Chronic Pain and DNA Methylation in the Mouse Prefrontal Cortex

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For my Father,

who turned in a M.Eng thesis that was 500 pages

and

For my Mother,

who completed her Ph.D, found her career, and had her son in the same summer

Genetics or epigenetics who knows, but it's their fault

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Abstract

Chronic pain is one of the leading causes of disability and reduced quality of life worldwide. As a result of chronic pain, the prefrontal cortex (PFC) undergoes significant structural and functional remodeling, resulting in the loss of grey matter, altered synapse formation, and changes in neurotransmitter and ion channel signalling. These changes are accompanied by widespread alterations in gene expression and can be reversed if pain is attenuated by therapeutic intervention. The combination of widespread changes in gene expression with a reversible phenotype implicates epigenetics as a potential regulatory mechanism underlying chronic pain development and maintenance. Previous research has demonstrated the involvement of DNA methylation, an epigenetic mechanism, in mediating chronic pain. However, its response across the chronic pain time course and to interventions is poorly understood. Increased understanding of PFC DNA methylation in response to chronic pain and therapeutic interventions will reveal mechanisms of chronic pain development and identify possible novel therapeutic targets.

This thesis hypothesized that the PFC undergoes dynamic changes in DNA methylation as chronic pain develops over time, and that pharmacological and non-pharmacological interventions would counteract or prevent pain-related changes in methylation. These hypotheses were investigated through three research aims:

1) Track and observe PFC DNA methylation in response to induced neuropathic pain for up to 12 months post-injury

2) After chronic pain has developed, determine the PFC DNA methylation response to a pharmacological intervention of s-adenosylmethionine (SAM)

3) After chronic pain has developed, determine the PFC DNA methylation response to a non-pharmacological intervention of voluntary exercise

We found that spared nerve injury (SNI) resulted in rapid and persistent changes in DNA methylation, with robust differential methylation observed at one day post-injury and up to 12 months post-injury. We identified hundreds of differentially methylated genes, including those with known functions in pain, affecting domains related to stimulus response at early time points, immune function at later time points and actin and cytoskeletal regulation throughout the time course (Manuscript I). This study confirmed the involvement of PFC DNA methylation throughout the chronic pain time course, and identified time point specific changes in DNA methylation across pain-related genes and domains.

To explore the response of DNA methylation to intervention, SAM and voluntary exercise were provided after SNI in two separate experiments. Chronic administration of SAM beginning 3 months after injury resulted in attenuation of neuropathic pain and differential methylation of over 4000 genomic regions. These regions were related to functional domains of intracellular signaling, cell locomotion and migration, cytoskeletal structure, and cell adhesion (Manuscript II). Providing access to voluntary exercise after injury also resulted in the attenuation of neuropathic pain and the differential methylation of over 5000 genomic regions. These regions were related to functional domains of ion transport and homeostasis, cell adhesion and locomotion, and immune functioning and morphogenesis (Manuscript III). In each experiment, providing therapeutic intervention resulted in the reversal of pain-related DNA methylation changes in over 1000 genomic

regions. These studies confirmed the responsiveness of PFC DNA methylation to intervention after chronic pain, and that therapeutic intervention reverses the methylation status of a subset of chronic pain affected genes.

The work presented in this thesis demonstrates that PFC DNA methylation is dynamic and responsive to the development of chronic pain and therapeutic intervention. These results increase the understanding of how chronic pain is regulated in the PFC during its development and treatment, and which functional domains are predominantly affected by DNA methylation. This thesis provides the foundation for future investigations to explore how epigenetic mechanisms mediate chronic pain development and for future therapies to target epigenetic mechanisms to alleviate chronic pain.

Résumé

La douleur chronique est l'une des causes principales de perte d'autonomie et de réduction de la qualité de vie dans le monde. En réponse à la douleur persistante, le cortex préfrontal (CPF) subit d'importants remodelages structuraux et fonctionnels, conduisant à une perte de matière grise, une altération de la formation des synapses et des changements dans la signalisation des neurotransmetteurs et des canaux ioniques. Ces changements s'accompagnent d'une altération généralisée de l'expression des gènes et peuvent être contrecarrés si la douleur est soulagée par une intervention thérapeutique. La combinaison de changements généralisés dans l'expression des gènes avec un phénotype réversible suggère que l'épigénétique est un mécanisme de régulation potentiel qui sous-tend le développement et le maintien de la douleur chronique. Des recherches antérieures ont démontré l'implication de la méthylation de l'ADN, un mécanisme épigénétique, dans la médiation de la douleur chronique, mais sa réponse au travers de l'évolution de la douleur chronique et aux interventions est mal comprise. Une meilleure compréhension de la méthylation de l'ADN du CPF en réponse à la douleur chronique et aux interventions thérapeutiques permettra de révéler les mécanismes sous-jacents du développement de la douleur chronique et contribueront à l'identification de nouvelles cibles thérapeutiques possibles.

Cette thèse repose sur l'hypothèse que le CPF subit des changements dynamiques dans méthylation de l'ADN au fur et à mesure que la douleur chronique se développe, et que des interventions pharmacologiques et non pharmacologiques

corrigeraient ou empêcheraient ces changements. Cette hypothèse a été explorée à travers trois objectifs de recherche:

1) Décrire et suivre sur 12 mois la méthylation de l'ADN du CPF en réponse à une douleur neuropathique induite.
2) Après le développement de la douleur chronique, déterminer la réponse de la méthylation de l'ADN dans le CPF suite à une intervention pharmacologique utilisant la s-adénosylméthionine (SAM).
3) Après le développement de la douleur chronique, déterminer la réponse de la méthylation de l'ADN dans le CPF en réponse à une intervention non pharmacologique basée sur l'exercice volontaire.

Nous avons constaté que la lésion partielle du nerf sciatique, ou SNI, entraînait des changements rapides et persistants de la méthylation de l'ADN au niveau du CPF, avec une puissante méthylation différentielle observée dès le premier jour et qui persistait jusqu'à 12 mois. Nous avons identifié des centaines de gènes différentiellement méthylés, incluant ceux ayant des fonctions connues dans la douleur, affectant les domaines liés à la réponse au stimulus dans les premiers points de temps, la fonction immunitaire dans les derniers points de temps et la régulation de l'actine et du cytosquelette tout au long de l'observation (Manuscrit I). Cette étude a confirmé l'implication de la méthylation de l'ADN du PFC au cours de l'évolution de la douleur chronique, et a également identifié des changements spécifiques de la méthylation de l'ADN de gènes et domaines liés à la douleur, à certains points temporels.

Pour explorer la réponse de la méthylation de l'ADN aux interventions, la SAM ou l'exercice volontaire ont été dispensés après lésion du nerf sciatique dans deux expériences distinctes. L'administration chronique de SAM, 3 mois après la blessure, a atténué la douleur neuropathique et la méthylation différentielle de plus de 4000 régions génomiques. Ces régions étaient liées aux domaines fonctionnels de la signalisation intracellulaire, de la locomotion et migration cellulaire, de la structure du cytosquelette et de l'adhésion cellulaire (Manuscript II). La possibilité de faire volontairement de l'exercice après la lésion a également atténué la douleur neuropathique et la méthylation différentielle de plus de 5 000 régions génomiques. Ces régions étaient liées aux domaines fonctionnels du transport ionique et de l'homéostasie, de l'adhésion et locomotion cellulaire, du fonctionnement immunitaire et de la morphogenèse (Manuscrit III). Dans chaque expérience, l'intervention thérapeutique a permis d'inverser les changements de méthylation de l'ADN liés à la douleur dans plus de 1000 régions génomiques. Ces études ont confirmé la réactivité de la méthylation de l'ADN du CPF aux interventions au cours de la douleur chronique, et qu'une intervention thérapeutique efficace inverse le statut de méthylation d'un sous-ensemble de gènes affectés par la douleur chronique.

Les travaux présentés dans cette thèse démontrent que la méthylation de l'ADN du CPF est dynamique et sensible au développement de la douleur chronique et aux interventionx thérapeutique efficaces. Ces résultats permettent de mieux comprendre comment la douleur chronique est régulée dans le CPF au cours de son développement et de son traitement, et identifient les domaines fonctionnels principalement affectés par

la méthylation de l'ADN. Cette thèse construit les bases des futures recherches qui exploreront les mécanismes épigénétiques intervenant dans le développement de la douleur chronique et des thérapies futures qui cibleront les mécanismes épigénétiques pour soulager la douleur chronique.

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Contribution of Authors

This manuscript-based thesis consists of three multi-authored manuscripts. Each manuscript includes several original and distinct contributions to knowledge that will be demonstrated and discussed throughout this thesis. For each manuscript, I (L.Topham) conducted the majority of data analysis design and work, and wrote the initial draft of each manuscript. Each manuscript was a collaborative effort of the authors to design experiments, collect and analyze data, and write and revise the final manuscripts. Below is a categorical list of each author's contribution to each manuscript.

Manuscript I: The Transition from Acute to Chronic Pain: Dynamic Epigenetic Reprogramming of the Mouse Prefrontal Cortex up to One Year Following Nerve Injury

Published in *Pain*, 2020

Study Design: L. Topham, S. Gregoire, M. Millecamps, E. Lax, M. Salmon-Divon, M. Szyf, L. Stone

Conducted In Vivo Experiments and Processed Tissue: S. Gregoire, M. Millecamps, HM. Kang

Analysed Data: L. Topham, HM. Kang

Wrote Manuscript: L. Topham, M. Szyf, L. Stone

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Manuscript II: Attenuation of neuropathic pain by s-adenosylmethionine is associated with genome-wide reversals of pathological changes in DNA methylation in mouse frontal cortex

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Study Design: L. Topham, S. Gregoire, M. Millecamps, E.Lax, M. Salmon-Divon, M.Szyf, L. Stone

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Analysed Data: L. Topham

Wrote Manuscript: L. Topham, L. Stone

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List of Abbreviations

1Yr – one year post-injury

5hmC – 5-hydroxymethyl cytosine

5mC – 5-methylcytosine

ACC – anterior cingulate cortex

CpG – cytosine guanine sequence

D1 – one day post-injury

DLPFC – dorsolateral prefrontal cortex

DM – differentially methylated

DNMT – DNA Methyltransferase

DRG – dorsal root ganglia

FDR – false discovery rate

HAT – histone acetyltransferase

HDAC – histone deacetylase

HMT – histone methyltransferase

LTD – long term depression

LTP – long term potentiation

M6 – six months post-injury

mPFC – medial prefrontal cortex

PAG – periaqueductal grey

PFC – prefrontal cortex

S1 – primary somatosensory cortex

S2 – secondary somatosensory cortex

SAM – s-adenosylmethionine

SNI – spared nerve injury

TET – ten-eleven translocation enzyme

TSS – transcription start site

W2 – two weeks post-injury

Chapter 1: Introduction

2.1. The Challenge of Chronic Pain and the Potential of Epigenetics

Chronic pain is a global challenge, affecting 10-20% of adults worldwide at any given time and with 80% of people experiencing some form of chronic pain during their lifetime. Chronic pain stretches across all socio-economic levels and as of 2016, was the leading cause of years lost to disability in both men and women [1-3]. The high prevalence of chronic pain leads to massive healthcare costs with billions spent yearly on its treatment, and billions more lost indirectly through missed days of work and resource opportunity cost [4, 5]. Individuals living with chronic pain also suffer from one of the poorest qualities of life among chronic conditions [6]. Individuals report poorer mental health and sleep, difficulties maintaining personal relationships, reduced productivity at work and are commonly comorbid for depression, anxiety, and cognitive deficits [7]. These factors exacerbate suffering, prolong recovery, and make chronic pain complex and difficult to treat.

One of the key aspects that differentiates the experience of chronic pain from acute pain is the greater impact of these cognitive components [8]. Both human pain patients and animal models report deficits in decision making, attention, working memory, and executive function [9-13]. The prefrontal cortex (PFC) is one of the key structures mediating these processes, and undergoes significant functional and anatomical remodeling during chronic pain in both human and animal populations [14-20]. Animal models have also noted widespread changes in PFC gene expression during chronic pain [21-23]. This combination of PFC remodelling and cognitive/affective comorbidities has

been proposed to contribute to chronic pain intractability and make it difficult to resolve chronic pain. However if chronic pain is successfully attenuated through treatment, PFC remodelling can be reversed in human pain patients [24-26]. The PFC's plasticity in response to pain combined with the observed genome-wide changes in expression implicate epigenetics as a potential regulatory mechanism.

Epigenetics refer to stable but malleable mechanisms of influencing gene expression, including histone modifications, chromatin conformation, and DNA methylation. These modifications regulate much of cellular differentiation during development, and crucially they remain responsive to environmental changes throughout life [27]. Stress, nutrition, behaviour, physical activity, and environmental pollutants have all been found to induce the epigenetic regulation of gene expression and lead to altered phenotypes [28]. Therefore, epigenetics are a mechanism by which the environment, including pain stimuli, can directly modulate and affect gene expression.

Given the difficulty of treating chronic pain and the limited development of novel therapies in recent years, examining the relationship between chronic pain and PFC epigenetics provides a twofold benefit. First, by understanding the epigenetic response to chronic pain, we can identify potential epigenetic mechanisms to target or manipulate in order to prevent the development and maintenance of chronic pain. Second, by examining the genome-wide epigenetic response to pain, we can observe which cellular functions are being differentially regulated and identify new genes and domains that may yield new therapeutic avenues.

2.2. Comprehensive Literature Review and Background

2.2.1. **Pain Pathways**

Pain is defined by the International Association for the Study of Pain (IASP) as “an unpleasant sensory and emotional experience associated with, or resembling that associated with, actual or potential tissue damage” [29]. Pain sensation, perception, and experience involves the entire nervous system starting with peripheral detection, progressing through spinal processing and modulation, and then ascending to supraspinal perception and interpretation.

2.2.1.1. Peripheral and Spinal Pain Transduction

Most pain begins as the peripheral detection of a nociceptive stimulus, that is, an actual or potential tissue damaging event. Nociceptive stimuli can be noxious thermally, mechanically, or chemically, and are detected by specialized peripheral sensory neurons called nociceptors. These afferent nociceptive signals are conducted by either Aδ or C-fibers of the dorsal root ganglia (DRG) from the peripheral nociceptors to the dorsal horn of the spinal cord. Aδ fibers are myelinated, transmit noxious mechanical or thermal stimuli, and terminate primarily either in lamina I and the outer layer of lamina II, or arborize throughout lamina II-V [30, 31]. C fibers are unmyelinated, terminate primarily in laminae I and II, and transmit noxious mechanical, chemical or thermal stimuli as well as itch. C fibers can be broadly classified into peptidergic and non-peptidergic subtypes, which have been proposed to mediate the perception of heat pain and mechanical pain respectively [32]. Once arriving at the dorsal horn, Aδ and C-fibers synapse with interneurons or ascending projection neurons. Interneuron signalling within the dorsal

horn is complex and serves to modulate and potentiate nociceptive signalling. Broadly, interneurons are excitatory or inhibitory, and can mediate allodynia and gate pain sensation [33-35]. Ascending projection neurons transmit nociceptive information to supraspinal structures, primarily ascending via the anteriolateral spinothalamic tract to the thalamus. However, projection neurons also travel via the spinoparabrachial-amygdala pathway to the lateral parabrachial nuclei and amygdala, and via the spinoreticular pathway to the periaqueductal grey (PAG).

2.2.1.2. Supraspinal Pain Circuits

From the lateral spinothalamic tract and thalamus, nociceptive information is sent to the primary (S1) and secondary (S2) somatosensory cortices, insula, and anterior cingulate cortex (ACC). Projections from the lateral parabrachial nuclei route nociceptive stimuli to the amygdala and subsequently to the basal ganglia. The dorsolateral (DLPFC) and medial prefrontal cortex (mPFC) integrate inputs from S1, S2, insula, ACC, amygdala, and basal ganglia [36, 37].

Human and animal studies have identified how each supraspinal area contributes to the perception and interpretation of nociceptive stimuli. The S1 and S2 cortices are responsible for the localization, intensity, and duration of pain [38, 39]. The ACC primarily encodes the aversive emotional and affective dimensions [40, 41], while the insular cortex is involved in both pain sensation and pain affect [42]. In humans, the DLPFC and mPFC are crucial as integrators of ascending sensory information, cognitive and emotional responses, and descending inhibitory control during pain [37]. Human research has linked DLPFC activity with pain suppression and maintenance of pain inhibition and has

hypothesized it to be a “pain control centre”. Bilateral DLPFC activation occurs during intentional pain suppression, is associated with reduced unpleasantness of pain, and is involved in mediating placebo effects on pain [43-45]. Greater connectivity between right and left DLPFC is correlated with greater pain tolerance while conversely, reduced bilateral DLPFC activity is correlated with increased pain catastrophizing during pain [46, 47]. In contrast to DLPFC, mPFC is more involved in the processing of negative emotions and appraisal of unfavourable outcomes in relation to oneself. mPFC activity is correlated with sustained high-intensity pain and pain intensity [48]. The rostral ACC is a subregion of mPFC and contributes to mPFC encoding of aversive stimuli. Rostral ACC, mPFC, and amygdala work together to encode aversive memories and may be involved in pain-related memory acquisition and extinction [36].

Through descending pathways, supraspinal structures modulate pain processing and transduction. The frontal cortices and ACC can act via the periaqueductal gray to attenuate pain sensation during placebo and the expectation of pain relief [45, 49]. Conversely, signalling via the rostral ventromedial medulla can facilitate pain and is required for maintaining central sensitization in the spinal cord [50].

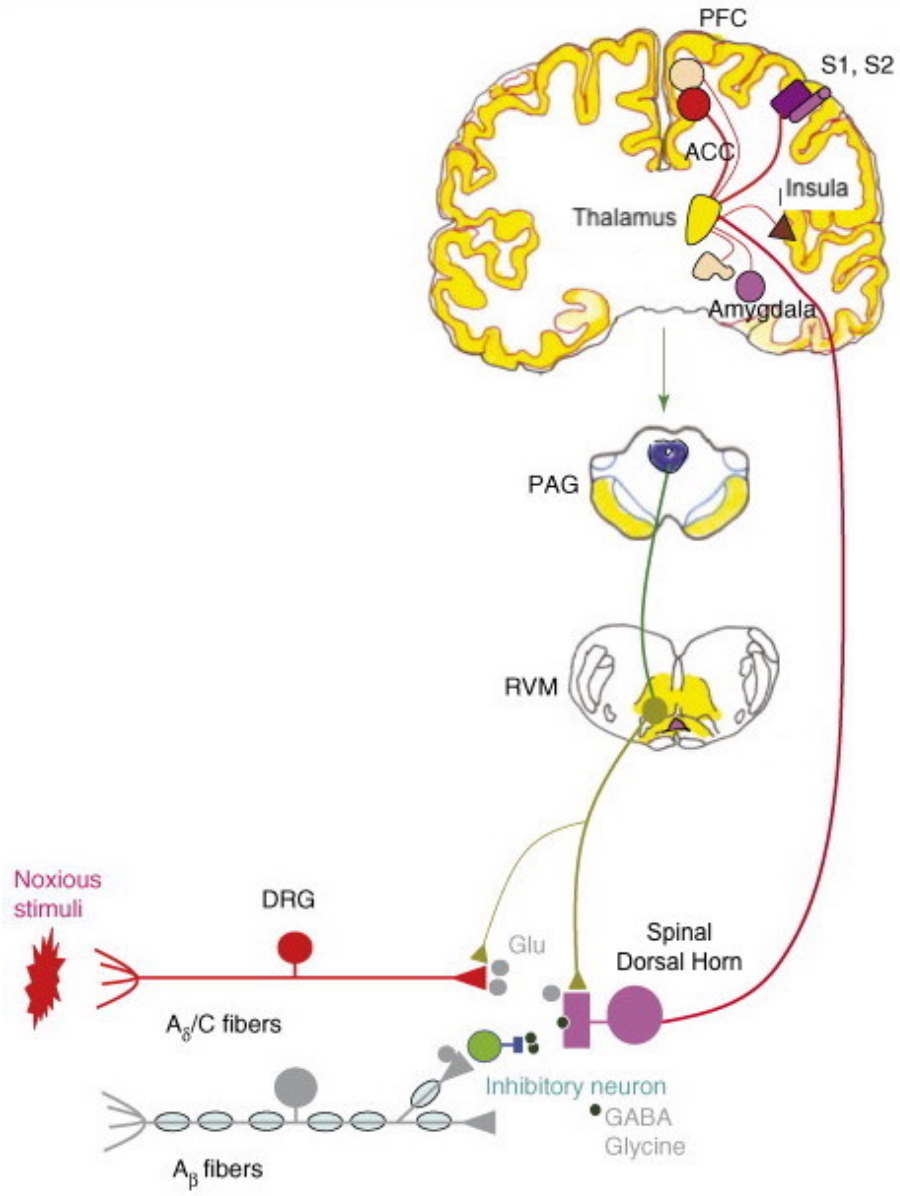


Figure 1: Nociceptive information is detected in the periphery and carried to the dorsal horn of the spinal cord by primary nociceptive afferents. Once in the dorsal horn, inhibitory interneurons and descending fibers modulate nociceptive information before it ascends to supraspinal areas. Supraspinal structures mediate pain perception and emotional and cognitive processing of nociceptive information. This image was adapted from [51], and used with permission of the publisher.

2.2.2. **Chronic Pain**

IASP has defined that for human patients, once pain has persisted or recurred for more than 3 months, it is considered to be chronic. Chronic pain can be considered a disease on its own, when it occurs as the sole or primary complaint, or as secondary and a symptom of another disease, such as cancer or trauma [52]. Animal models have revealed a number of mechanisms that underlie chronic pain syndromes. The use of animal models provides better control over the time course and development of chronic pain, and more consistent presentations of chronic pain between subjects. Neuro- or peripheral inflammation, and peripheral and central sensitization are mechanisms that most chronic pain syndromes have in common, all of which can lead to enhanced pain sensation.

