

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Fig. 1 – Kay C. Montgomery during his years in the University of Chicago (ca. 1946–1949; top) and Yale University (1953, with spouse), courtesy of Dr. Scott L. Montgomery.

foundations. He was also a dedicated teacher popular among students. In 1955–1956, Montgomery fell victim to deep, chronic depression brought on by a combination of family difficulties and his failure to gain tenure at Yale University (despite his impressive publication record, ground-breaking research, and commitment to teaching excellence). In July of 1956, aged 35, he committed suicide, thus ending a young but highly promising career.

Several important findings form Montgomery's legacy. In his most famous "approach–avoidance" theory (Montgomery, 1954, 1955; Montgomery and Monkman, 1955), Montgomery postulated that animal exploration is determined by the balance between two conflicting motivations—an exploratory drive (curiosity) and fear evoked by novelty. An exploratory drive differs from other (homeostatic) drives in that it is aroused by novel external stimulation (rather than internal state of the organism, such as hunger), and is satiated quickly by continuous exposure to the same stimulus situation (Bindra, 1957; Bindra and Spinner, 1958; Cofer, 1959; O'Keefe and Nadel, 1978). In line with this theory, Montgomery has also made an important contribution to the neurobiology of learning. In their classical study, Montgomery and Segall (1955) showed T-maze learning in rats may be reinforced by an exploratory drive—the opportunity to explore a complex Dashiell-type maze (also see Walker, 1957 for discussion).

Importantly, these theories are nowadays widely used in behavioral neuroscience. Several traditional anxiety tests, including the elevated plus (Handley and Mithani, 1984; Rodgers and Cole, 1993; Rodgers et al., 1995)-, zero (Cook et al., 2001; Shepherd et al., 1994)- and T-mazes (Carvalho-Netto and Nunes-de-Souza, 2004; Glickman and Jensen, 1961), are all based on Montgomery's observations of innate fear in rodents (Montgomery, 1953b,c,d) exposed to the elevated unprotected alley in the Y-maze. Numerous modifications of these tests have been validated (Hagenbuch et al., 2006; Rodgers et al., 1995), finding extensive applications in screening of novel anxiety-active drugs (Rodgers et al., 1995), various strains (Flint, 2002, 2003; Trullas and Skolnick, 1993) and mutant or transgenic animals (Carobrez and Bertoglio, 2005; Cryan and Holmes, 2005; Dulawa et al., 1999; Pogorelov et al., 2005). As these observations suggested that exploration is gradually inhibited by anxiety, and therefore may represent its indirect measure (Ohl, 2005) (see, however, Ennaceur et al., 2006 for discussion of fear vs. anxiety in animal responses to novelty), it may also be concluded that all current novelty-based anxiety paradigms are, in fact, based on Montgomery's theory of motivational conflict.

Moreover, Montgomery shared strong interest in the impact of various motivations on animal exploration. In several early studies (Adlerstein and Fehrer, 1955; Dashiell, 1925), food deprivation was reported to increase exploration. In contrast, assessing the effects of hunger and thirst on Y-maze exploration in female rats, Montgomery obtained somewhat opposite data (Montgomery, 1953c; Montgomery and Zimbardo, 1957). Subsequently, replicating Montgomery's experiments in male rats, Glickman and Jensen (1961) showed complex bi-directional effects of food deprivation on exploration (also see Maren and Fanselow, 1998; Zimbardo and Miller, 1958). Although this aspect is still the matter of further studies, Montgomery succeeded in linking several different drives in their actions on animal exploration and learning. In research with Zimbardo, Montgomery showed that when hungry or thirsty male rats were put in a novel environment where cups of food or water were readily available throughout, all rats explored the novel setting before ever stopping to eat or drink (Zimbardo and Montgomery, 1957a). They reasoned that in the wild, such exploration was an essential precaution to assure the safety of the setting prior to engaging in consummatory behavior that might make them vulnerable to predators.

Another topic of his research was the effects of early environment on animal exploration. In 1957, Zimbardo and Montgomery (1957b) suggested the interesting hypothesis that animals reared in a sensory and behaviorally enriched environment will explore more when subsequently put into a complex environment, but may explore less in a relatively simple novelty situation-compared to rats reared after weaning in deprived environments of either behaviorally restricted or both sensory and behaviorally restricted. (also see rev. Gorry et al., 1971). Clearly, this notion is of great importance for today's neuroscientists, as behavior- and brain-modulating role of environmental enrichment in animals (Wolfer et al., 2004; Wurbel, 2001) is becoming widely recognized.

Today, Montgomery's pioneering works continue to influence generations of researchers working in this field. Only for the last 20 years covered by the ISI Web of Science (2006), Montgomery's papers (Montgomery, 1951a,b,c, 1952a,b; Montgomery and Heinemann, 1952; Montgomery, 1953a,b,c,d, 1954, 1955; Montgomery and Monkman, 1955; Montgomery and Segall, 1955; Montgomery and Zimbardo, 1957; Zimbardo and Montgomery, 1957a,b) were cited more than 1200 times, outlining their lasting actuality for neurobehavioral neuroscience. His research, along with other contemporaries studying curiosity behavior, helped shift the focus away from deficit models of behavior, such as acting to reduce negative drive states, to a more positive conception of animal and human behavior motivated by self-enrichment tendencies. Montgomery's notion of the importance of situational models (where the environment itself has an incentive value to the animal), his influence on the structure of current experimental setups, his research on the impact of early environment and hunger on exploration, all resonate well with current approaches in behavioral neuroscience and neurogenetics. One unexpected extension of his focus on the significance of external, environmental factors on influencing behavior can be found in contemporary social psychology. Its situationist approach contrasts with the dispositional approach that locates the sources of behavior entirely within the organism's inner characteristics, often ignoring the power of situational forces (Zimbardo, in press).

However, it is also possible that Montgomery's theories are not being interpreted in the richness which we believe they deserve. For example, as already mentioned, in addition to his classic "fear–curiosity" theory, Montgomery recognized that animals may optimize their security through careful exploration of novel environments in order to rule out predator dangers (e.g., Zimbardo and Montgomery, 1957a). As this also suggests an important role of biological processes, such as the Darwinian pressures on animals, Montgomery's approach to animal exploration (taking into account both psychological and biological factors) may have been even more comprehensive and foresighted than it is generally recognized.

Clearly, Montgomery's seminal works shall be considered as an important part of history of behavioral neuroscience of exploration and motivation (Cryan and Holmes, 2005). While further complexity and paradoxes of animal exploration (Kalueff et al., 2006; Lester, 1968; Rodgers et al., 1995; Ruarte et al., 1997) continue to puzzle behavioral neuroscientists today, Montgomery's life work was an important step in our understanding (Ennaceur et al., 2006; Ohl, 2005) of animal exploratory behaviors.

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