Immune cells and nociceptors are mutually responsive, with each capable of modulating and enhancing each other's activity. Animal models have observed that the secretion of pro-inflammatory mediators by immune cells such as nerve growth factor (NGF), tumor necrosis factor alpha (TNF-α), and interleukin 1-beta (IL-1β) can lead to increased sensitization of peripheral nociceptors and central neurons [53]. In turn, peripheral and central neurons can attract and activate local and circulating immune cells through neurogenic secretion of chemokines such as CCL2 [54].

Peripheral sensitization is the reduced activation threshold and increased membrane excitability of peripheral nociceptors. Peripheral sensitization is responsible for primary hyperalgesia, pain hypersensitivity located at the site of damaged or inflamed tissue. Peripheral sensitization is driven by increased insertion or changes in sensitivity

of transducer and voltage-gated ion channels into nociceptor membranes, triggered by inflammatory mediators [55]. Central sensitization is the increased responsiveness of central nociceptive neurons to afferent input.

Central sensitization contributes to secondary hyperalgesia and allodynia, defined as pain hypersensitivity in non-inflamed or non-damaged tissue, and pain sensitivity to sub-threshold stimulation respectively. Central sensitization is mediated in part by the increased activity and density of AMPA and NMDA receptors in the post-synaptic membrane of dorsal horn neurons, leading to heightened excitability to afferent input. Loss of inhibitory GABAergic or glycinergic signalling from dorsal horn interneurons also can contribute to central sensitization [56]. Central sensitization can occur independently of peripheral input, with central lesions driving central sensitization and subsequent peripheral pain sensitivity [57, 58]. In this thesis, we will focus on **chronic peripheral neuropathic pain** as the primary chronic pain syndrome.

2.2.2.1. Peripheral and Spinal Mechanisms and Response

Neuropathic pain is characterized in human pain patients by spontaneous burning and electric shock like sensations, and neuropathic pain remains difficult to treat due to the heterogeneity of potential etiologies [59]. Peripheral neuropathic pain arises from damage to peripheral afferents through diseases such as diabetes or direct trauma. This damage generally results in the ectopic generation of action potentials along damaged and neighbouring nociceptive afferents. Animal models show that this ectopic nerve activity is predominantly driven by the abnormal expression and activity of voltage-gated sodium channels, with dysregulation of potassium channels and transport contributing to

altered membrane excitability [60-63]. The ongoing activity of peripheral afferents is associated with increased presynaptic release of glutamate in the dorsal horn through increased expression of voltage-gated calcium channels and the loss of inhibitory G-protein coupled receptors such μ-opioid receptors [64, 65]. Post-synaptic activity is also sensitized through the increased activity and expression of AMPA and NMDA receptors, and a number of calcium induced signalling pathways that initiate synaptic plasticity [66-68]. Central sensitization and hyperexcitability in the dorsal horn is also potentiated by the loss of GABAergic interneurons in the dorsal horn [69, 70].

Nerve lesions also initiate peripheral and central inflammation mechanisms which potentiate aberrant signalling. Immune involvement in neuropathic pain is complex as macrophages and microglia can promote both pro-inflammatory, pro-nociceptive or anti-inflammatory, pro-recovery responses. Peripheral nerve injury results in macrophage infiltration, T cell activation, and the expression of pro-inflammatory cytokines at the site of injury. In vivo animal models demonstrate pro-inflammatory cytokines can directly sensitize and induce ectopic signalling in primary nociceptive afferents [71, 72]. Microglia in the dorsal horn perform a similar function to macrophages, becoming activated after nerve injury and secreting pro-inflammatory cytokines. Microglial surface receptors such as P2X4, P2X7, and toll like receptors (TLRs) initiate the release of cytokines including brain derived neurotrophic factor (BDNF), TNF-α, and IL-1β. These cytokines increase excitatory nociceptive neuron activity by increasing the strength of excitatory glutamatergic signalling, and disinhibition via elevated intracellular chloride levels on inhibitory neurons [73-76].

2.2.2.2. Supraspinal Mechanisms and Response

Human studies have revealed that continued nociceptive afferent input and central sensitization of the dorsal horn results in increased ascending excitatory signalling to supraspinal structures and altered pain circuit activation and physiological response [77-80]. Broadly, supraspinal pain processing is thought to transition away from the sensory-discriminative circuit that is predominant in acute pain, involving S1, S2, and insula, and towards an emotional-affective circuit in chronic pain, involving prefrontal cortex, amygdala, and ACC [36, 78]. The duration of pain also contributes to the degree of change observed in supraspinal circuits [80, 81]. While many supraspinal structures undergo physiological and functional changes, this thesis will focus on the **prefrontal cortex**.

2.2.2.3. Prefrontal Cortex Pain Mechanisms and Response

During chronic pain, human PFC is abnormally active and shows altered functioning compared to normal brain functioning during acute pain [82]. DLPFC activity is normally inversely correlated with pain sensation in healthy individuals, however in fibromyalgia [83], this correlation is disrupted. mPFC normally shows activation in response to painful stimuli, however in chronic pain this activation is enhanced [48, 84]. Even in the absence of painful stimuli, during chronic pain the PFC shows abnormal functional connectivity with multiple regions involved in the default mode network [85]. This abnormal activity is accompanied by widespread functional and anatomical reorganization in response to chronic pain.

Broadly, after the onset of chronic pain, a number of imaging studies have detected the loss of grey matter in PFC. Human studies of chronic pain reveal losses in DLPFC and mPFC in back pain [17, 19, 82, 86-88] , fibromyalgia [15], osteoarthritis [26], migraine [89], visceral pain [90, 91], and neuropathic disorders [92]. Despite differing paradigms in grey matter measurement like grey matter density or volume, or cortical thickness, these studies all display some grey matter loss. Grey matter decrease is not uniform across PFC areas or to the same degree, however this could be expected given the heterogeneity of the evaluated pain disorders, variable duration of chronic pain, and interindividual differences. The degree of PFC grey matter loss is correlated in some conditions with ratings of pain intensity and with pain duration [15, 82, 93-95].

The abnormal activity and grey matter loss observed in human studies is replicated in rodent models of chronic pain. When translating human studies to rodents, it should be noted that rodents lack a human-equivalent DLPFC, however rodent mPFC is thought to be anatomically similar and mediate similar attention, working memory, and decision making processes [96, 97].

Functional imaging studies of rodent models first observe abnormal activity in PFC 28 days post-injury and in some cases up to 4 months [98, 99]. Detecting the loss of PFC grey matter by structural MRI can take 3-4 months [20]. However, molecular and electrophysiology studies have found altered synapse signalling and formation in mPFC as soon as one week after induction of a pain model. One to two weeks after neuropathic injury, pyramidal neurons in layers 2/3 of mPFC have larger basal dendrites and spine density, enhanced presynaptic release of glutamate, and postsynaptic AMPA, NMDA,

and HCN current, correlated to the degree of pain hypersensitivity [99-102]. Metabotropic glutamate receptor mGluR5 is also elevated in rat mPFC 4-6 months after neuropathic injury, with pharmacological inhibition capable of ameliorating pain hypersensitivity and overexpression inducing pain in naïve animals [103]. Concurrently, layer 5 mPFC pyramidal neurons show a decrease in response to glutamatergic input [104, 105]. This decreased response may be a result of GABAergic interneuron feed forward inhibition, with increased GABAergic signalling correlated with increased neuropathic pain and vice versa [106]. The precise causes of these circuit level changes in mPFC signalling have yet to be determined. They may be the result of layer specific input from other brain areas, such as hippocampus and amygdala [107, 108].

The root mechanisms of grey matter loss remain unclear. An initially proposed mechanism was cellular death or atrophy as a result of excitotoxicity [37]. Neuronal loss can be demonstrated by decreased concentrations of neuronal marker N-acetyl-aspartate (NAA), however results are mixed with some studies finding decreased NAA [109-111], while others do not find any differences between healthy and chronic pain individuals [112].

An interesting component of chronic pain-related changes in PFC is the reversal of grey matter loss when an intervention successfully attenuates pain. In human pain patients, surgical interventions that reduce pain result in increased DLPFC and ACC grey matter at patient follow up 4 and 6 months post injury [25, 26, 113]. If the source of pain resolves naturally without any outside intervention, this is also sufficient to reverse pain related losses of grey matter [86, 114]. Finally, cognitive interventions designed to reduce

the anticipatory fear and emotional impact also increased DLPFC and ACC grey matter and reduced reports of pain symptoms and pain experience [24]. The reversibility of chronic pain related maladaptive changes in grey matter has also been demonstrated in animal models, where pain relief following treatment with metformin restores axon initial segment length in layer 5/6 of the infralimbic cortex and reverses pain related cognitive impairment [115].

Given the reversibility of grey matter losses after successful pain attenuation, widespread PFC cell death is unlikely to be the primary mechanism underlying grey matter loss. While the mechanisms underlying grey matter loss remain unknown, hypotheses include a widespread loss of synapses mediated by glia or long-term depression resulting from excessive neuronal excitation [26, 116, 117], changes in PFC microvasculature [95, 118], or changes in extracellular fluid volume [113]. Similarly, the mechanisms underlying the recovery of grey matter after intervention are also unknown. Grey matter recovery may occur via a functional reversal of the mechanisms that were initially responsible for grey matter loss, or may involve entirely new functional pathways.

2.2.2.4. Therapeutic Interventions Against Chronic Pain

Therapeutic interventions against chronic pain have progressed through multiple phases as clinical and basic science have made additional discoveries regarding mechanisms underlying chronic pain. Opiates, particularly morphine, were and are the gold standard for relieving acute pain. However, their use in chronic pain has diminished as clinicians have become more aware of their strong addictive potential and long-term risks [119, 120]. Opiates are effective because they mimic endogenous opioid peptides

and act upon endogenous opiate receptors, in particular the μ-opioid receptor. The PAG plays an important role by activating descending inhibition of pain through the rostral ventral medulla to spinal cord [121]. Morphine analogues such as buprenorphine or opioid receptor agonists such as tramadol or methadone are more commonly prescribed to better manage the risk of addiction, respiratory depression, and gastrointestinal side effects, however these side effects remain a concern [122].

Non-steroid anti-inflammatory drugs (NSAID) and selective COX-2 inhibitors are targeted at reducing pro-inflammatory responses to reduce pain. NSAIDs benefit from limited abuse potential and relatively safe risk/benefit profiles. The basic mechanism of action of NSAIDs is to inhibit cyclooxygenase 1 or 2 and prevent prostaglandin-mediated inflammation [123]. However, NSAIDs increase risk of nephro- and gastrointestinal toxicity with chronic use, and place immunocompromised patients and the elderly at particular risk for opportunistic infections [124]. Moreover, their anti-inflammatory mechanism of action limits their efficacy to treating inflammatory chronic pain conditions like osteo- or rheumatoid arthritis, or mild to moderate presentations of other chronic pain disorders.

Tricyclic and serotonin-norepinephrine reuptake inhibitors (SNRIs) anti-depressants are often utilized and may simultaneously address chronic pain and depression. Tricyclic anti-depressants have well documented effects against chronic pain and are particularly recommended against neuropathic pain [125, 126]. Interestingly, anti-depressants still inhibit pain when the patient is not in a depressive state, and mediate their analgesic effect faster than their anti-depressive effect [127, 128]. A proposed

mechanism is the action of inhibited reuptake of noradrenalin on α_2-adrenergic receptors in the dorsal horn of the spinal cord. Pre-synaptically, this action inhibits voltage-gated calcium channels from initiating the release of excitatory neurotransmitters and post-synaptically, it may open inward rectifying K^+ channels causing hyperpolarization [129]. Other mechanisms include NMDA and AMPA receptor inhibition [130], increased GABA-B receptor function [131], and sodium channel blockade [132].

Pharmacological treatments have demonstrated effectiveness in reducing chronic pain, however many of them act to reduce pain sensation but do not treat the underlying cause. Moreover, many of these treatments have negative side-effects with prolonged use. Other pharmacological interventions that were not discussed here include gabapentin and pregabalin, anti-psychotics, other anti-convulsants, benzodiazepines, and cannabinoids.

Cognitive and mind-body based techniques have been introduced as non-pharmacological interventions against chronic pain and include cognitive behavioural therapy (CBT), meditation, hypnosis, and relaxation. These interventions are varied and do not have a unified protocol. Most techniques focus on controlling a cognitive component such as attention or problem solving, and an emotional component such as distress or anxiety awareness and reduction [133]. CBT and meditation have significant but small effects on pain and disability, and moderate effects on mood and catastrophizing compared to non-treatment controls. However when compared to active treatment such as pharmacological intervention or physical therapy, CBT and mediation only confer significant improvements to catastrophizing and ratings of disability [134].

CBT or mediation practitioners have lower pain unpleasantness ratings correlated with stronger ACC and ventromedial PFC activity [135]. Crucially, practitioners do not have to be actively meditating to benefit from lower rated pain unpleasantness, suggesting that meditation and CBT confer persistent changes. As mentioned above, CBT can reverse chronic pain induced losses in grey matter [24]. Follow up research is needed to dissect which elements of CBT are most effective, and if certain chronic pain disorders or certain patient populations benefit more from one element of CBT or another.

Exercise and movement interventions are other commonly prescribed non-pharmacological interventions. Exercise interventions include aerobic, strength, flexibility or core and balance training programs, as well as yoga, tai chi, and Pilates. However, exercise interventions are greatly varied and can focus on different aspects and levels of physical fitness, which can result in varying levels of pain reduction. However physical activity generally reduces pain, has a variable effect on mood and quality of life, and improves physical functioning [136]. Clinicians and physiotherapists must tailor exercise protocols to the specific presentation of chronic pain. However even low-to-moderate intensity exercise (50-60% of maximum heart rate) is sufficient to improve pain sensitivity and is recommended for certain conditions instead of strenuous exercise [137-139]. The mechanisms of exercise-based pain attenuation remain unclear. Exercise can improve poor sleep, reduce reported depression, and can promote the release of anti-inflammatory cytokines over pro-inflammatory cytokines in chronic pain individuals [140-142].

2.2.3. **Epigenetics**

Epigenetics refers to a group of mechanisms that alter the phenotype of a cell or organism without modifying the genotype. Epigenetic mechanisms allow for stem cells with the same genome to differentiate along different cell type fates. Epigenetics represent a mechanism that can enact stable and long-term changes in response to developmental or environmental signals [143]. Epigenetic changes are mitotically heritable, meaning daughter cells will express the same phenotype that their mother cells developed. There is also evidence for epigenetic changes to be meiotically heritable, allowing for the parental environment to shape and alter offspring phenotype [144]. Epigenetic regulation occurs via three predominant interrelated mechanisms: DNA methylation, histone modification, and chromatin conformation. In this thesis, we will focus on **DNA methylation** as the primary epigenetic mechanism.

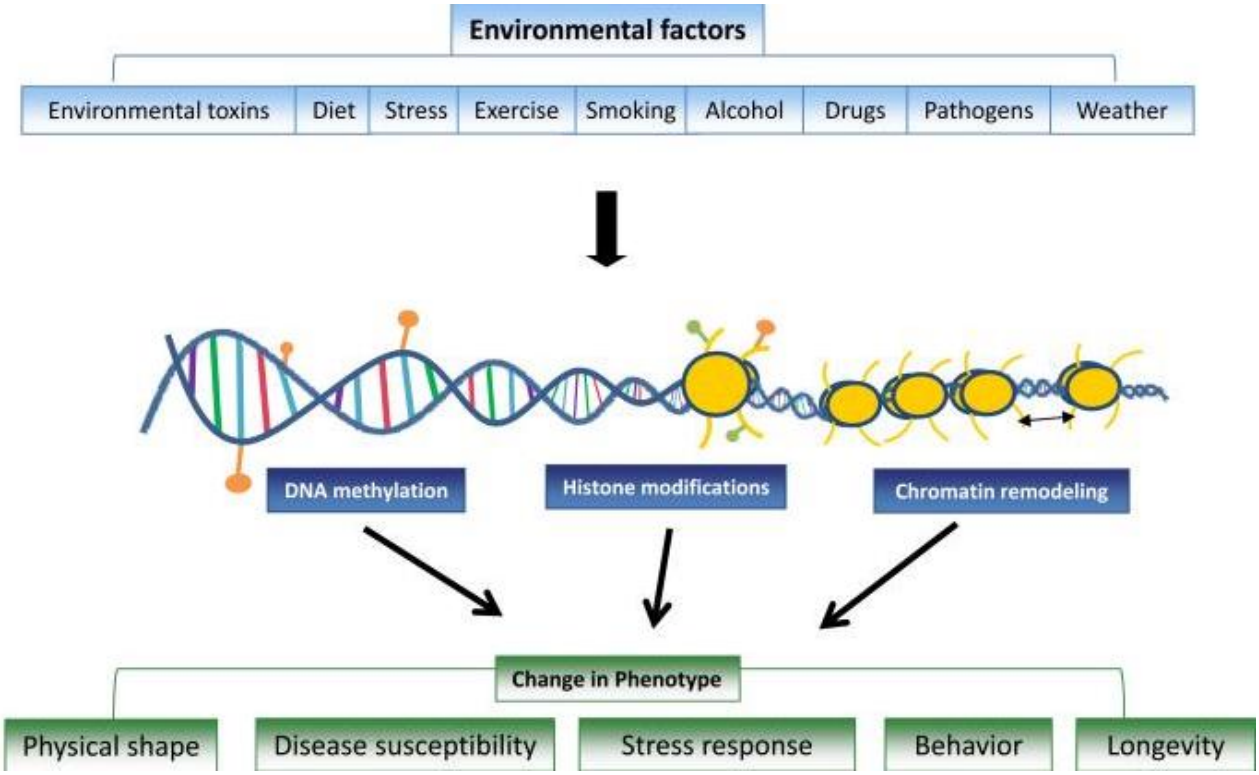


Figure 2: Epigenetics mediates the effect of environmental factors and can induce stable and long term changes in phenotype. This image was adapted from [145], and was used with permission from the publisher.

2.2.3.1. DNA Methylation

DNA methylation is the direct chemical modification of a DNA nucleotide. In differentiated eukaryote cells, DNA methylation primarily occurs on cytosine nucleotides in a dinucleotide cytosine guanine sequence (CpG) [146]. In these cells, ~80% of the available CpG sites are methylated [147]. The basic methylation mechanism involves the covalent transfer of a methyl group from the universal methyl donor, s-adenosyl methionine (SAM), to the 5' carbon of a cytosine nucleotide to form 5-methylcytosine (5mC) [148]. DNA methylation occurs as either maintenance methylation, that is, faithful replication of methyl marks from parent to daughter DNA strands during mitosis, or *de novo* methylation, which is the novel placement of methyl marks on available CpG positions.

2.2.3.1.1. DNA Methylation Mechanisms

The addition of methyl groups to cytosine nucleotides is mediated by DNA Methyltransferases (DNMTs). At present, six DNMT enzymes have been identified: DNMT1, DNMT2, DNMT3a, DNMT3b, DNMT3c, and DNMT3L. DNMT2 is a tRNA methyltransferase, while DNMT3c thus far is believed to be specific to male murine germ cells, therefore they will not be discussed further [149, 150]. DNMT1, 3a, and 3b all share a conserved catalytic domain responsible for performing methyltransferase activity. DNMT1 is responsible for maintenance methylation and is the most abundantly expressed DNMT in mammalian cells. DNMT1 is localized to the replication fork during S-phase and binds with UHRF1, which targets DNMT1 to methylate hemi-methylated DNA [151]. In contrast, DNMT3a and 3b are responsible for *de novo* methylation [152].

There are exceptions to this division of labour between DNMT1 and DNMT3a and 3b [153-155], however the above model is the general rule. The mechanisms for targeting DNMT3a and 3b *de novo* methylation are complex and may involve multiple overlapping systems. DNMT3a and 3b both form a complex with DNMT3L, however they target different genetic loci. DNMT3a preferentially targets DNA marked by unmethylated histone 3 lysine 4 tails (H3K4), and prefers CpG sites with a CG(C/T) motif [156-159]. In contrast, DNMT3b preferentially targets DNA marked by trimethylated histone 3 lysine 36 (H3K36me3) and trimethylated histone 3 lysine 9 (H3K9me3), and prefers CpG sites with a CG(G/A) motif [158, 160, 161]. In development, DNMT3a is required for *de novo* methylation at transcription start sites (TSS), while DNMT3b predominantly acts upon the X chromosome [161]. Finally, DNMT3L is an important regulatory co-factor of DNMT3a and 3b. DNMT3L is catalytically inactive, however as mentioned above, it forms a complex with DNMT3a and 3b, enhances their methylation activity, and is crucial for appropriate targeting of methylation [162, 163].

The removal of methyl groups from DNA can occur via two active mechanisms First, 5mC bases can spontaneously deaminate and convert to thymine, at which point they are identified and removed via base excision repair [164]. The second and more common mechanism is via ten-eleven translocation (TET) enzymes. TET enzymes perform iterative oxidation to convert 5mC through a series of intermediaries in order: 5-hydroxymethyl cytosine (5hmC), 5-formyl cytosine (5fC), and 5-carboxyl cytosine (5caC) [165-167]. The enzyme thymine DNA glycosylase (TDG) recognizes 5fC and 5caC and excises them to allow cytosine to be reinserted via base excision repair [168, 169]. There

are three main TET enzymes, TET1, TET2, and TET3. TET enzymes have a number isoforms that limit its expression or activity to specific tissues or developmental phases. TET1s is the dominant TET1 isoform in mouse somatic tissue and TET1 mediates activity-induced DNA demethylation in mouse neuronal tissue [170, 171]. TET3 isoform TET3FL is thought to preferentially target TSS CpG islands in neuronal tissue and maintain their unmethylated state [172].

2.2.3.1.2. Regulatory Role

DNA methylation can occur at any CpG site within the genome, and indeed, 70~80% of the genome is methylated in differentiated somatic cells. In gene promoters, DNA methylation is associated with a repressed and closed chromatin conformation and inhibition of gene expression [173]. In promoter regions with a low CpG content, DNA methylation rapidly results in gene repression [174]. However, other promoter regions contain CpG rich sequences called CpG islands that are frequently unmethylated, and have low rates of CpG mutation [175]. In fact, nearly 70% of all promoters have a CpG island [176], and 50% of all CpG islands are associated with a TSS [177]. CpG islands are actively demethylated and serve to enhance promoter function by increasing DNA strand accessibility and allowing transcription factors to bind [175, 178]. DNA methylation outside of promoters can also influence gene transcription. Enhancers are distal regulatory elements that can enhance gene transcription through transcription factor binding and recruitment of co-activators [179]. DNA methylation at enhancers is also associated with repressed gene expression [180, 181]. Conversely, gene body DNA methylation is associated with increased transcription [182, 183].

DNA methylation inhibits gene expression via two primary mechanisms. First, methylated cytosine can sterically interfere with DNA-binding transcription factor recognition of their target sequence [184, 185]. Accordingly, mammalian transcription factor binding sites tend to be more CG rich than the genome [175]. Second, the recruitment of methyl-binding proteins can initiate repressive mechanisms [186, 187]. DNA methylation is recognized by three families of methyl binding proteins: MBD, UHRF, and zinc-finger proteins. The function of the UHRF family is outlined above, and targets DNMT1 to hemi-methylated DNA. The zinc-finger proteins include Kaiso, ZBTB4, and ZBTB38, and they act to repress DNA transcription by binding to methylated DNA [188-190]. However, the MBD family is the best characterized and consists of MBD1, MBD2, MBD3, MBD4, and MeCP2. MBD1, MBD2, and MeCP2 can bind directly to methylated DNA and may have specific preferences for different methylated sites across the genome [191]. MBD3 lacks the ability to bind methylated DNA, and MBD4 acts as a base excision glycosylase specific for thymine [187]. These zinc-finger and MBD proteins recruit various repressor complexes that contain histone methyltransferases (HMT), histone deacetylases (HDAC), DNMTs, and chromatin remodelling proteins that work together to repress gene transcription [173, 192-195].

Genome methylation is profoundly and globally altered during development and differentiation, and then undergoes smaller local modifications across the lifespan in response to environmental stimuli. Broadly, during development there is an initial global demethylation of the genome after fertilization and formation of the blastocyst. After implantation and as embryonic stem cells begin to differentiate along their cell fates, DNA

methylation increases as unnecessary cellular functions are repressed [196]. DNA methylation resulting from differentiation is highly stable, such that 70%-80% of methylated DNA will not change methylation status afterwards [197]. Outside of development, there is a large body of evidence linking changes in DNA methylation in response to environmental stimuli. Changes in DNA methylation are documented after stress, chronic pain, addiction, nutritional changes, physical exercise, exposure to pollutants, and a number of other sources [28, 198-200]. The mechanisms that differentially methylate specific genes in response to environmental stimuli are still unknown. One hypothesis points to the direct action of environmental chemicals on DNMT or TET activity or reducing the availability of SAM. The transcription factor occupancy hypothesis proposes that transcription factor binding enables or prevents DNMT to methylate specific sites by controlling access to target DNA. Via this mechanism, environmentally stimulated transcription factors would bind to their target sequences and preserve an unmethylated state to allow for continued gene expression [201, 202].

2.2.3.2. Other Epigenetic Mechanisms

2.2.3.2.1. Histone Modifications

Histones are octamer protein complexes composed of four subunits, H2A, H2B, H3, and H4, that organize DNA into nucleosomes and allow DNA to be compacted into condensed chromatin. Histones have protruding tails where post-translational modifications are placed to signal and modulate chromatin structure and DNA activity and accessibility. Modifications include methylation, acetylation, phosphorylation, ubiquitination, SUMOylation, and citrullination. Three positions of the H3 subunit tail at

lysine 4 (H3K4), lysine 9 (H3K9), and lysine 27 (H3K27) have the most well studied relationships with DNA methylation, gene expression, and chromatin structure. H3K4 trimethylation (H3K4me3) marks the TSS of active genes and is positively correlated with gene expression [203]. H3K4 monomethylation (H3K4me1) is associated with enhancers, with the presence or absence of H3K27 acetylation (H3K27ac) denoting active or primed enhancers, respectively [204]. H3K4me1 and H3K4me3 marks are associated with open or euchromatin, and prevent promoter and enhancer DNA methylation by inhibiting DNMT3L interaction with H3K4 [159].

Conversely, H3K9 trimethylation (H3K9me3) and H3K27 trimethylation (H3K27me3) are markers for closed or heterochromatin formation and gene repression. H3K9me3 marks constitutive heterochromatin, the conserved repeat-rich genomic regions at centromeres and telomeres that are resistant to transcription factors [205]. H3K9 methylation is mediated by the HMTs SETDB1, Suv39h1/2, G9a and GLP [206]. H3K27me3 marks facultative heterochromatin, the cell-type specific repression of lineage inappropriate genes that remain accessible to transcription factors [207]. H3K27 methylation is mediated by the Polycomb complex PRC2 and its methyltransferases EZH1 and EZH2 [208]. Constitutive heterochromatin maintains genomic structure and stability, while facultative heterochromatin is the counterbalance to euchromatin and serves to stably repress target genes.

Histone acetylation is a general marker for active gene expression. H3K4 acetylation (H3K4ac) is generally found in the promoter and actively transcribed regions of genes, while H3K9 acetylation (H3K9ac) and H3K27 acetylation (H3K27ac) are located

around the TSS [209]. Histone acetylation is performed by histone acetyltransferases (HAT) and removal of acetyl groups is performed by HDACs. Numerous other histone marks such as H3K9me1, H3K27me1, H3K36me3, H3K79me1, H4K20me1, or H3K79me3 and H4K20me3 contribute to the nuanced activation or repression of gene expression respectively [210, 211].

2.2.3.2.2. Chromatin Conformation

As demonstrated above, local open or closed chromatin structure mediated by histone modifications can regulate gene expression. However, the higher-order supramolecular chromatin structure also can promote or repress gene expression. Euchromatin and heterochromatin are organized into distinct regions in the nucleus, with heterochromatin localized to the periphery and nucleolus, and euchromatin localized to the region in between [212]. As chromatin changes between euchromatin or heterochromatin, these open or closed chromatin regions are relocalized to the appropriate area [213]. By localizing euchromatin to a central region, distal enhancers are able to loop around and contact their target promoters and promote gene expression [214]. Regions with a high frequency of interactions are called topologically associated domains (TAD). TADs can prevent or promote enhancer and promoter interaction, and can prevent euchromatin reverting to heterochromatin. The DNA-binding protein CCCTC-binding factor (CTCF) delineates and regulates loops within TADs and works with cohesin to promote and mediate enhancer-promoter interactions by altering loop size. Active transcription of genes can also help delineate TADs [212].

2.2.3.3. Epigenetic Interactions

Despite the separate discussion of the above mechanisms, all epigenetic elements are closely interrelated and reciprocally mediate each other. It is difficult to place these mechanisms in a regulatory hierarchy as DNA methylation and histone modifications simultaneously depend on and alter each other [215, 216]. In some cases, histone status initiates DNA methylation [217], whereas in others DNA methylation changes histone modifications [218]. Co-repressor complexes like Sin3 or NuRD are composed of MBDs, HDACs, HMTs, and possibly DNMTs, which all act to induce and maintain a closed chromatin conformation [219]. Despite being currently unable to answer the epigenetic chicken or egg, what is certain is that these mechanisms work in tight concert to control gene expression.

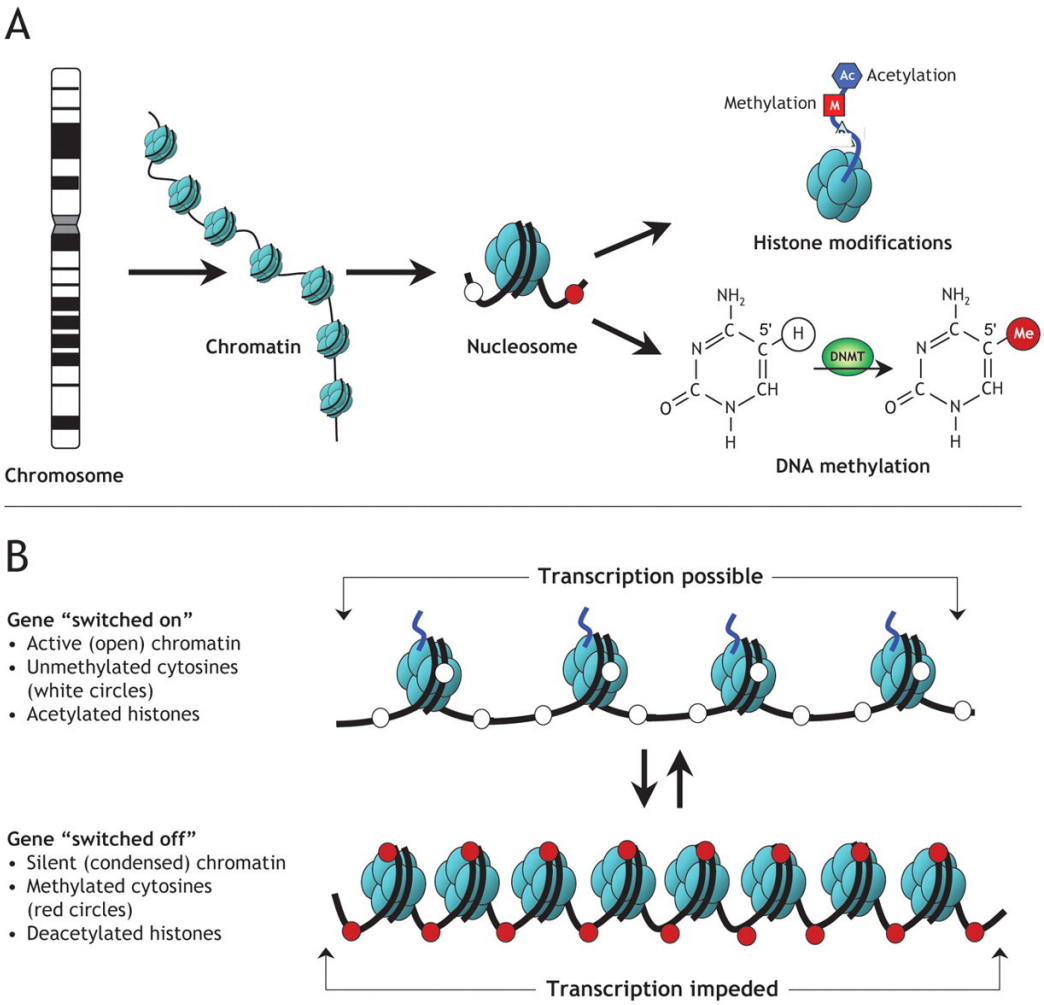


Figure 3: Chromosomes are composed of smaller subunits called nucleosomes, composed of a histone and a length of DNA. Histone modifications such as methylation and acetylation, and DNA methylation are two forms of epigenetic marks. These marks change the conformation of chromatin to open or closed, and permit or repress gene transcription respectively. Image taken from [220], with permission from the publisher.

2.2.4. **DNA Methylation, Gene Expression, and Pain**

Chiechio et al. 2009 conducted one of the first investigations of epigenetic mechanisms and chronic pain to find that HDAC inhibitors could produce analgesia in a mouse model of chronic inflammatory pain [221]. Since then, a number of human and animal studies have deepened our understanding and revealed the widespread contribution of DNA methylation and epigenetics to chronic pain throughout the body.

2.2.4.1. Human Studies

In human studies, measures of genome wide and gene specific DNA methylation are generally derived from circulating whole blood. Human studies have often focused on correlating single pain-related gene methylation to levels of pain sensitivity. TRPA1 receptor methylation has been studied in detail, with an inverse correlation to heat and mechanical pain thresholds in healthy individuals [222, 223]. Accordingly, TRPA1 gene expression inversely correlated with TRPA1 promoter methylation and positively correlated with heat pain threshold [222]. This relationship is maintained in chronic pain patients, with increased TRPA1 methylation associated with larger pain ratings in neuropathic pain and Crohn's patients [224-226]. μ-opioid receptor OPRM1 promoter methylation is positively correlated with reports of pre-operative pain and the probability of developing chronic post-surgical pain in adolescents [227]. Increased OPRM1 methylation also correlated with increased clinical pain in opiate-treated patients. It is unclear if increased OPRM1 methylation may be a result of opiate treatment rather than directly related with chronic pain [228]. Decreased BDNF methylation in exon IX,

correlating with elevated serum BDNF, has also been found to predict widespread hyperalgesia in fibromyalgia patients [229].

Genome-wide studies of human pain conditions have revealed the breadth of DNA methylation changes in response to chronic pain. In a study comparing complex regional pain syndrome (CRPS) and non-CRPS neuropathic pain patients, 48 differentially methylated CpG sites were identified and were enriched in immune domains [230]. 41 out of the 48 CpG positions were hypomethylated. In fibromyalgia patients, 1610 differentially methylated positions were identified compared to healthy controls, again with 69% of positions showing hypomethylation. The 960 genes correlated with these positions were enriched for MAPK signalling, regulation of the actin cytoskeleton, and focal adhesions [231]. Finally, in a study of 1708 twins, 24 differentially methylated positions were estimated to explain 6% of the variance in chronic widespread musculoskeletal pain. These differentially methylated positions were enriched for gene ontology terms related to nervous system activity and development [232]. These studies clearly demonstrate a strong relationship and response between DNA methylation and chronic pain, where changes in promoter methylation lead to changes in pain rating and in potential pain relevant mechanisms.

2.2.4.2. Animal Studies

Animal studies allow for the direct sampling of tissues of interest as well as a greater control over chronic pain presentation and paradigm. In rodent prefrontal cortex, chronic neuropathic pain is associated with widespread changes in DNA methylation. At six months post-onset of neuropathic pain, two studies have found global PFC DNA

methylation decreased and correlated with mechanical and cold sensitivity [233, 234]. The PFC methylation response nine months after neuropathic pain onset was analysed in detail and over 10000 differentially methylated promoters were identified at a false discovery rate < 0.1. These differentially methylated promoters were associated with long-term potentiation, neuritogenesis, DNA binding, and cell death [200].

DRG and spinal cord also undergo widespread differential methylation at multiple time points after onset of neuropathic pain. One day after neuropathic pain onset in DRG, over 8000 differentially methylated CpGs in promoters, introns, and exons were identified, over 80% were hypermethylated, and with axon guidance as the most significantly enriched function. Follow up RNA-seq analysis showed some correlation between promoter or gene body methylation status and mRNA expression, however the relationship is inconsistent [235]. The observed hypermethylation in DRG early after onset of neuropathic pain has been replicated, however at three weeks after onset, DRG differential methylation shifts towards hypomethylation. At this time point, the dorsal horn of the spinal cord and prefrontal cortex are skewed towards hypermethylation [236]. The dynamism of DNA methylation response to chronic pain highlights the need to track methylation changes across multiple phases and time points of chronic pain development.

A number of studies have also investigated interventions targeting DNA methylation and methylation mechanisms. Increased DNA methylation and MeCP2 binding in spinal cord two weeks after neuropathic pain onset was treated with intrathecal 5-azacytidine, a DNMT inhibitor. 5-azacytidine administration reduced global DNA methylation in the spinal cord and attenuated measures of pain sensitivity [237].

Meanwhile, chronic systemic SAM treatment increased PFC DNA methylation and counteracted the global PFC DNA methylation decrease observed six months after injury while also attenuating pain sensitivity [234]. These two studies demonstrate that interventions targeting DNA methylation must understand the direction of aberrant differential methylation to be effective. Non-pharmacological interventions have also been investigated and found to be effective. The global PFC DNA methylation decrease observed six months after nerve injury can be reversed and pain behaviour attenuated if animals are provided environmental enrichment three months after pain onset [233].

2.3. Rationale

Chronic pain is a prevalent and costly disease that has limited therapeutic options and induces widespread functional and anatomical changes in pain transduction systems throughout the body. DNA methylation, as a dynamic and environmentally responsive mechanism of regulating gene expression, has great potential to help researchers understand how chronic pain develops and is maintained. At the start of this thesis, the relationship between chronic pain and DNA methylation was only beginning to be understood, and subsequent work has only underscored this potential. By examining and tracking how chronic pain affects DNA methylation in the PFC, we may better identify and understand its underlying mechanisms. Beyond improving our understanding of chronic pain development and maintenance, DNA methylation can also help us observe the reaction of the PFC to therapeutic interventions. As a stable mark of changes in gene

expression, we can understand why and how certain interventions mediate their effects and attempt to identify ways to make them more effective.

2.4. Hypothesis

The prefrontal cortex undergoes dynamic DNA methylation responses as chronic pain begins and develops over time. Pharmacological and non-pharmacological interventions that reduce pain sensitivity will counteract or reverse these methylation responses.

2.5. Specific Aims

1) Track and observe PFC DNA methylation in response to induced neuropathic pain for up to 12 months post-injury
2) After chronic pain has developed, determine the PFC DNA methylation response to a pharmacological intervention
3) After chronic pain has developed, determine the PFC DNA methylation response to a non-pharmacological intervention

Chapter 2: Timecourse of DNA Methylation Response Across Chronic Pain

3.1. Preface

The development and progression of chronic pain is associated with a number of functional and structural changes in PFC grey matter. Changes in neuronal architecture, cortical excitability, and loss of grey matter have all been noted from the onset of chronic pain to months later in the chronic pain time course. Widespread changes in the PFC transcriptome have also been noted after the onset of chronic pain. DNA methylation has been proposed as a candidate mechanism to mediate and regulate these changes, and indeed a number of studies have explored changes in PFC DNA methylation in response to chronic pain. However, previous studies focused on a single time point and did not track the full time course of chronic pain development and progression. Examining PFC DNA methylation across the time course of chronic pain development will further our understanding of how DNA methylation responds to chronic pain, and identify functional domains and mechanisms affected by DNA methylation.

In this study we hypothesized that as chronic pain develops and progresses over time, the PFC will undergo a number of changes in DNA methylation. We characterized PFC DNA methylation at one day, two weeks, six months, and one year after spared nerve injury.

3.2. Manuscript I:

The Transition from Acute to Chronic Pain: Dynamic Epigenetic Reprogramming of the Mouse Prefrontal Cortex up to One Year Following Nerve Injury

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Abstract:

Chronic pain is associated with persistent structural and functional changes throughout the neuroaxis, including in the prefrontal cortex (PFC). The PFC is important in the integration of sensory, cognitive and emotional information and in conditioned pain modulation. We previously reported wide-spread epigenetic reprogramming in the PFC many months following nerve injury in rodents. Epigenetic modifications, including DNA methylation, can drive changes in gene expression without modifying DNA sequences. To date, little is known about epigenetic dysregulation at the onset of acute pain or how it progresses as pain transitions from acute to chronic. We hypothesize that acute pain following injury results in rapid and persistent epigenetic remodelling in the PFC that evolves as pain becomes chronic. We further propose that understanding epigenetic remodelling will provide insights into the mechanisms driving pain-related changes in the brain. Epigenome-wide analysis was performed in the mouse PFC 1 day, 2 weeks, 6 months, and 1 year following peripheral injury using the spared nerve injury (SNI) in mice. SNI resulted in rapid and persistent changes in DNA methylation, with robust differential methylation observed between SNI and sham-operated control mice at all time points. Hundreds of differentially methylated genes were identified, including many with known function in pain. Pathway analysis revealed enrichment in genes related to stimulus response at early time points, immune function at later time points and actin and cytoskeletal regulation throughout the time course. Given these results, importance of pain time course as a factor is emphasized for both pain research and treatment.

1. Introduction

Chronic pain is a global challenge, affecting between 10-20% of adults and costing billions each year in patient care and lost productivity [1, 2, 4]. Chronic pain is modulated by a complex mix of biological, psychological and social factors. At the molecular level, hundreds of genes become differentially expressed in chronic pain conditions [22, 200, 238-240]. Understanding chronic pain is further complicated by time-dependent recruitment of mechanisms and pathways mediating the transition from acute to chronic pain [241, 242]. Improved understanding of pathological gene dysregulation from acute to chronic pain is desperately needed to prevent the development of prolonged, intractable pain.

Epigenetic mechanisms allow for malleable and reversible gene regulation without modification of DNA sequences. DNA methylation is an epigenetic regulator of gene expression wherein a methyl group is added to cytosine DNA nucleotides. When methylation occurs in gene promoter regions, the gene is typically repressed via hindrance of transcription factor binding, recruitment of methyl binding proteins, and chromatin remodeling, ultimately preventing RNA polymerase-mediated transcription [243, 244].

DNA methylation is environmentally sensitive, with methylation profiles changing in response to addiction, early life stress, and neurodegenerative disease [198, 245, 246]. Chronic pain is also associated with changes in DNA methylation in both humans and animal models across many tissues including the prefrontal cortex (PFC), dorsal root ganglia, and spinal cord [22, 200, 235, 236]. DNA promoter methylation at specific genes

can be linked to the degree of mechanical hypersensitivity [200], and chronic treatment with methyl donor S-adenosylmethionine increased global DNA methylation in the PFC and attenuated mechanical hypersensitivity [234]. Investigation of DNA methylation's role in chronic pain advances our understanding of pain progression and may reveal potential therapeutic avenues.

Among the structures involved in chronic pain, the PFC is crucial as an integrator of ascending sensory information, cognitive and emotional responses, and descending inhibitory control [37, 247, 248]. In human patients and animal subjects, long-term pain results in a persistent functional and anatomical reorganization of the PFC [15, 20, 82, 249], with patients showing more PFC activation than healthy controls [14, 48]. Chronic pain patients are commonly comorbid for depressive and anxiety disorders [250] that are heavily correlated with PFC abnormal functioning [251, 252]. As a central mediator in the pain pathway, therapeutic mechanisms targeting PFC may have efficacy across different pain disorders and simultaneously address associated cognitive and emotional comorbidities.

Previous work has shown extensive changes in DNA methylation and dynamic structural and functional reorganization in the PFC to be associated with chronic pain. To track epigenetic reprogramming in the PFC in acute and chronic pain, we captured the pattern of genome-wide DNA methylation across time from 1 day to 1 year following peripheral nerve injury in mice. Our analysis revealed a dynamic pattern of DNA methylation across the time course, implicating hundreds of differentially methylated genes at each time point. Subsequent analysis revealed time point-specific changes that

reveal potential underlying mechanisms. Our data show that epigenetic reprogramming occurs early during the transition from acute to chronic pain and is consistent with a potential causal role.

2. Materials and Methods

2.1 Animals

78 male CD-1 mice (Charles River Laboratories, St-Constant, QC, Canada) mice were used in this study. Animals were received at 6-8 weeks of age and housed 3-4 per cage on a 12h light/dark cycle in a temperature controlled room in ventilated polycarbonate cages (Allentown, Allentown, NJ) with corncob bedding (7097, Teklad Corncob Bedding, Envigo, UK) and cotton nesting squares for enrichment. Mice were given access to food (2092X Global Soy Protein-Free Extruded Rodent Diet, Irradiated) and water *ad libitum*. Animals were habituated to the housing conditions for at least one week prior to any experimental interventions.

Animals designated for DNA methylation analysis were randomly assigned to receive either the spared nerve injury (SNI) model of neuropathic pain or sham surgery control and the model was allowed to develop for one day (D1), two weeks (W2), six months (M6), or one year (1Yr) post-injury. Final numbers per group (Sham/SNI) – D1:4/4; W2:6/6; M6:6/6; 1Yr:4/6; 42 animals in total.

Animals designated for immunohistochemistry were randomly assigned to either SNI or sham surgery and allowed to progress to two weeks or six months post-injury. Final numbers per group (Sham/SNI) – W2:10/8; M6:10/8; 36 animals in total.

All experiments were approved by the Animal Care Committee at McGill University, and conformed to the ethical guidelines of the Canadian Council on Animal Care and the guidelines of the Committee for Research and Ethical Issues of the International Association for the Study of Pain [253].

2.2 Induction of spared nerve injury

Nerve injury was induced using the Spared Nerve Injury model of neuropathic pain, as adapted for mice [254, 255] at 10 to 12 weeks of age. Under deep isoflurane anesthesia, an incision was made on the medial surface of the thigh, exposing the three branches of the sciatic nerve. SNI surgery consisted of ligation and transection of the left tibial and common peroneal branches of the sciatic nerve, while sparing the sural nerve. The tibial and common peroneal branches were tightly ligated with 6:0 silk (Ethicon) and sectioned distal to the ligation. Sham surgery consisted of exposing the nerve without damaging it.

2.3 Behavioural assessment of mechanical sensitivity

After a habituation period of 1 hour to the testing environment of Plexiglas boxes placed on a wire mesh grid, von Frey filaments (Stoelting Co, Wood Dale, IL) were applied to the plantar surface of the hind paw to the point of bending for 3 seconds or until withdrawal. Mechanical sensitivity was determined as the 50% withdrawal threshold

using the up-down method [256]. The stimulus intensity ranged from 0.04 to 4.0 g, corresponding to filament numbers 2.44 to 4.56. Testers were blind to the condition of the animal.

2.4 Immunofluorescent histochemistry

Animals were deeply anesthetized with an intraperitoneal injection of ketamine (100 mg/kg), xylazine (10 mg/kg), and acepromazine (3 mg/kg). Animals were perfused with 100 mL vascular rinse (0.2M phosphate buffer with sodium nitrate), followed by 200 mL Lana's fixative (4% paraformaldehyde, 14% saturated picric acid, 0.16M phosphate buffer, pH 6.9), and then 100 mL 10% sucrose solution in phosphate buffered saline. Tissue was cryoprotected in 10% sucrose solution at 4°C for three days, and then coronally divided at Bregma into forebrain and hindbrain sections. Brain tissue was coronally sectioned at 14µm on a cryostat (Leica), and PFC sections, defined as +1.54 mm to +1.98 mm from Bregma, were collected. Prelimbic and infralimbic areas were defined according to Paxinos and Franklin [257].

Tissue was incubated with blocking buffer (1% Normal Donkey Serum, 1% Bovine Serum Albumin, 0.3% Triton X-100, 0.01% Sodium Azide) for 1 hour before primary antibody incubation overnight at 4°C. Tissue sections were either singly stained with rabbit anti-NeuN (1:1000, Abcam, Ab177487), or double stained with mouse anti-NeuN (1:1000, Millipore, MAB377) and either rabbit anti-GFAP (1:1000, Neomarkers, RB087AO) or rabbit anti-Iba1 (1:1000, Wako, 019-19741). Rabbit anti-NeuN was used to quantify neuronal cell counts while mouse anti-NeuN was used as a counter stain to define cortical layers in double-stained sections. Secondary antibodies (donkey anti-rabbit Alexa 594

(1:200, Jackson ImmunoResearch, 711-585-152) and donkey anti-mouse Alexa 488 (Jackson ImmunoResearch, 714-545-150) were incubated for 90 min at room temperature. Sections were counterstained with DAPI (1:50000, Sigma, D9542) and coverslipped with AquaPolymount (18606, PolySciences).

2.5 Immunohistochemistry quantification

FIJI [258] and manual cell counting were used to quantify the number of total cells, neurons, astrocytes, and microglia in prelimbic and infralimbic brain areas. DAPI was used as a marker of total cell population, NeuN-immunoreactivity (-ir) defined neuronal populations, GFAP-ir defined astrocyte populations, and Iba1-ir defined microglial populations. NeuN staining was also used to separately designate layer I, superficial (layers II-III) and deep (layer V) cortical layers to aid the placement of three regions-of-interest (ROIs) per layer. Cell quantification was based on colocalization of the cell type specific marker with DAPI, and cell counts were averaged across three ROIs per layer. The averaged ROI area per cortical layer: layer I: 6724 μm^2; superficial (layers II-III): 15790.14 μm^2, deep (layer V): 10526.76 μm^2. An overall cell count was calculated by adding the counts from all three layers. Total ROI area: 33040.9 μm^2. ROI sizes were identical between prelimbic and infralimbic areas.

2.6 Isolation of prefrontal cortex, DNA capture and bisulfite sequencing

Mouse PFC was dissected following isoflurane anesthesia and decapitation. PFC was defined as a region with an anterior boundary of the frontal pole, approximately +3.00 Bregma, posterior boundary of +1.42 Bregma, lateral boundaries of +1 mm from midline, and a ventral boundary wherein the olfactory bulb, caudate putamen, and areas below

the rhinal fissure and lateral ventricles were all removed [257]. This defined area isolates the prelimbic, orbital, and infralimbic cortices corresponding to the mouse medial PFC. Once dissected, tissue was homogenized and genomic DNA was extracted using the Qiagen DNeasy Blood and Tissue kit and protocol.

Genome-wide methylation analysis was performed using the Roche SeqCap Epi Developer M Enrichment system on bisulfite-treated DNA (Roche Nimblegen; WI, USA), with custom designed primers targeting promoter and enhancer regions of the genome. Probe design was based on the mm9 reference genome and associated H3K4me1 and H3K4me3 binding (probe BED file available in **Supplemental Table 1**). Briefly, 1 μg of genomic DNA per sample was fragmented into 200bp lengths, and adapter and index sequences were ligated to each end of the fragment according to the KAPA Library Preparation Kit protocol. Sample DNA was then bisulfite converted following the EZ DNA Methylation-Lightning Kit (Zymo Research; CA, USA). Sample DNA was then PCR amplified, hybridized with custom capture probes, and PCR amplified again in accordance with Roche SeqCap Epi system protocols [259]. Sample captured bisulfite-converted DNA sequencing was performed by Genome Quebec on the Illumina HiSeq 2500 following Illumina guidelines. Paired-end sequencing reads of 125bp in length were generated.

2.7 DNA methylation pre-processing

Capture sequencing data was pre-processed using the McGill University Genome Quebec Innovation Centre GenPipes Methyl-Seq Pipeline [260]. The pipeline proceeds through Trimmomatic, Bismark Align, Picard Deduplication, and Bismark Methylation Call

[261, 262]. Baseline pipeline parameters were set as a minimum sequence quality of PHRED score > 30, alignment reference genome was mm10 (GRCm38), and minimum read coverage per base was set at 10 reads. A detailed outline of the Methyl-Seq pipeline steps and process can be found at https://bitbucket.org/mugqic/genpipes. Before analysis, collected sequence data was filtered to remove a blacklist of regions identified to have anomalous, unstructured, and high signal/read counts in next gen sequencing [263]. The blacklist used was specific for mm10 and the BED file can be found in **Supplemental Table 2.**

2.8 Differential methylation analysis

Generalized linear model analysis was used to compare Sham to SNI methylation values at each time point. Differential methylation analysis was performed using R and the edgeR package [264]. Samples were normalized to library size, where library size was set to be the average of the total read counts for methylated and unmethylated CpGs. For a CpG site to pass through to analysis, it was required to be sequenced at a depth of at least 10 reads in each sample within a time point.

At each time point, CpGs were defined as being differentially methylated if the false discovery rate (FDR) was less than < 0.1 and a difference in methylation between Sham and SNI of > 5%. While the selection of an FDR threshold of 0.1 carries greater risk of type I error than the more typical threshold of 0.05, it is preferable for the exploratory purposes of this study. Differential methylation between Sham and SNI was determined by calculating the M-Value ($\log_2$ of the ratio (methylated cytosines / unmethylated cytosines)) of each CpG site in Sham and SNI, and then detecting statistically significant

differences. The methylation percentage (percentage of (methylated cytosines / total cytosines)) at each site was also calculated. Differentially methylated samples were further divided into hypermethylated CpGs or hypomethylated CpGs with the Sham CpG methylation percentage acting as the reference point. If the SNI CpG methylation is 5% or larger than the Sham, the CpG position is considered to be hypermethylated. If the SNI CpG methylation is reduced by -5% or more compared to Sham, the CpG position is considered to be hypomethylated.

CpGs were annotated to their associated genes and genomic regions using the topTags function of edgeR [264] and annotatePeaks function of the ChIPseeker [265] R packages, using a TxDb object created from the Gencode “mmusculus_gene_ensembl” Biomart database. Each CpG position was annotated and tracked individually throughout the analysis. For homology conversion, gene symbols from non-mouse species were converted to known mouse homologs based on the Mouse Genome Database (MGD) – Vertebrate Homology, Mouse Genome Informatics, The Jackson Laboratory, Bar Harbor, Maine [266].

The data discussed in this publication have been deposited in NCBI's Gene Expression Omnibus [267] and are accessible through GEO Series accession number GSE146215.

2.9 Statistical analysis

Two-tailed Student’s t-test was used for group differences between Sham and SNI in the von Frey mechanical sensitivity behavioural assay (Figure 1). A two-tailed Welch’s

t-test was used to test for differences in cell type counts between Sham and SNI (Figure 2). Differences between the magnitude of differential methylation across time points was identified using a Welch's ANOVA followed by Games-Howell's post-hoc test for multiple comparisons (Figure 3). Pairwise comparisons of CpG positions at each time point utilized a negative binomial generalized linear model to fit the data and differential methylation was determined utilizing the likelihood ratio test. Analyses were corrected for multiple comparisons using the Benjamini-Hochberg FDR (Figure 4). Post-hoc supervised hierarchical clustering analysis was performed using Ward's method and 1 – Pearson correlation as the distance metric (Figure 5-8A). Hypergeometric test was used to test for significant enrichment of pain-related and other experimentally identified genes.

2.10 Gene ontology analysis

Differentially methylated genes identified at each time point were submitted to Metascape [268], a web-based Gene Ontology tool. The CORUM, the Reactome Gene Sets, the KEGG Pathway, Functional Set and Structural Complex, and the GO Biological Processes, Cellular Component and Molecular Function databases were selected as ontology databases. An ontology was considered enriched at a p-value < 0.05, minimum gene count of 3, and a minimum enrichment factor > 1.5. At each time point, 15 representative gene ontologies were selected on the basis of p-value, number of differentially methylated genes within the ontology, and being a parent term to other identified ontologies. At most, only 66% of differentially methylated genes within a representative ontology are identical to the differentially methylated genes identified in any other representative ontology.

3. Results

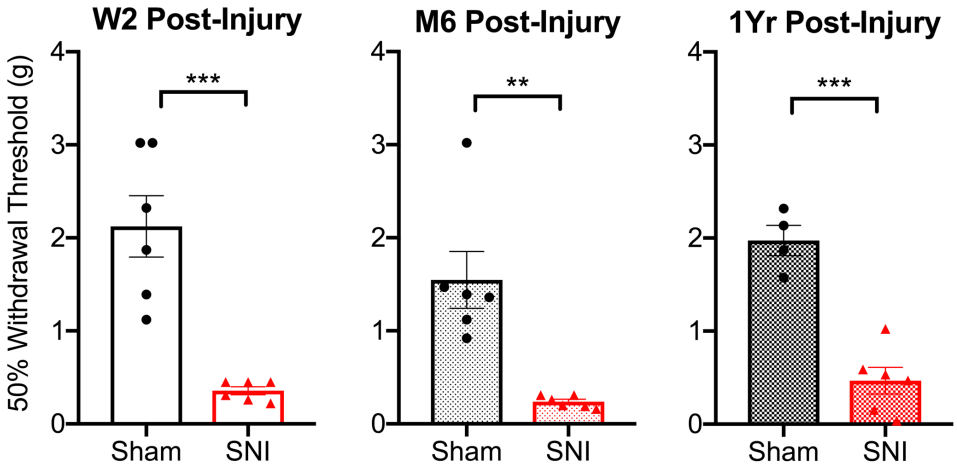
3.1 Spared nerve injury results in long-term neuropathic pain but has no impact on the proportions of neurons, astrocytes and microglia in the prefrontal cortex

Before performing bisulfite sequencing, we validated the presence of long-term neuropathic pain **(Figure 1).** To control for non-epigenetic mechanisms that might drive differential DNA methylation, we verified that the proportions of neurons, astrocytes and microglia do not differ between Sham and SNI animals at W2 and M6. As each cell type has its own DNA methylation profile, differential methylation between Sham and SNI animals could result from the gain or loss of specific cell populations.

3.1.1 Behavioural signs of neuropathic pain persist up to one year following spared nerve injury

To confirm long-term neuropathic pain, mechanical sensitivity was assessed using the von Frey assay at 2 weeks, 6 months, and 1 year following SNI. SNI animals were more sensitive to mechanical stimuli applied to the plantar surface of the hindpaw ipsilateral to the injury at all time points when compared to their respective sham animals (Two-tailed Student's t-test. *W2*: $t_{10} = 5.3$, $p = 0.0003$; *M6*: $t_{10} = 4.2$, $p = 0.002$; *1Yr:* $t_8 = 6.8$, $p = 0.0001$) (**Figure 1**). The reduction in 50% withdrawal thresholds in SNI animals indicates the presence of a persistent and stable mechanical hypersensitivity for up to 1 year.

Figure 1



[**Figure 1 – Mechanical hypersensitivity persists for up to 1 year following spared nerve injury (SNI)**. Nerve injured mice were hypersensitive to mechanical stimuli compared to sham mice at two weeks (W2), six months (M6), and one year (1Yr) post-SNI. Bars represent mean ± SEM withdrawal threshold expressed in grams. *Two-tailed Student's t-test,** = $p < 0.01$; *** = $p < 0.001$, n = 4-6/group.*]

3.1.2 Spared nerve injury has no impact on the proportions of neurons, astrocytes and microglia in the prefrontal cortex

The neuronal, astrocytic, and microglial cell populations were quantified in the PFC by immunohistochemistry to quantify SNI-related changes 2 weeks and 6 months following surgery. Overall cell counts were calculated independently in prelimbic and infralimbic cortical areas as well as at three cortical depths: layer I, superficial layers (layer

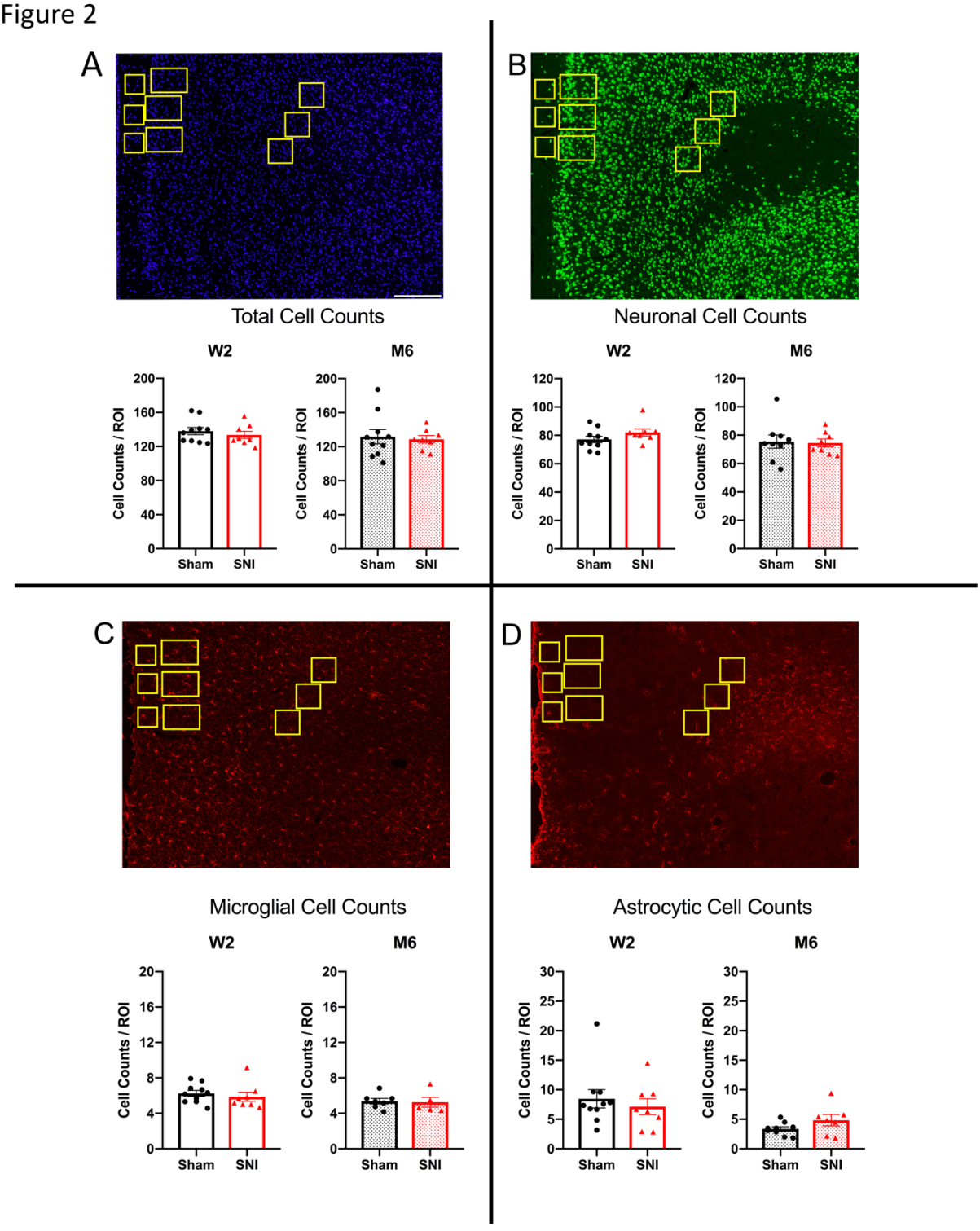
II-III), and deep layers (layer V). No significant differences were detected between SNI and Sham for any cell types in either the prelimbic (Two-tailed Welch's t-test. **DAPI** *W2***:** $t_{15.80} = 0.7$ p = 0.48; *M6***:** $t_{13.21} = 0.3$, p = 0.75. **NeuN** *W2***:** $t_{15.16} = 1.5$, p = 0.16; *M6***:** $t_{12.96} = 0.2$, p = 0.86. **GFAP** *W2***:** $t_{16} = 0.6$, p = 0.53; *M6***:** $t_{7.80} = 1.4$, p = 0.19. **Iba1** *W2:* $t_{12.48} = 0.6$, p = 0.55; *M6:* $t_{6.51} = 0.2$, p = 0.86) **(Figure 2)** or infralimbic **(Supplemental Figure 1)** regions at either time point.

3.2 Spared nerve injury produces rapid, large and persistent changes in DNA methylation in the prefrontal cortex

Differentially methylated (DM) CpG sites were identified by bisulfite capture sequencing by comparing SNI vs. Sham. In this study only DM CpGs that were annotated to promoter regions were selected for analysis due to the inverse relationship between CpG DNA methylation and gene expression (in general, less methylation = increased gene expression; more methylation = reduced gene expression [269]).

Table 1 shows the number of DM CpG sites after adjusting for multiple comparisons. At each of the four time points evaluated, at least 350 DM CpGs were identified at an FDR adjusted p-value threshold of 0.1. Increasingly stringent thresholds still identify a large number of differentially methylated positions. Notably, a subpopulation of DM CpGs remain significant at an FDR adjusted p-value < $1x10^{-7}$, representing a substantial and consistent change between Sham and SNI and strong effect of injury.

Figure 2


A
B
Total Cell Counts
Neuronal Cell Counts
W2
M6
Cell Counts / ROI
Sham
SNI
C
D
Microglial Cell Counts
Astrocytic Cell Counts

[**Figure 2 – Immunohistochemistry reveals no changes in neuronal, microglial or astrocytic cell proportions two-weeks and six-months following spared nerve injury (SNI)**. A) Total (DAPI, Blue), B) Neuronal (NeuN-immunoreactivity (-ir), Green), C) microglial (Iba1-ir, Red), and D) astrocytic (GFAP-ir, Red) cell counts in Sham and SNI cortex at W2 or M6 time points. Displayed are average cell counts from all cortical layers from prelimbic area of the prefrontal cortex. Quantified ROI area is equivalent to 33040.9 μm^2. Bars represent mean ± SEM cell counts; *Two-tailed Welch's t-test. No significant differences observed. n = 8-10/group*.]

FDR	**D1**	**W2**	**M6**	**1Yr**
1.0×10^{-7}	31	28	214	25
1.0×10^{-6}	43	42	259	41
1.0×10^{-5}	62	58	344	62
1.0×10^{-4}	87	91	424	100
0.001	120	141	605	156
0.01	205	232	883	257
0.1	**396**	**370**	**1418**	**435**
0.2	508	487	1767	541

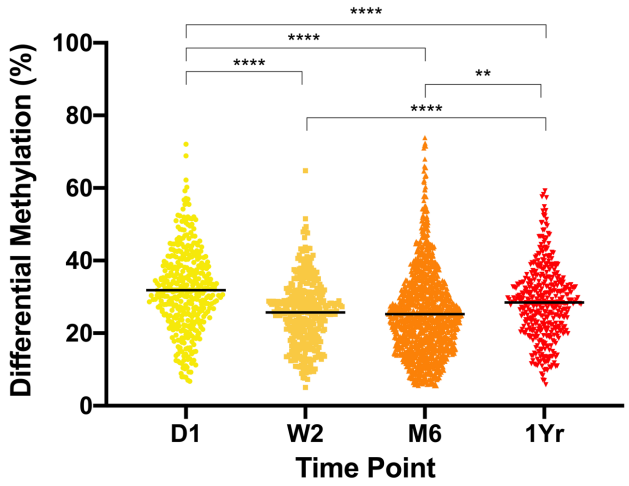
[**Table 1 – Spared nerve injury (SNI) results in highly significant differentially methylated (DM) CpG positions in prefrontal cortex.** SNI induces DM CpGs at all time points. Bolded figures indicate DM CpGs at FDR adjusted p-value experimental threshold

of 0.1. *Likelihood ratio test with Benjamini-Hochberg false discovery rate correction for multiple comparisons.*]

The magnitude of differential methylation at each time point of all DM CpGs is displayed in **Figure 3.** The average magnitude of differential methylation between Sham and SNI is approximately 25-30% at all time points. This is a robust shift in methylation state for most DM CpG positions and is on par with that observed in the brain for major depressive disorder [270].

The effect of peripheral injury on PFC methylation is immediate, with the largest degree of differential methylation between Sham and SNI detected at D1 post-injury, indicating a rapid response to injury. D1 had a significantly higher average methylation change between Sham and SNI than the other time points (Welch's ANOVA followed by Games-Howell's post-hoc test: D1 vs. W2/M6/1Yr, $p < 0.0001$), with 75% of CpGs having a greater than 25% change in methylation, and 25% of CpGs having a change larger than 38%. The W2 and 1Yr time points were the most tightly clustered, with 50% of DM CpGs within 6-7% of their mean differential methylation. Despite having the lowest average percent differential methylation, the M6 time point had a large subpopulation skewed towards high levels of methylation change. These highly DM CpGs may play an important role in the transition from subacute to chronic pain.

Figure 3

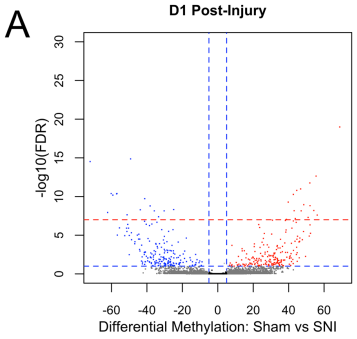


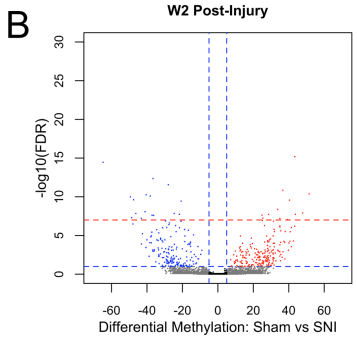
[**Figure 3 – Magnitude of differential methylation following spared nerve injury (SNI)** Differential methylation is expressed in terms of absolute percentage of change between Sham and SNI at 1 day (D1), 2 weeks (W2), 6 months (M6) and 1 year (1Yr) post-surgery. Each dot is an individual CpG. *Welch's ANOVA with Games-Howell's test for multiple comparisons.. **p<0.01, ****p< 0.0001. n = 4-8/group.*]

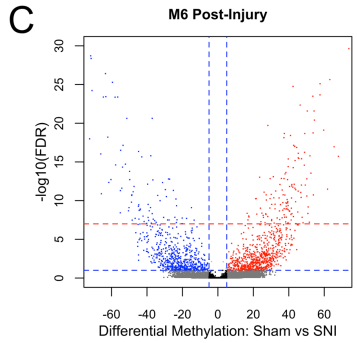
The effect of injury upon PFC methylation is also persistent, with differential methylation observed throughout the time course. Within each time point there were no significant differences in the number of hyper- vs. hypo-methylated CpGs. (**Figure 4A-E**). This balance suggests locus-specific methylation targeting as opposed to a global increase or decrease in DNA methylation.

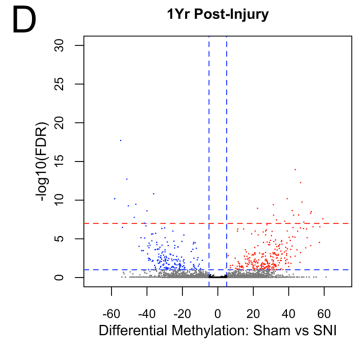
To explore how patterns of methylation evolve at individual CpGs across time, we grouped all CpGs that were differentially methylated at a minimum of 3 out of the 4 time points **(Figure 4F).** While the direction of differential methylation is largely consistent across time for some CpGs, others display dynamic patterns as a function of chronicity. For example, the actin cytoskeleton remodeling gene, WAS/WASL interacting protein family member 2 (*Wipf2*), is consistently hypomethylated, while the cell adhesion gene Contactin 1 (*Cntn1*), fluctuates between hypo- and hypermethylation across the entire time course. Taken together, the DNA methylation response to peripheral nerve injury is rapid, large, dynamic, and persists throughout the entire time-course.

Figure 4





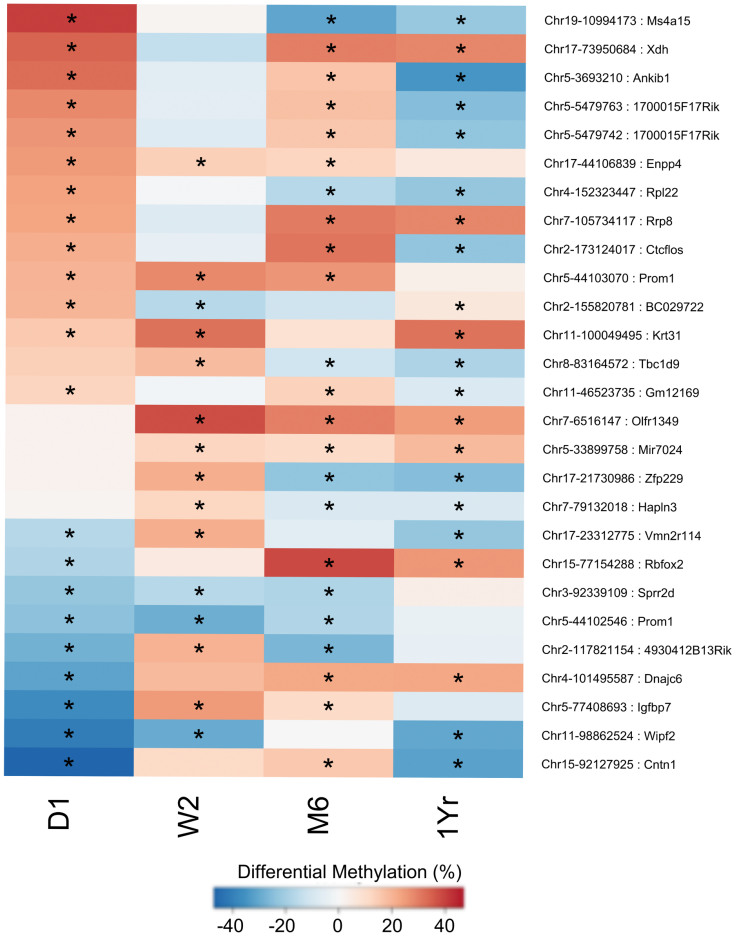




E

CpG Status	D1 Post-Injury		W2 Post-Injury		M6 Post-Injury		1Yr Post-Injury	
	Raw Counts	Percent (%)	Raw Counts	Percent (%)	Raw Counts	Percent (%)	Raw Counts	Percent (%)
Hyper-methylated	206	0.05	202	0.04	784	0.09	259	0.04
Hypo-methylated	190	0.05	168	0.03	634	0.07	176	0.03
Diff Meth >5% Non-significant	84530	21.35	68970	14.26	116706	13.11	98202	16.92
No Differences	311006	78.55	414272	85.66	771649	86.72	481827	83.01
Total CpGs evaluated	395933	100	483612	100	889777	100	580465	100

F



[**Figure 4 – Hyper- and hypo-methylated CpGs following spared nerve injury (SNI).** The magnitude of the statistical significance between methylation differences in promoter region CpGs at A) 1 day (D1), B) 2 weeks (W2), C) 6 months (M6) and D) 1 year (1Yr) post-surgery. CpGs are displayed in terms of positive or negative methylation difference with Sham as the reference point vs. SNI, against –log10(FDR) on the y-axis. Blue horizontal dashed line indicates an FDR adjusted p-value threshold of 0.1, red horizontal dashed line indicates an FDR adjusted p-value threshold of $1x10^{-7}$. The blue vertical dashed line indicates methylation difference thresholds of 5% and -5%. Red dots = hyper-methylated CpGs: blue dots = hypo-methylated CpGs; grey dots = non-significant with methylation differences of >5%, black dots = CpGs that are not different: black. E) The raw counts and percentage of detected CpGs. F) Single CpG positions that were significantly different at three or more time points were tracked across time and display varying patterns of differential methylation. Values are displayed as differential methylation. ** = FDR adjusted p-value < 0.1.*]

3.3 Spared nerve injury results in time point-specific differential methylation of individual genes and functional pathways in the prefrontal cortex.

To determine the functional impact of these substantial shifts in the PFC methylation landscape, we performed gene annotation and downstream analyses to identify associated genes and gene ontologies.

DM CpGs were annotated to their corresponding gene based on the mm10 reference genome. We found that 61.3% of annotated CpGs were the only DM CpG annotated to a gene promoter within a time point. In contrast, 35.5% of annotated CpGs were part of clusters of 2-6 DM CpGs annotated to a promoter region and the remaining 3.3% of CpGs existed within clusters of 7+ CpGs, corresponding to the promoters of 4 genes*: Organic Solute Carrier Partner 1 (Oscp1), Midline1 (Mid1), Toll-like receptor 6 (Tlr6) and 1110020A21Rik.*

Of the genes identified with multiple DM CpGs within a time point, the vast majority (88.5%) were either all hyper- or all hypo-methylated within that promoter, suggesting that the resulting dysregulated genes are likely to be either up- or down-regulated.

Supervised clustering was performed at each time point to visualize clusters of covarying DM CpGs and the characteristic methylation profile of Sham and SNI animals (**Figure 5A-8A**).

To identify the most differentially methylated genes at each time point, a promoter region index was determined by multiplying the adjusted p-value of each CpG by the number of CpGs within the promoter region. The top 25 differentially methylated genes at each time point as determined by promoter region index can be viewed in **Figures 5B-8B**, listing the average adjusted p-value, average differential methylation, number of DM CpGs identified within the gene promoter, and number of hyper- or hypo-methylated DM CpGs. In cases with mixed differential methylation in the promoter, the average methylation for both hyper-methylated and hypo-methylated CpGs are shown separately.

Full lists displaying individual DM CpGs and their annotated genes are available in **Supplemental Table 3.**

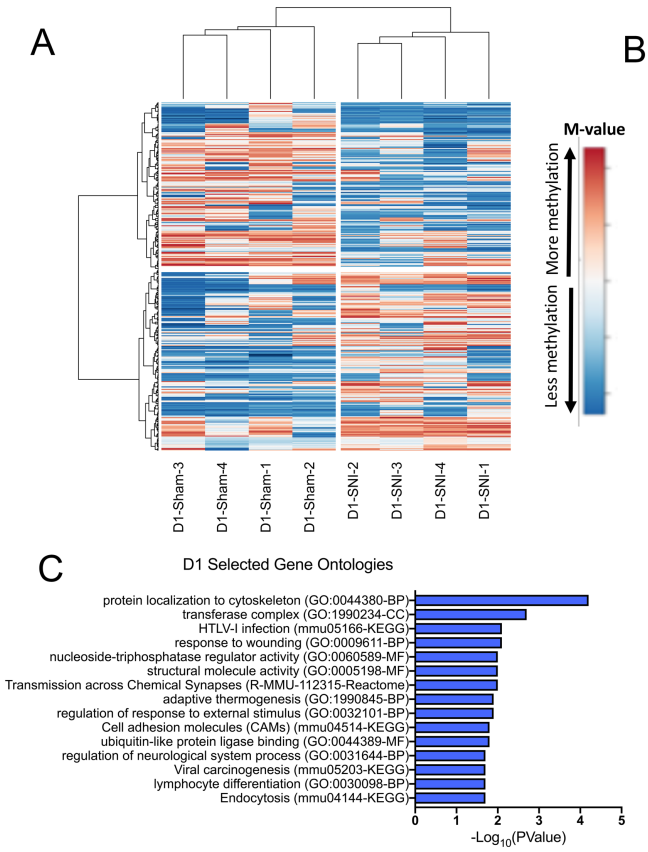
To identify broader effects of differential gene methylation and therefore potential functional dysregulation, gene ontologies enriched for differentially methylated genes were also identified (**Figure 5C-8C**). The full list of enriched ontologies by time point can be observed in **Supplemental Table 4.**

3.3.1 One day post-injury

At D1, 396 DM CpGs identified 327 unique genes undergoing differential methylation in their promoter region. The top 25 differentially methylated genes were related to cell-cell interaction (*Ccdc85a, Cntn1*), cell structure (*Banf2, Cep63, Mid1*), and immune response (*Cystlr2, H2-Q4, Icos, Mapkbp1, Unc5cl*) (**Figure 5B)**. *Mapkbp1, H2-Q4, Icos*, *Unc5cl*, have involvement in TLR, NFκB, and TNF signaling pathways, with additional immune related genes *Acod1, Cd14, Itch, H2-K1, H2-M1, Mapkapk3, Mapkapk5,* and *Tnfrsf13c* also identified as differentially methylated at this time point. While not part of the top 25 differentially methylated genes, actin and cytoskeletal dynamics genes (*Acta2, Diaph1, Dvl1, Macf1, Wipf2*) are also observed.

Gene ontology analysis identified functional pathways enriched for differentially methylated genes involved in response to stimulus, cellular structure remodeling, and extracellular matrix formation **(Figure 5C)**.

Figure 5



B

Gene Name	Average FDR	Average Differential Methylation	# of DM CpGs	Hyper - Hypo
4933421I07Rik	4.26E-03	-32.99	3	0-3
Ahr	9.75E-04	37.45	2	2-0
Banf2	5.77E-10	47.65	2	2-0
BC051537	1.18E-05	-33.49	2	0-2
Ccdc85a	2.29E-05	48.14	2	2-0
Cdc23	3.80E-08	45.41	2	2-0
Cep63	4.05E-03	37.18	3	3-0
Cntn1	6.61E-11	-59.23	1	0-1
Cysltr2	4.79E-04	-53.38	3	0-3
Dcaf11	5.28E-10	39.76	1	1-0
Ddx51	2.55E-03	26.26	3	3-0
Fam109b	1.63E-09	-38.18	1	0-1
H2-Q4	5.03E-03	23.35 / -24.90	2	1-1
Icos	1.92E-05	46	2	2-0
Klk1b24	1.86E-06	-45.84	2	0-2
Mapkbp1	4.16E-11	-60.19	1	0-1
Mid1	3.61E-02	23.58	12	12-0
Mir6993	2.65E-09	52.75	3	3-0
Nacad	4.60E-04	42.72 / -30.28	2	1-1
Olfr1387	5.32E-11	42.67	1	1-0
Olfr316	3.83E-03	-40.88	2	0-2
Sec23b	2.25E-11	-64.6	2	0-2
Smim26	1.02E-19	68.83	1	1-0
Ucp3	1.88E-10	-41.24	1	0-1
Unc5cl	6.11E-06	-46.68	2	0-2

[**Figure 5 – Differentially methylated genes and gene ontologies at 1 day (D1) following spared nerve injury (SNI). A)** Supervised hierarchical clustering of DM CpGs at each time point displays common patterns of differential methylation between individual animals in the same treatment group. Each column is an individual animal and each row represents a CpG position, with blue being less methylation and red being more methylation. Values are displayed as M-Value: $\log_2$ (# methylated CpGs / # unmethylated CpGs) Clustering method: Ward, distance metric: 1-Pearson correlation. **B)** Top 25 differentially methylated genes, **C)** Top 15 selected gene ontologies identified. *Enriched*

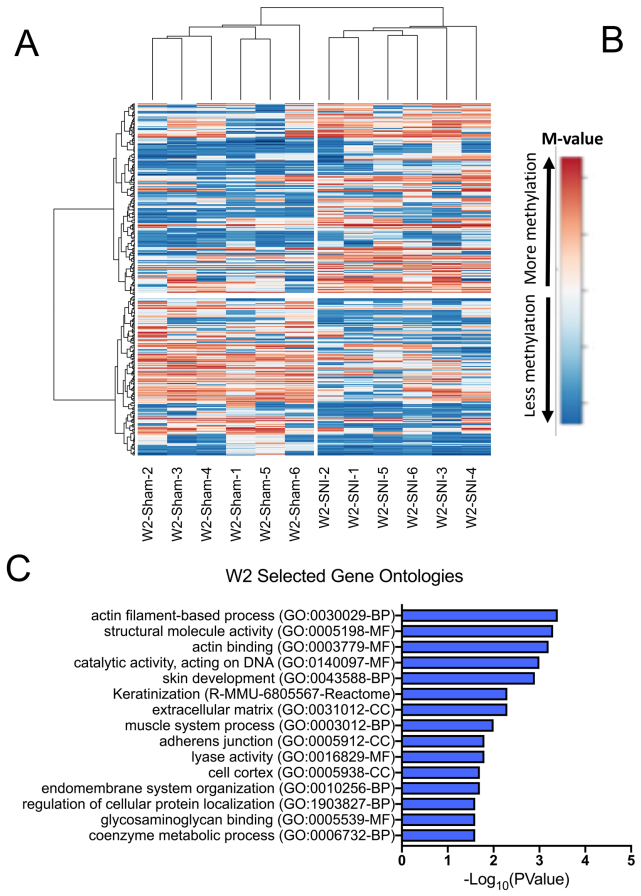
ontology: minimum gene count of 3, p < 0.05, and a minimum enrichment of 1.5. n = 4 mice/group.]

3.3.2 Two weeks post-injury

At W2, 370 DM CpGs identified 311 unique genes undergoing differential methylation in their promoter region. The top 25 differentially methylated genes had involvement in actin processes (*Mical3*), cell surface molecules (*Gpc6, Prom1*), and immune regulation (*Btla, Ccl7*) (**Figure 6B**), In addition to the top 25, the W2 time point revealed genes involved in cellular structure and organization processes, such as actin and cytoskeleton (*Capza3, Epb41l1, Fhdc1, Myh2, Mprip, Shroom3, Tns1, Tns4, Wipf2)*, extracellular matrix (*Col4a1, Col6a4, Halpn3, Rpsa*) and cell-cell interactions (*Nectin2, Lgals4*). Also of interest is the differential methylation of *Ramp1,* which is crucial for the maturation and transport of CALCRL and its function as the CGRP receptor.

At W2, identified gene ontologies are involved with cellular structure remodeling, extracellular matrix, response to stimulus, and changes to internal cellular functioning (**Figure 6C**).

Figure 6



B

Gene Name	Average FDR	Average Differential Methylation	# of DM CpGs	Hyper - Hypo
6430550D23Rik	4.88E-07	-28.65	3	0-3
Btla	7.98E-11	-38.14	1	0-1
Ccl7	3.37E-02	-29.42	3	0-3
Cep250	1.62E-04	-19.89	2	0-2
Cts3	1.55E-06	-40.65	3	0-3
Epn3	5.40E-07	-37.22	2	0-2
Fpgs	3.33E-07	34.94	2	2-0
Gm5111	1.34E-03	15.22	3	3-0
Gpc6	3.46E-15	-64.76	1	0-1
Klk1b24	4.81E-05	35.93	2	2-0
Krt31	2.69E-10	40.41	1	1-0
Lmcd1	4.88E-05	28.04	2	2-0
Mical3	3.01E-04	27.84	2	2-0
Nkain1	3.52E-04	35.37	2	2-0
Olfr371	6.72E-16	43.4	1	1-0
Oscp1	1.03E-02	11.35	9	9-0
Pdk1	1.03E-10	-49.34	1	0-1
Pprc1	1.84E-03	-14.72	3	0-3
Prom1	1.27E-06	35.46 / -36.23	2	1-1
Slc35a5	4.52E-13	-36.6	1	0-1
Snord1b	1.41E-11	36.61	1	1-0
Sprr2d	7.14E-06	-23.66	2	0-2
Tesk1	7.06E-09	-26.29	2	0-2
Them7	6.25E-04	34.93 / -46.31	2	1-1
Vmn1r65	3.40E-03	23.92	2	2-0

[**Figure 6 – Differentially methylated genes and gene ontologies 2 weeks (W2) following spared nerve injury (SNI). A)** Supervised hierarchical clustering of DM CpGs at each time point displays common patterns of differential methylation between individual animals in the same treatment group. Each column is an individual animal and each row represents a CpG position, with blue being less methylation and red being more methylation. Values are displayed as M-Value: $\log_2$(# methylated CpGs / # unmethylated CpGs) Clustering method: Ward, distance metric: 1-Pearson correlation. **B)** Top 25 differentially methylated genes, **C)** Top 15 selected gene ontologies identified. *Enriched*

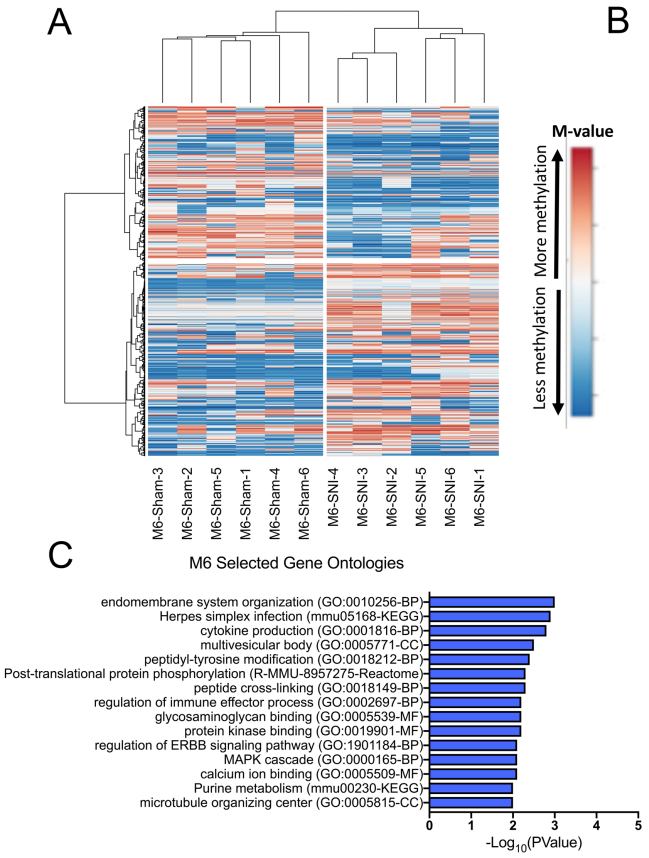
ontology: minimum gene count of 3, p < 0.05, and a minimum enrichment of 1.5. n = 6 mice/group]

3.3.3 Six months post-injury

At M6, 1418 DM CpGs identified 1001 unique genes undergoing differential methylation in their promoter region. The top 25 differentially methylated genes were involved in E3 ubiquitination (*Mid1, Trim21, Trim30d*), and immune functioning (*Gdf15, Fam129c, Arhgef2*) (**Figure 7B**), In addition to the top 25, the M6 time point also displays a substantial number of immune genes across many different pathways (*Cd6, Ltbp1, Trem2;* TNF: *Traf3ip1, Traf6;* Interleukin: *Il12b, Il12rb1, Jak3;* TLR: *Lbp, Acod1, Myd88, Tlr6*). Actin regulation and formation is also affected, with numerous differentially methylated GTPases and guanine exchange factors (*Arhgap8, Arhgap15, Arhgap17, Arhgap33os, Arhgef2, Arhgef10l, Arhgef17, Arhgef19*).

At M6, the gene ontologies are related to immunological responses and systems, transcription factors, signaling cascades, and enzymatic processes (**Figure 7C**).

Figure 7



B

Gene Name	Average FDR	Average Differential Methylation	# of DM CpGs	Hyper - Hypo
1700060C16Rik	5.21E-19	-71.68	2	0-2
Ankle1	2.46E-19	47.1	3	3-0
Ap1m1	1.40E-07	34.87	3	3-0
Arhgef2	1.54E-02	28.69 / -20.80	5	1-4
C2cd5	3.14E-29	-71.65	2	0-2
Ddx51	3.23E-05	22.4	4	4-0
Fam129c	1.11E-04	28.74	4	4-0
Gdf15	4.91E-18	46.19	2	2-0
Gm5415	5.50E-18	64.36	2	2-0
Gm7457	7.86E-18	-60.25	4	0-4
Gys2	6.46E-07	-46.81	2	0-2
Kcnn1	9.42E-13	42.37	2	2-0
Ldhb	4.21E-24	-57.26	2	0-2
Lsm4	1.17E-11	44.35	4	4-0
Mid1	2.12E-02	-15.1	27	0-27
Mir1969	3.80E-13	42.9	2	2-0
Mir6769b	1.07E-19	45.88	2	2-0
Mir7041	2.98E-04	40.15 / -38.86	6	3-3
Mroh1	2.45E-12	-53.98	3	0-3
Olfr374	4.88E-16	43.48	3	3-0
Olfr898	7.58E-04	23.55	3	3-0
Oscp1	1.27E-02	-10.77	22	0-22
Spx	8.20E-09	-51.85	4	0-4
Trim21	3.44E-04	30.96	5	5-0
Trim30d	1.14E-08	-45.27	3	0-3

[**Figure 7 – Differentially methylated genes and gene ontologies 6 months (6M) following spared nerve injury (SNI). A)** Supervised hierarchical clustering of DM CpGs at each time point displays common patterns of differential methylation between individual animals in the same treatment group. Each column is an individual animal and each row represents a CpG position, with blue being less methylation and red being more methylation. Values are displayed as M-Value: $\log_2$(# methylated CpGs / # unmethylated CpGs) Clustering method: Ward, distance metric: 1-Pearson correlation. **B)** Top 25 differentially methylated genes, **C)** Top 15 selected gene ontologies identified. *Enriched*

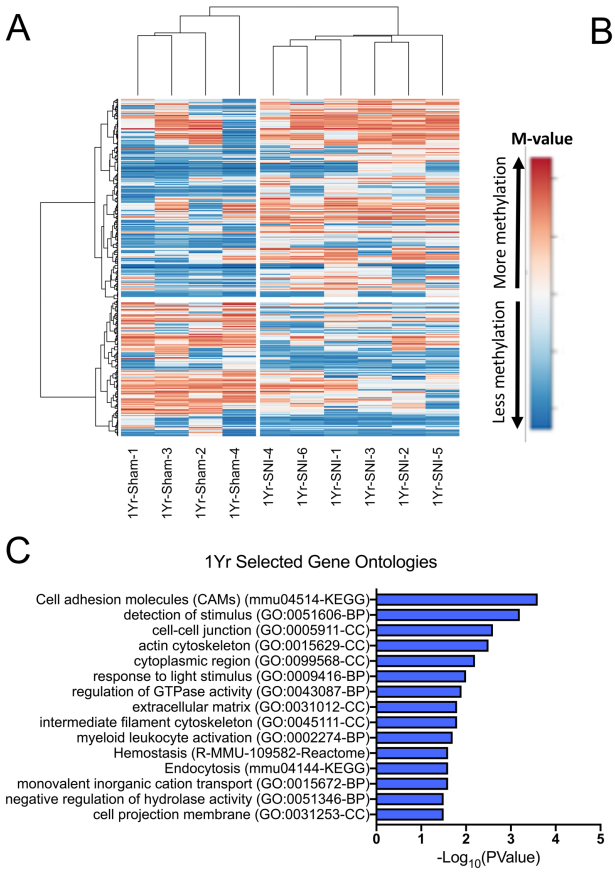
ontology: minimum gene count of 3, p < 0.05, and a minimum enrichment of 1.5. n = 6 mice/group]

3.3.4 One year post-injury

At 1Yr, 435 DM CpGs identified 359 unique genes undergoing differential methylation in their promoter region. The top 25 differentially methylated genes are involved in actin regulation (*Mprip, Parva, Txnrd1*), histone methylation (*Smyd1*), and the acid sensing channel *Asic3* (**Figure 8B**)*,* In addition to the top 25, genes were identified that are involved with cell adhesion molecules (*Cldn13, Cldn15, Hapln3, Madcam1, Nectin2, Nfasc*) and extracellular matrix (*Col17a1, Lama3*).

At 1Yr, the top selected gene ontologies are related to cellular signaling, extracellular matrix formation, and cellular function regulation (**Figure 8C**).

Figure 8



B

Gene Name	Average FDR	Average Differential Methylation	# of DM CpGs	Hyper - Hypo
1110020A21Rik	1.96E-02	18.35	7	7-0
2010003K11Rik	6.58E-11	39.14	1	1-0
2700038G22Rik	2.67E-07	46.03	2	2-0
AI506816	1.08E-03	50.11	2	2-0
Asic3	1.73E-03	-42.49	3	0-3
Btnl6	7.67E-07	12.8	2	2-0
Chpf2	5.48E-10	-50.52	1	0-1
Cngb1	6.59E-03	-33.27	4	0-4
Enpp1	6.85E-07	43.73	2	2-0
Erich3	1.65E-07	-56.02	2	0-2
Etnk2	4.04E-03	33.51	2	2-0
Gba2	3.25E-05	43.51 / -40.35	3	2-1
Golt1a	1.14E-14	43.69	1	1-0
Lrrn2	1.80E-10	47.46	1	1-0
Mir6982	4.32E-04	30.61 / -26.94	2	1-1
Mir7675	1.95E-18	-54.84	1	0-1
Mprip	3.55E-03	31.01	4	4-0
Ms4a15	7.17E-05	33.49 / -28.01	3	1-2
Olfr311	1.15E-09	22.41	1	1-0
Parva	1.50E-11	-36.22	1	0-1
Smyd1	1.77E-02	26.79	3	3-0
Tango6	1.91E-13	-51.34	1	0-1
Tmem68	1.08E-03	33.06 / -24.31	3	2-1
Tnni3	3.39E-10	-46.28	1	0-1
Txnrd1	2.88E-05	30.03	2	2-0

[**Figure 8 – Differentially methylated genes and gene ontologies 1 year (1Yr) following spared nerve injury (SNI). A)** Supervised hierarchical clustering of DM CpGs at each time point displays common patterns of differential methylation between individual animals in the same treatment group. Each column is an individual animal and each row represents a CpG position, with blue being less methylation and red being more methylation. Values are displayed as M-Value: $\log_2$(# methylated CpGs / # unmethylated CpGs) Clustering method: Ward, distance metric: 1-Pearson correlation. **B)** Top 25 differentially methylated genes, **C)** Top 15 selected gene ontologies identified. *Enriched*

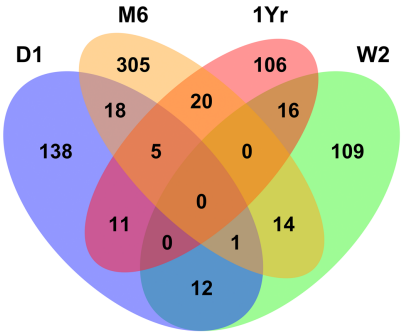
ontology: minimum gene count of 3, $p < 0.05$, and a minimum enrichment of 1.5. n = 4-6 mice/group]

3.4 Spared nerve injury results in function-specific responses across the time course

To identify trends in the functional responses to peripheral nerve injury across time, we overlapped all gene ontologies that were significantly enriched in differentially methylated genes at all time points. Overall, of the 775 enriched gene ontologies identified across all four time points, 658 gene ontologies were unique to one time point, 91 overlapped across two time points, 6 were found at three time points, and none were found to overlap across all four time points (**Figure 9A**). Displayed are the top 5 overlapping ontologies between time points, as determined by greatest averaged p-values and a minimum of 3 enriched genes at each time point in the ontology (**Figure 9B**). When identifying the overlapping gene ontologies at each time point, early time points D1 and W2 display ontologies more related to responding to external stimuli and damage, while later time points M6 and 1Yr display ontologies more related to adaptive immune response and T-cell mediated cytotoxicity. In all overlapping ontologies between time points, there is a strong contribution of actin and cytoskeleton related ontologies. These dysregulated pathways may contribute to functional and structural cortical remodeling previously reported in chronic pain conditions.

Figure 9

A



B

Overlap	Gene Ontology	Description
D1 + W2	GO:0005198	structural molecule activity
	GO:0001750	photoreceptor outer segment
	R-MMU-6805567	Keratinization
	GO:1903034	regulation of response to wounding
	GO:0045178	basal part of cell
D1 + M6	GO:0048668	collateral sprouting
	GO:0072698	protein localization to microtubule cytoskeleton
	mmu05332	Graft-versus-host disease
	GO:0032606	type I interferon production
	mmu05330	Allograft rejection
D1 + 1Yr	mmu04514	Cell adhesion molecules (CAMs)
	mmu04725	Cholinergic synapse
	R-MMU-112314	Neurotransmitter receptors and postsynaptic signal transmission
	mmu05032	Morphine addiction
	GO:0007044	cell-substrate junction assembly
W2 + M6	GO:0018149	peptide cross-linking
	GO:0031424	keratinization
	GO:0010256	endomembrane system organization
	GO:0001533	cornified envelope
	R-MMU-6809371	Formation of the cornified envelope
W2 + 1Yr	GO:0003779	actin binding
	GO:0030864	cortical actin cytoskeleton
	GO:0044448	cell cortex part
	GO:0005938	cell cortex
	GO:0030029	actin filament-based process
M6 + 1Yr	GO:0002711	positive regulation of T cell mediated immunity
	mmu04612	Antigen processing and presentation
	GO:0030865	cortical cytoskeleton organization
	GO:0002709	regulation of T cell mediated immunity
	GO:0001912	positive regulation of leukocyte mediated cytotoxicity
D1 + W2 + M6	GO:0032101	regulation of response to external stimulus
D1 + W2 + 1Yr	NA	NA
D1 + M6 + 1Yr	GO:0044380	protein localization to cytoskeleton
	GO:0031343	positive regulation of cell killing
	GO:0001916	positive regulation of T cell mediated cytotoxicity
	GO:0001914	regulation of T cell mediated cytotoxicity
	GO:0046579	positive regulation of Ras protein signal transduction
W2 + M6 + 1Yr	NA	NA
All Timepoints	NA	NA

[**Figure 9: Overlap of dysregulated gene ontologies across time following spared nerve injury (SNI). A)** Gene ontology analysis reveal that 658 of 775 identified enriched ontologies are unique to one time point, with only 91 ontologies overlapping at two or more time points. **B)** The top 5 gene ontologies per overlap as determined by greatest averaged p-value and a minimum of 3 enriched genes at each time point in the ontology]

3.5 Pain-related genes show time point-specific patterns of differential methylation

To determine if any of the identified DM genes had been previously linked to pain, we cross-referenced with datasets of previously identified pain-related genes (**Figure 10**). Ultsch, Kringel [271] previously identified 535 human and mouse genes associated with pain. After conversion to mouse gene homologs, we identified 31 differentially methylated pain-related genes representing a significant enrichment (hypergeometric test, $p = 0.03$). The Human Pain Genes Database (HPGD) has identified 361 genes in humans wherein SNPs have been found to affect the sensation of pain [272]. 289 HPGD genes had known mouse homologs, of which 15 differentially methylated genes were found in our dataset, however was not significantly enriched (hypergeometric test, $p = 0.21$).

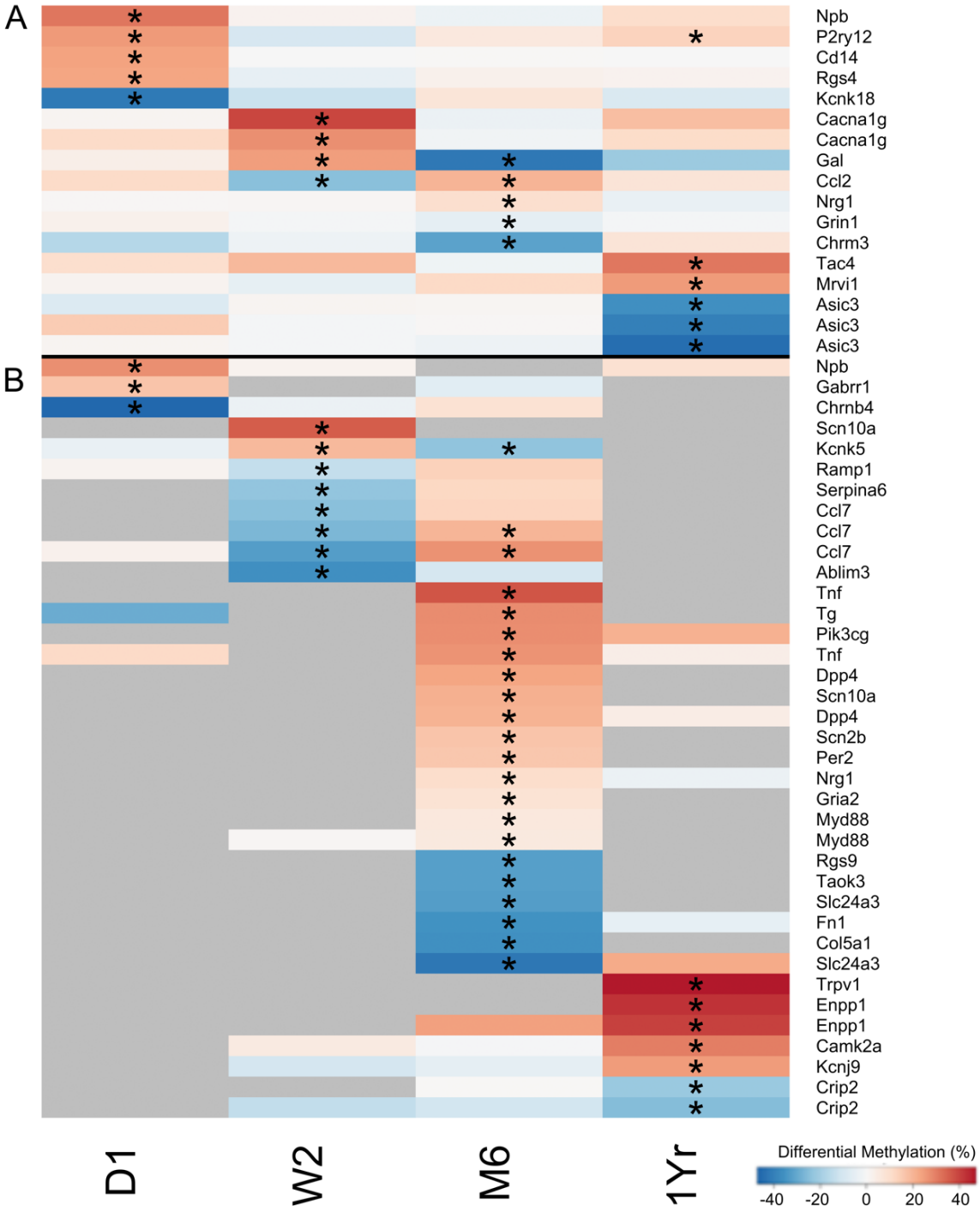
When tracking the differential methylation pattern of pain-related genes across the time course, most only show differential methylation at one time point. At D1, pain-related genes were involved in immune response (*Cd14*), and a number of ion channels (*Chrnb4, Gabrr1, Kcnk18*). At W2, pain-related genes were related to actin (*Ablim3*), immune regulation (*Ccl2, Ccl7*), and ion channels (*Cacna1g, Kcnk5, Scn10a*) At M6, identified pain-related genes are involved in immune responses (*Ccl2, Ccl7, Dpp4, Myd88, Pik3cg, Tnf*), cell-cycle regulation (*Taok3*), and ion channels and transport (*Chrm3, Kcnk5, Scn2b, Scn10a, Slc24a3*). At 1Yr, pain-related genes were involved in ion channels (*Asic3, Kcnj9,* Trpv1), peptide signaling (Tac4), and G-protein coupled receptor signaling (*P2ry12*).

For pain-related CpGs that were able to be captured at all time points, only three CpGs had differential methylation at more than one time point (*P2ry12, Gal,* and *Ccl2*) (**Figure 10A)**. Interestingly, galanin (*Gal)* and chemokine ligand 2 (*Ccl2)*, both show

reversals of their methylation state from W2 to M6. The methylation reversal of these two pain genes may indicate that the recruitment of pain-related processes may change across the time course, and genes have a temporal impact upon chronic pain development. While limited by a lack of data at all time points, a similar time point specific pattern of significant differential methylation was observed for CpGs that were not captured at all time points (**Figure 10B).** Therefore while a gene may be pain-related, its contribution to a pain phenotype may be restricted or limited in time.

We also cross-referenced our M6 experimental genes with two gene sets identified in our previous studies. Massart et al. 2016 examined rat PFC DNA methylation at 9 months post-SNI and identified 3981 genes that undergo differential methylation, with 3011 identified mouse homologs [200]. Our dataset was significantly enriched for genes identified in Massart et al. (hypergeometric test, $p = 0.02$) with 107 overlapping genes and 56 genes with consistent differential methylation profiles between the two species (**Supplemental Table 5**). Alvarado et al. 2013 examined mouse PFC mRNA expression using RNAseq at 6-8 months post-SNI and identified 641 differentially expressed genes [22]. Our dataset was again enriched for genes identified by Alvarado et al. (hypergeometric test, $p = 8 \times 10^{-4}$), with 27 overlapping genes and 12 differentially methylated genes consistent with the predicted change in mRNA expression (**Supplemental Table 6**).

Figure 10


A
B
Npb
P2ry12
Cd14
Rgs4
Kcnk18
Cacna1g
Cacna1g
Gal
Ccl2
Nrg1
Grin1
Chrm3
Tac4
Mrvi1
Asic3
Asic3
Asic3
Npb
Gabrr1
Chrnb4
Scn10a
Kcnk5
Ramp1
Serpina6
Ccl7
Ccl7
Ccl7
Ablim3
Tnf
Tg
Pik3cg
Tnf
Dpp4
Scn10a
Dpp4
Scn2b
Per2
Nrg1
Gria2
Myd88
Myd88
Rgs9
Taok3
Slc24a3
Fn1
Col5a1
Slc24a3
Trpv1
Enpp1
Enpp1
Camk2a
Kcnj9
Crip2
Crip2
D1
W2
M6
1Yr
Differential Methylation (%)
-40
-20
0
20
40

[**Figure 10: Identification and time course of differentially methylated CpGs associated with pain-related genes.** Displayed are CpG positions that were annotated to a pain-related gene identified by Ultsch, Kringel [271] or the Human Pain Genes Database (HPGD) [272]. **A)** For CpGs that were captured at all time points, pain-related genes show mostly single time point differential methylation. **B)** For CpG positions that were not captured at all time points, there is a trend towards single time point differential methylation. Values are displayed as differential methylation. ** = FDR adjusted p-value < 0.1. Grey = no data for that gene/time point*.]

The NMDA receptor subunit *Grin1* was identified in all three datasets, showing both consistent methylation across species and the predicted impact on mRNA expression. Gene regulatory gene *Eif3g*, and neurite outgrowth inhibitor *Rtn4* were among the genes consistent between M6 genes and Massart et al. Among the gene consistent between M6 and Alvarado et al. were the cell-cell junction desmosome gene *Dsg1c*, the actin regulatory gene *Cobl*, and the calcium/calmodulin dependent protein kinase *Camk1d*.

4. Discussion

This study evaluated DNA methylation as a mechanism for the long term embedding of injury-related pain in PFC and subsequent evolution of chronic pain. Previous studies have demonstrated DNA methylation responses to chronic pain in rodent PFC [22, 200], however a number of questions still remain. Are changes in DNA methylation a consequence of chronic pain or do changes precede its emergence? How rapidly do DNA methylation changes occur, and are they persistent throughout chronic pain's time course? Are these changes limited to pain genes, or do they affect entire domains and gene families? What can these changes tell us about how chronic pain develops and embeds itself? Finally, and most importantly, which of these processes should be targeted for intervention?

To answer these questions we tracked PFC DNA methylation profiles for one year post-SNI. We provide first evidence that the PFC methylome is reprogrammed immediately after injury at D1. These data, together with results showing rapid DNA methylation changes in dorsal horn and DRG after injury [236, 273], suggest DNA methylation changes precede the emergence of chronic pain. Second, we show SNI triggers a cascade of dynamic and evolving DNA methylation changes that continue up to one year post-injury, suggesting DNA methylation changes accompany the onset and establishment of chronic pain phenotypes. Third, we identified hundreds of genes and gene ontologies that experience differential methylation. While some may be relevant at only one time point, others are differentially methylated throughout the time course,

potentially serving as the genomic memory of the initial injury and necessary for chronic pain development.

4.1 CpG methylation dynamics

We first analyzed differential CpG methylation between Sham and SNI at each time point independently. At one day post-injury, we observed differential methylation of hundreds of specific CpG positions in the PFC. The D1 time point had the second largest proportion of differentially methylated CpGs identified and the largest average differential methylation, illustrating that the response of the PFC methylome to injury is rapid and substantial. Each time point evaluated had a large population of DM CpGs that displayed a substantial significant difference (FDR adjusted p-value < 1E-7) and large changes in differential methylation (> 40%), indicating strong methylation changes take place throughout the chronic pain time course.

The presence of both hyper-methylated and hypo-methylated CpG positions at each time point implies targeted regulation rather than genome-wide increases or decreases in methylation. There is also a slight trend towards overall promoter hyper-methylation, which may indicate a reduction in overall rates of transcription or a greater number of silenced genes. We previously observed that global DNA methylation decreases after SNI [22], however this difference can be explained by the non-specific demethylation of non-promoter regions in the genome.

4.2 Differentially methylated genes, pathways, and functions

We identified 1633 total unique genes that experience differential promoter methylation, of which 31 and 15 genes were members of the pain-related gene lists by Ultsch et al. or Human Pain Genes Database, respectively. Thus, chronic pain effects not just a few candidate genes but also functionally related groups of genes. Each time point had at least 300 differentially methylated genes identified, and over 150 enriched gene ontologies. At the early time points of D1 and W2, we observed a greater number of ontologies involved in the response to external stimuli, while at the later time points of M6 and 1Yr, inflammatory processes and T-cell adaptive immune responses are implicated. Interestingly, across all four time points numerous ontologies involved in actin dynamics or cytoskeletal regulation were identified. Actin reorganization has been previously identified as a key step in inflammation related persistent pain in glial cells in the spinal cord [274], and sensory neurons in the periphery [275]. The reorganization of nociceptive circuits and dendritic pruning in response to peripheral neuropathic pain is well established [100, 276, 277], and may be a form of maladaptive synaptic plasticity. The consistent differential methylation of actin and cytoskeleton related genes throughout the time course up to one year post-injury suggests an ongoing cortical plasticity and remodeling in response to peripheral injury, and that chronic pain induces progressively greater deviations from normal cortical functioning.

A number of our differentially methylated genes were consistent with results from previous studies. The NMDA receptor subunit *Grin1* was hypo-methylated in both mouse and rat PFC 6 and 9 months post-SNI respectively, with corresponding increases in Grin1

mRNA expression in mouse cortex during the same time frame [22, 200]. Other studies have demonstrated post-injury changes in PFC in NMDA receptor currents, and modulation of PFC NMDA activity can result in pain-attenuation [100, 278]. Hypo-methylation of Grin1 may drive pain-related neuroplasticity, and suggests that NMDA-dependent synaptic changes in chronic pain may be epigenetically-mediated. Other genes including *Camk1d, Kcnip2,* and *Cobl* were also consistent between differential methylation and mRNA expression. These converging lines of evidence across different studies highlight potentially pivotal pain-related genes.

4.3 Time point specific methylation patterns across the chronic pain time course

DM CpGs follow distinctive trajectories of differential methylation across the progression from acute to chronic pain. These differential methylation profiles are a time stamp for the contributions of each gene during chronic pain development and shed light on the post-injury response. Genes with DM CpGs that maintain a methylated state throughout the time course, such as *Wipf2, Rrp8, Xdh, or Sprr2d* may encode a persistent genomic memory of the initial injury, triggering and maintaining a chronic pain state.

It is important to also consider the time point specific differential methylation of genes. Nearly all identified pain-related genes were differentially methylated at a single time point, implying a time-dependent recruitment or dysregulation of normal functioning. *Grin1, Nrg1, Asic3, Gabrr1, Scn10a, Ramp1, Myd88, Trpv1, and Tnf* had differential methylation at only one observed time point. All have well documented impacts on pain

sensation across domains of ion channel activity and trafficking, inflammatory responses, and neurotransmitter regulation [279-293].

The time point specific gene differential methylation and ontology enrichment underscore the importance of understanding temporal dynamics and effects upon normal functioning during the transition to chronic pain. Here we describe the methylation response of the PFC across all phases of the pain phenotype. At one day post-injury, differential PFC methylation is likely driven by the acute abnormal sensory afferent signalling and systemic effects of peripheral inflammation. As pain becomes more chronic by two weeks post-injury, central mechanisms including central sensitization and neuroinflammation initiate changes in synaptic signalling and neuron-glia interactions in PFC. By six months and one year post-injury in late-stage chronic pain, dysregulation of descending inhibitory and facilitatory pain pathways, long-term neuroinflammation and neuroplasticity lead to characteristic depression, anxiety, cognitive impairment, and loss of PFC density.

4.4 Limitations

First, only male mice were studied. Our results lack female methylation responses to chronic pain development, especially important given known sex differences in pain processing [294]. Second, our experiment focused on promoter region methylation, potentially missing DNA methylation regulation in non-promoter regions or by other processes. DNA methylation in the first intron of coding genes or gene body can affect gene expression [183, 295]. Moreover, DNA methylation does not have a linear

relationship to gene expression, with other regulatory processes such as RNA transcription or protein translation involved, thus requiring a future analysis of gene expression. Third, our tissue samples are derived from whole brain tissue homogenates, and therefore mixtures of different brain cell types, each with their own cell type specific profiles of DNA methylation. Thus, the differential methylation signal may be diluted by conflicting methylomic data. While the lack of significant changes in the proportions of neurons, astrocytes and microglia mitigates this limitation **(Figure 2),** changes in other non-neuronal cell types (e.g. oligodendrocytes, vascular cells) is not accounted for in the current study. Fourth, the alpha threshold was set at an FDR of 0.1 in this study. It is acknowledged that the selection of an FDR threshold of 0.1 carries a greater risk of type I error (false positive), it is preferable for the exploratory purposes of this study where type II error (false negative) is a greater concern. We recognize these limitations and present these results as a first step towards understanding the epigenetic reprogramming associated with the development and maintenance of chronic pain.

5. Conclusions

Our findings provide evidence for rapid epigenetic reprogramming in the PFC methylome in response to peripheral nerve injury. Thus, epigenetic reprogramming precedes rather than follows chronic pain, consistent with a causal role. Reprograming persists as pain becomes chronic, thereby suggesting an important role for DNA methylation in the initiation, progression and maintenance of chronic pain. While some changes in DNA methylation were persistent, dynamic reprogramming was also observed.

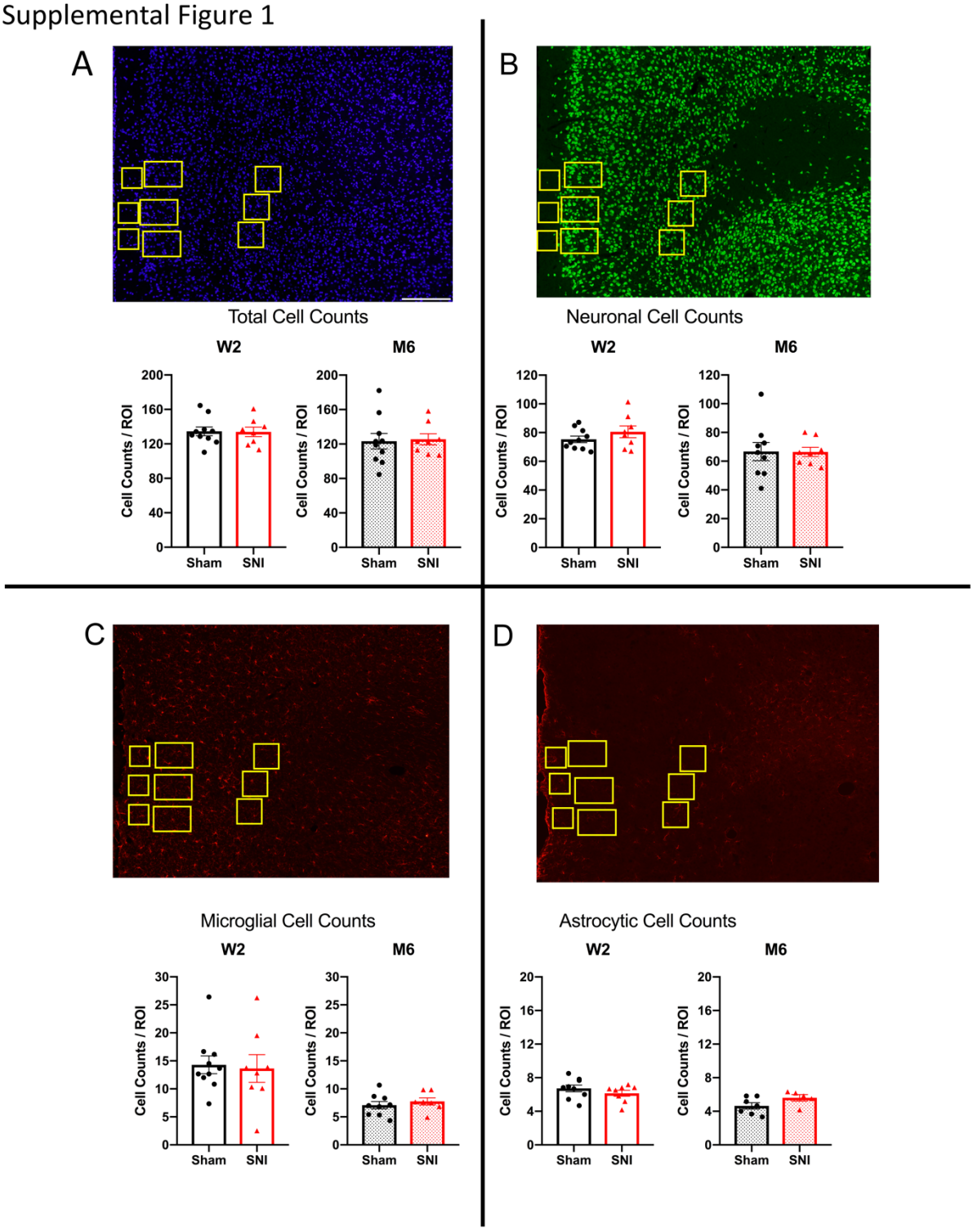
These patterns may reflect underlying differences between acute, sub-chronic and chronic pain, suggesting that therapeutic interventions may have efficacy dependent on pain duration. Pathway analysis revealed enrichment in genes related to stimulus response at early time points, immune function at later time points and actin and cytoskeletal regulation throughout the time course. These findings highlight the importance of understanding the time course of acute to chronic pain and suggesting broader pain interventions than single gene or protein targets are required.

Acknowledgements:

The authors would like to thank the Louise and Alan Edwards Foundation, the Canadian Institutes of Health Research, and the Fonds de la Recherche en Sante du Quebec for their financial support. The authors would also like to thank the McGill Animal Resources Centre, Compute Canada, the McGill University Genome Quebec Innovation Centre and the Canadian Center for Computational Genomics. The Canadian Center for Computational Genomics (C3G) is a Genomics Technology Platform (GTP) supported by the Canadian Government through Genome Canada. Finally, the authors would like to thank Virginie Calderon, Odile Neyret, Francois Lefebvre, and Xiaojian Shao for invaluable advice and technical support. The authors declare no conflicts of interest.

Supplemental Figures

Supplemental Figure 1



[**Supplemental Figure 1 – Immunohistochemistry reveals no changes in neuronal, microglial or astrocytic cell proportions two-weeks and six-months in infralimbic cortex following spared nerve injury (SNI)**. A) Total (DAPI, Blue), B) Neuronal (NeuN-immunoreactivity (-ir), Green), C) microglial (Iba1-ir, Red), and D) astrocytic (GFAP-ir, Red) cell counts in Sham and SNI cortex at W2 or M6 time points. Displayed are average cell counts from all cortical layers from prelimbic area of the infralimbic cortex. Quantified ROI area is equivalent to 33040.9 μm^2. Bars represent mean ± SEM cell counts; *Two-tailed Welch's t-test. No significant differences observed. n = 8-10/group*.]

Supplemental Table 1 – Probe Bed File. Genomic coordinates for the bisulfite capture-sequencing probes

See Appendix 1 of Thesis

Supplemental Table 2 – Blacklist Bed File. Genomic coordinates for regions known to have anomalous, unstructured, and high signal/read counts in next gen sequencing

See Appendix 2 of Thesis

Supplemental Table 3 – All differentially methylated CpGs and annotated genes identified

See Appendix 3 of Thesis

Supplemental Table 4 – All enriched gene ontologies identified

See Appendix 4 of Thesis

Supplemental Table 5 – Genes with consistent differential methylation profiles between M6 and those identified previously in Massart et al. 2016

See Appendix 5 of Thesis

Supplemental Table 6 – Genes consistent with the predicted change in mRNA expression between M6 and those identified previously in Alvarado et al. 2013

See Appendix 6 of Thesis

Chapter 3: DNA Methylation Response to SAM Treatment of Chronic Pain

4.1. Preface

Chronic pain is associated with persistent changes in PFC structure and function. Previous work has demonstrated a clear association with DNA methylation in the PFC, the development and progression of chronic pain and the differential methylation of chronic pain-related functional domains. Interestingly, successful pain attenuation through therapeutic intervention reverses chronic pain associated losses in PFC grey matter in human patients. As a stable but malleable mechanism of gene regulation, DNA methylation is an excellent potential candidate mechanism to underlie this reversal in PFC. Indeed, research in addiction and stress have demonstrated that successful intervention will reverse DNA methylation changes associated with the disease. However, no study has determined gene specific changes in PFC DNA methylation in response to a successful pain attenuating intervention.

Previous work has demonstrated that chronic systemic administration of the methyl donor s-adenosylmethionine is capable of attenuating chronic peripheral neuropathic pain, and affecting global PFC DNA methylation levels. We hypothesized that chronic administration of s-adenosylmethionine would result in the counteraction or reversal of chronic pain related changes in PFC DNA methylation, and sought to determine affected functional domains.

4.2. Manuscript II:

Attenuation of neuropathic pain by s-adenosylmethionine is associated with genome-wide reversals of pathological changes in DNA methylation in mouse frontal cortex

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Abstract:

Chronic pain is associated with persistent but reversible structural and functional changes in prefrontal cortex (PFC). This stable yet malleable plasticity implicates epigenetic mechanisms, including DNA methylation, as a potential mediator of chronic pain-induced changes. We have previously demonstrated that oral administration of the methyl donor s-adenosyl methionine (SAM) is capable of attenuating long-term peripheral neuropathic pain and affecting global PFC DNA methylation. However, little is known of the mechanisms underlying SAM-mediated pain attenuation. To elucidate these mechanisms, we performed epigenome-wide analysis of mouse PFC after 4 months of SAM treatment initiated 3 months following induction of peripheral nerve injury. Over 4000 differentially methylated genomic regions were detected in both Injury and SAM treatment conditions, and enriched gene ontologies included intracellular signaling, cell locomotion and migration, cytoskeletal structure, and cell adhesion. Following SAM treatment, 1415 differentially methylated regions, representing 1030 genes, showed a reversal of chronic pain-related differential methylation. Over 100 genes with known pain-related function were differentially methylated following nerve injury, with many also experiencing a reversal after SAM treatment. These results demonstrating the reversal of PFC DNA methylation concurrent with pain reduction underscore the potential of DNA methylation targeted therapies in treating chronic pain.

1. Introduction

The PFC is essential for executive function and synthesizing the diverse range of information the brain receives [296, 297], and is a crucial area for processing of nociceptive and aversive stimuli [298]. The PFC is part of a cortical and subcortical network that is activated by pain [14, 299] and may mediate its affective-motivational and cognitive components [300-302]. These higher-order aspects of pain can exacerbate an individual's perception of pain and contribute to pain-related comorbidities and reduced quality of life [37, 303-305]. As a result of chronic pain, the PFC undergoes structural and anatomical changes over time resulting in the loss of grey matter, reorganization of synaptic connections, and changes in gene expression [21-23, 100, 104].

Reduced PFC grey matter occurs in a number of different pain conditions in humans and animal models [15-20, 82]. Interestingly, treatments that attenuate pain are capable of reversing chronic pain-induced losses of cortical thickness or grey matter in the PFC [24-26, 86, 115]. PFC gene expression is also heavily modified in response to chronic pain with genome-wide changes in mRNA expression level detected in long-term neuropathic pain [22, 23]. The plasticity and possible reversibility of these changes is not only encouraging with regard to effectively treating chronic pain, but suggests the involvement of epigenetic mechanisms.

Epigenetic regulation of gene expression allows for malleable control over gene expression without modifying the underlying genetic sequence. DNA methylation is the covalent addition of methyl residues to cytosine nucleotides and when it occurs in the

promoter region of a gene, typically results in epigenetic repression of gene expression [243, 244]. DNA methylation is mediated by DNA methyltransferases (DNMT) and its methyl donating substrate, s-adenosylmethionine (SAM) [306, 307]. SAM is marketed as a nutritional supplement for a wide range of pain-related or comorbid conditions including depression, cognitive deficits, migraine, back pain and osteoarthritis [308-310].

A number of studies have demonstrated that chronic pain development is accompanied by changes in DNA methylation throughout pain transmission pathways including dorsal root ganglion [236, 311], spinal cord [312], and brain including PFC [22, 200, 234, 313]. Studies examining promoter region DNA methylation found gene-specific changes that correlated to mRNA transcript levels [200], and were dynamically regulated up to one year post-injury [313]. Moreover, successful attenuation of pain by environmental enrichment reduced global PFC DNA methylation levels in the PFC [22, 234]. However, no study has yet examined gene specific PFC DNA methylation after the effective treatment of pain.

We recently demonstrated that systemic chronic treatment with the methyl-donor SAM attenuated the sensory and cognitive impact of nerve injury in mice [234]. Here, we focused on understanding the impact of systemic SAM treatment at the molecular level via analysis of genome-wide PFC DNA methylation. We demonstrate that, consistent with previous findings, spared nerve injury (SNI) induces changes in DNA methylation. We further demonstrate that SAM treatment counteracts nerve injury-related changes in DNA methylation and we identify functional pathways affected by this reversal.

2. Materials and Methods

2.1 Animals

Male CD-1 mice (Charles River Laboratories, St-Constant, QC, Canada) were used in this study. Animals were received at 6-8 weeks of age and housed 3-4 per cage on a 12h light/dark cycle in a temperature controlled room in ventilated polycarbonate cages (Allentown, Allentown, NJ) with corncob bedding (7097, Teklad Corncob Bedding, Envigo, UK) and cotton nesting squares for enrichment. Mice were given access to food (2092X Global Soy Protein-Free Extruded Rodent Diet, Irradiated) and water *ad libitum*. Animals were habituated to the housing conditions for at least one week prior to any experimental interventions.

All experiments were approved by the Animal Care Committee at McGill University, and conformed to the ethical guidelines of the Canadian Council on Animal Care and the guidelines of the Committee for Research and Ethical Issues of the International Association for the Study of Pain [253].

2.2 Neuropathic pain model: Spared Nerve Injury

Animals were randomly assigned to receive either spared nerve injury (SNI) or sham surgery. Nerve injury was induced using the Spared Nerve Injury model of neuropathic pain, as adapted for mice [254, 255] at 10 to 12 weeks of age. Under deep isoflurane anesthesia, an incision was made on the medial surface of the thigh, exposing the three branches of the sciatic nerve. SNI surgery consisted of ligation and transection of the left tibial and common peroneal branches of the sciatic nerve, while sparing the

sural nerve. The tibial and common peroneal branches were tightly ligated with 4:0 silk (Ethicon) and sectioned distal to the ligation. Sham surgery consisted of exposing the nerve without damaging it.

2.3 Drug treatment: Chronic administration of s-adenosylmethionine

Three months after SNI or sham surgery, animals were randomly assigned to receive saline vehicle or SAM (kind gift of Life Science Labs Supplements, LLC, Lakewood, NJ) treatment for 4 months. A solution of SAM (20 mg/kg) was freshly prepared each treatment day in 0.9% NaCl, and each animal received an oral administration of 8 μL 3 times per week for 4 months. The chosen dose and the protocol used were influenced by previous studies [314-316].

2.4 Behavioural assessment of mechanical sensitivity

Baseline behavioral assessments were performed 3 months after SNI or sham surgery to confirm the development of neuropathic pain. Behavioural testing group sizes: Sham-Vehicle: n = 6, Sham-SAM: n = 6, SNI-Vehicle: n = 7, SNI-SAM: n = 8. Mechanical sensitivity was then reassessed every 2 weeks across the 4 months of treatment. After a 1 hour habituation period to the testing apparatus, von Frey filaments (Stoelting Co, Wood Dale, IL) were applied to the plantar surface of the hind paw until filaments were bent for either 3 seconds or hind paw withdrawal. Mechanical sensitivity was determined as the 50% withdrawal threshold using the up-down method [256]. The stimulus intensity ranged from 0.04 to 4.0 g, corresponding to filament numbers 2.44 to 4.56. The experimenter was blind to treatment group.

2.5 Isolation of prefrontal cortex, DNA capture, and bisulfite sequencing

Following completion of SAM treatment, mouse PFC was dissected following isoflurane anesthesia and decapitation. DNA methylation analysis group sizes: Sham-Vehicle: n = 3, Sham-SAM: n = 3, SNI-Vehicle: n = 4, SNI-SAM: n = 4. PFC was defined as a region with an anterior boundary of the frontal pole, approximately +3.00 Bregma, posterior boundary of approximately +1.00 Bregma, lateral boundaries of +1 mm from midline, and a ventral boundary wherein the olfactory bulb, caudate putamen, and areas below the rhinal fissure and lateral ventricles were all removed [257]. This defined area isolates the prelimbic, orbital, and infralimbic cortices corresponding to the mouse medial PFC. Once dissected, tissue was homogenized and genomic DNA was extracted using the Qiagen DNeasy Blood and Tissue kit and protocol.

Genome-wide methylation analysis was performed using the Roche SeqCap Epi Developer M Enrichment system on bisulfite-treated DNA (Roche Nimblegen; WI, USA), with custom designed primers targeting promoter and enhancer regions of the genome. Probe design was based on the mm9 reference genome and associated H3K4me1 and H3K4me3 binding (probe BED file available in **Supplemental Table 1**). Briefly, 1 μg of genomic DNA per sample was fragmented into 200bp lengths, and adapter and index sequences were ligated to each end of the fragment according to the KAPA Library Preparation Kit protocol. Sample DNA was then bisulfite converted following the EZ DNA Methylation-Lightning Kit (Zymo Research; CA, USA). Sample DNA was then PCR amplified, hybridized with custom capture probes, and PCR amplified again in accordance with Roche SeqCap Epi system protocols [259]. Sample captured bisulfite-converted

DNA sequencing was performed by Genome Quebec on the Illumina HiSeq 2500 following Illumina guidelines. Paired-end sequencing reads of 125bp in length were generated.

2.6 DNA methylation pre-processing

Capture sequencing data was pre-processed using the McGill University Genome Quebec Innovation Centre GenPipes Methyl-Seq Pipeline [260]. The pipeline proceeds through Trimmomatic, Bismark Align, Picard Deduplication, and Bismark Methylation Call [261, 262]. Baseline pipeline parameters were set as a minimum sequence quality of PHRED score > 30, alignment reference genome was mm10 (GRCm38), and minimum read coverage per base was set at 10 reads. A detailed outline of the Methyl-Seq pipeline steps and process can be found at https://bitbucket.org/mugqic/genpipes. Before analysis, collected sequence data was filtered to remove a blacklist of regions identified to have anomalous, unstructured, and high signal/read counts in next gen sequencing [263]. The blacklist used was specific for mm10 and the BED file can be found in **Supplemental Table 2.**

2.7 Differential methylation analysis

Differential methylation analysis was performed using R and the MethylKit package [317]. For a CpG site to pass through to analysis, it was required to be sequenced to a minimum depth of at least 10 reads in each sample. Coverage values between samples were normalized using a scaling factor derived from differences between the median of coverage distributions. Tiling windows were used to summarize methylation information over the genome. Tiles were set to be 250 base pairs (bp) in length and advance in 125

bp steps. Methylated and unmethylated cytosine counts within each tile are summed to provide an overall methylation proportion within the tile. Only CpGs that were annotated to a promoter region, defined as 2000 bp upstream or 200 bp downstream from the transcription start site, were selected for analysis. MethylKit uses logistic regression to model a log odds ratio based on methylation proportion within each tile. Calculated p-values are adjusted to q-values using the SLIM method [318].

Tiles were defined as being differentially methylated between groups if the adjusted p-value was less than < 0.1 and had a difference in methylation $> 5\%$. While the selection of an FDR threshold of 0.1 carries greater risk of type I error, false positive, than the more typical threshold of 0.05, it is preferable for the exploratory purposes of this study. Differentially methylated tiles can be further divided into hypermethylated or hypomethylated. In comparisons between groups, the control group acts as the reference point, i.e. Control: Sham-Vehicle, Experimental: SNI-Vehicle. Therefore, if the experimental group tile methylation is 5% or larger than the control, the tile is considered to be hypermethylated, and if the treatment tile methylation is reduced by -5% or more compared to control, the tile is considered to be hypomethylated.

Tiles were annotated to their associated genes and genomic regions using the annotatePeaks function of the ChIPseeker [265] R package, using a TxDb object created from the Gencode “mmusculus_gene_ensembl” Biomart database. Each tile position was annotated and tracked individually throughout the analysis. For homology conversion, gene symbols from non-mouse species were converted to known mouse homologs based

on the Mouse Genome Database (MGD) – Vertebrate Homology, Mouse Genome Informatics, The Jackson Laboratory, Bar Harbor, Maine [266].

To simplify the analysis of reversals in differential methylation, we filtered for genes that had uniform differential methylation, meaning all tiles annotated to the gene were all hypermethylated or all hypomethylated. Genes with variable differential methylation, where the gene simultaneously had some hypermethylated tiles and some hypomethylated tiles, were not examined in the reversal analysis.

2.8 Statistical analysis

Two-way repeated measures ANOVA with Bonferroni post-hoc test was used to detect group differences in the von Frey mechanical sensitivity behavioural assay. Pairwise comparisons of tiles between experimental groups utilized logistic regression to model the log-odds ratio of methylation proportion per tile. Analyses were corrected for multiple comparisons using the SLIM method [318]. The hypergeometric test was used to test for significant enrichment of pain-related genes.

2.9 Gene ontology analysis

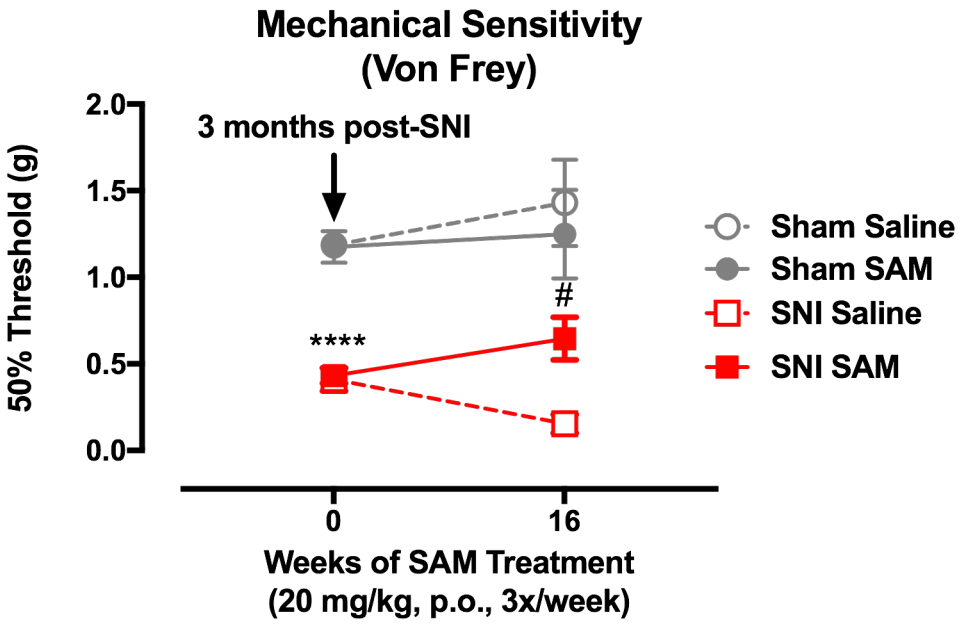
Differentially methylated genes identified were submitted to gProfiler [319], a web-based gene ontology tool. The GO Biological Processes and Molecular Function databases were selected as ontology databases. Ontology p-values were adjusted using the g:SCS correction for multiple comparisons [320] and an ontology was considered enriched at an adjusted p-value < 0.05. To allow for a specific view of affected functions

and pathways, the displayed gene ontologies are limited to a maximum size of 2000 genes.

3. Results

3.1 Spared Nerve Injury results in mechanical hypersensitivity that is attenuated by chronic SAM treatment.

Pain hypersensitivity induced by SNI in mice occurs immediately and can persist for up to one year post-injury [313]. Chronic administration of methyl donor s-adenosylemethionine (SAM) 3 months post-SNI injury decreases mechanical hypersensitivity in the ipsilateral injured paw compared to saline vehicle treated animals (**Figure 1**).



[**Figure 1**: *Chronic systemic administration of s-adenosyl methionine attenuates peripheral neuropathic pain*. Repeated administration of SAM (20 mg/kg, oral gavage, 3 doses per week) over a 16 week period was initiated 3 months post- sham or SNI-surgery (Time 0). SNI-related mechanical hypersensitivity was attenuated compared to vehicle-treated animals. Sham-Vehicle: n = 6, Sham-SAM: n = 6, SNI-Vehicle: n = 7, SNI-SAM: n = 8. 2-way RM ANOVA with Bonferroni post-hoc test. ** : $p < 0.01$ sham-vehicle vs SNI-vehicle; # : $p < 0.05$ SNI-vehicle vs SNI-SAM. SNI: spared nerve injury; SAM: s-adenosylmethionine; p.o. : Per os (oral administration). Adapted from Gregoire et al. 2016 [234]]

3.2 Spared Nerve Injury and chronic SAM administration lead to widespread changes in DNA methylation in the prefrontal cortex

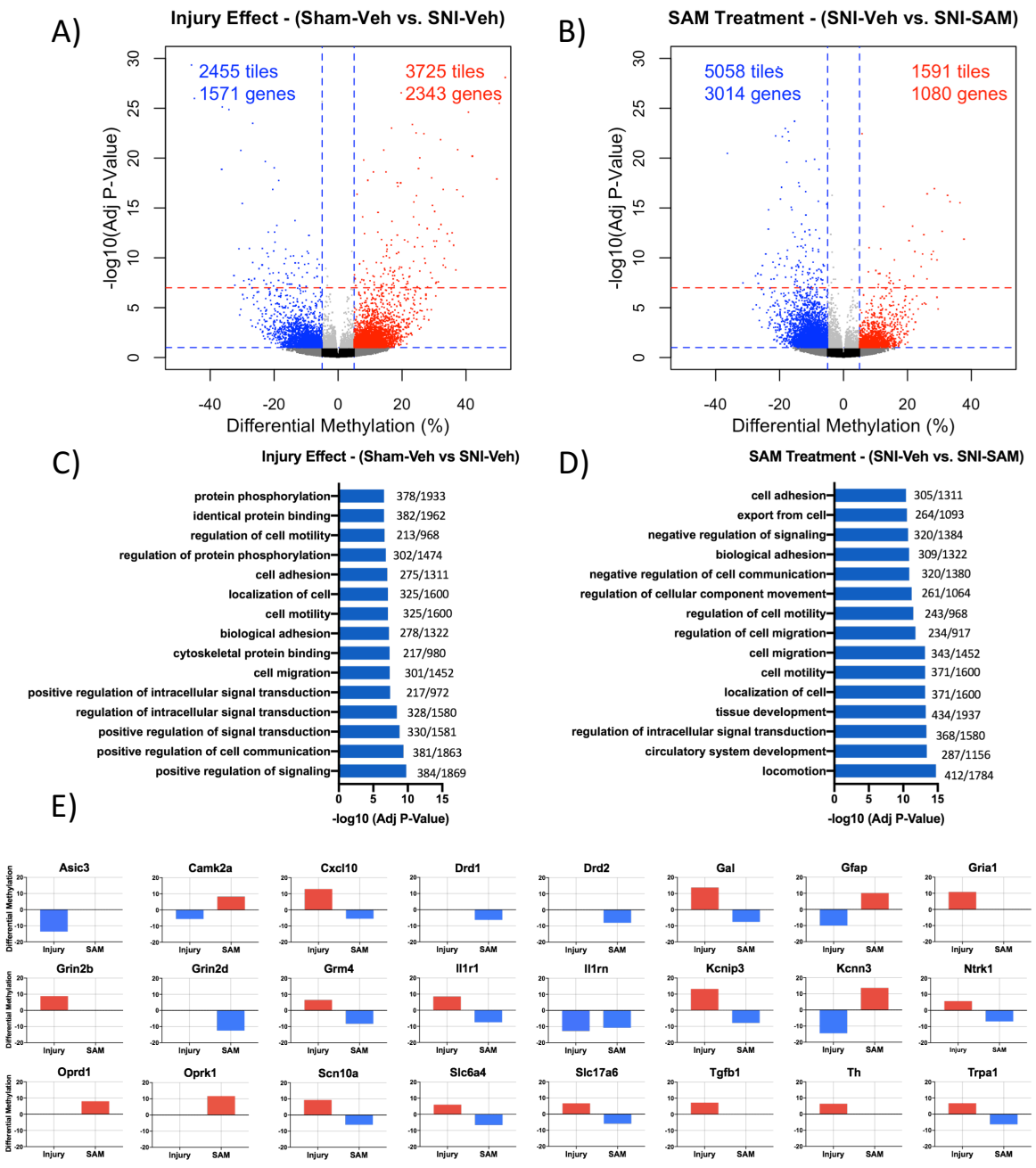
We have previously demonstrated changes in PFC promoter region methylation in response to SNI at multiple time points post-injury [313]. Here we examined global PFC promoter methylation post-injury and post-SAM administration to determine the effect of SAM on injury related changes in PFC promoter methylation.

To understand the effects of peripheral nerve injury, SNI-vehicle animals were compared against Sham-vehicle animals 7 months post-injury, with 191,013 tiling regions covering 22,683 unique gene promoters. We observed a trend towards promoter region hypermethylation with 3725 hypermethylated tiles and 2455 hypomethylated tiles, representing 2343 and 1571 unique genes, respectively (**Figure 2A**). 157 hypermethylated tiles and 95 hypomethylated tiles with robust differential methylation were detected (adjusted p-value < $1x10^{-7}$). These tiles represent 95 and 57 genes respectively and include PI3K gene *Pik3cd* (25.1% differentially methylated (DM)), toll-like receptor *Tlr6* (19.6% DM), and potassium ion channel subunit *Kcng2* (-29.9% DM). 213 ontologies were enriched for differentially methylated genes. The top 15 enriched ontologies are predominantly involved in signaling and intracellular signal transduction, cell migration, cytoskeletal protein binding, and biological adhesion (**Figure 2C**).

To explore the effect of SAM treatment in neuropathic pain, we compared SNI-SAM animals to SNI-vehicle animals, with 186,896 tiling regions evaluating 22,530 unique gene promoters. In contrast to sham vs. SNI, when SNI injured animals underwent chronic SAM administration, tiles in PFC promoter regions were predominantly

hypomethylated. 1591 hypermethylated tile regions and 5058 hypomethylated tile regions representing 1080 and 3014 unique genes were detected, respectively (**Figure 2B**). We detected 48 hypermethylated tiles and 142 hypomethylated tiles with robust differential methylation (adjusted p-value < $1x10^{-7}$). These tiles represent 33 and 78 genes respectively and include the TFIID subunit *Taf4b* (28.3% DM), interleukin 36β gene *Il1f8* (25.1% DM), and oxytocin receptor *Oxtn* (-9.6% DM). We identified 363 ontologies that were enriched in differentially methylated genes following SAM treatment. These ontologies are involved in locomotion and cell motility, circulatory system and tissue development, intracellular signal transduction, and cellular transport (**Figure 2D**).

To identify pain-related genes, differentially methylated genes were compared to curated lists of pain-related genes identified by Ultsch et al [271] or the Human Pain Genes Database (HGPD) [272]. Nerve injury resulted in differential methylation that was enriched for pain-related genes, with 110 differentially methylated pain-related genes identified by Ultsch and 59 differentially methylated pain genes identified by the HPGD (Ultsch: p = 0.0002; HPGD: p = 0.0103. Hypergeometric Test). In the SAM treatment effect, 112 DM pain genes were identified from the Ultsch list, and 62 from the HPGD list (Ultsch: p = 0.0012; HPGD: p = 0.0128. Hypergeometric Test). A number of pain related genes displayed reversals in differential methylation after SAM treatment, such as the CamKII subunit *Camk2a*, TrkA receptor *Ntrk1*, $Na_v1.8$ channel *Scn10a*, and serotonin transporter *Slc6a4* (**Figure 2E**).



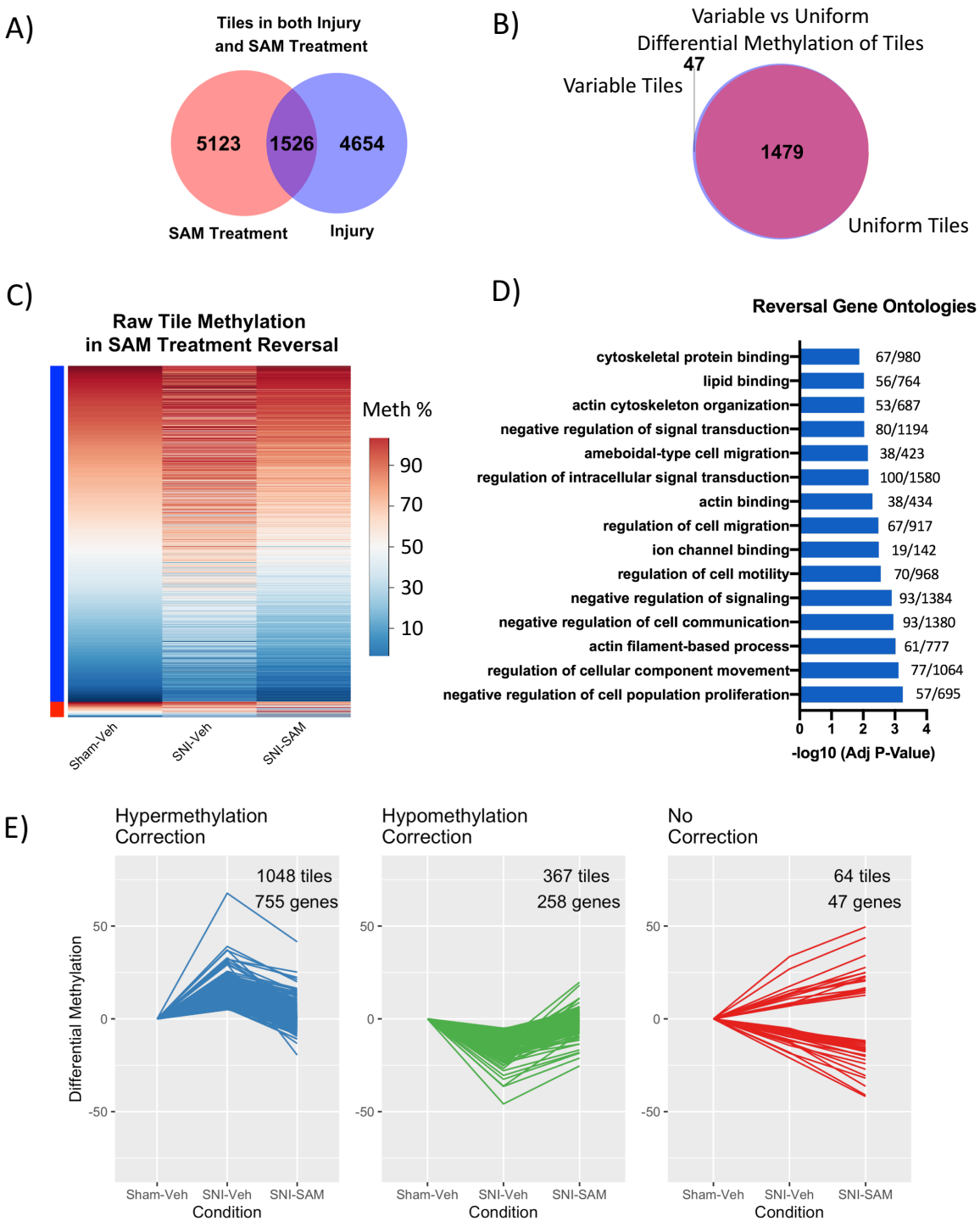
[**Figure 2**: *Injury and SAM treatment induce strong changes in PFC DNA methylation across multiple functional pathways and pain-related genes*. The magnitude and statistical significance of promoter region tile differential methylation during A) Injury and B) SAM treatment of Injury. Tiles are displayed in terms of positive or negative methylation

difference with control as the reference point compared to experimental, against –log10(adjusted p-value). Blue horizontal dashed line indicates an adjusted p-value threshold of 0.1, red horizontal dashed line indicates an adjusted p-value threshold of $1x10^{-7}$. The blue vertical dashed line indicates methylation difference thresholds of 5% and -5%. Red: hypermethylated; blue: hypomethylated; dark grey: non-significant but with methylation differences of > 5%; light grey: significant but with methylation differences of < 5%, black = not different. The top 15 enriched gene ontologies for differentially methylated genes in C) Injury and D) SAM treatment. Displayed ontologies are filtered for a maximum size of 2000 genes and are from Biological Processes or Molecular Function domains. Listed are the number of differentially methylated genes / total number of genes in each ontology E) Differential methylation of 24 pain genes of interest where displayed differential methylation is the average of all identified tiles per gene. Hypermethylated pain genes are displayed in red, hypomethylated genes are displayed in blue. Pain genes have been previously identified by either Ultsch et al. 2013 [271] or the Human Pain Genes Database [272]. Sham-Vehicle: n = 3, SNI-Vehicle: n = 4, SNI-SAM: n = 4.]

3.2 SAM treatment is associated with a reversal of SNI-induced differential methylation

To further understand the effect of SAM on injury-driven changes in DNA methylation, we identified 1526 tile regions that experience differential methylation in both injury effect and SAM treatment comparisons (**Figure 3A**). Of these 1526 tiles, 1479 tiles (representing 1030 genes) had uniform differential methylation when annotated to their gene, while 47 tiles (15 genes) had variable differential methylation (**Figure 3B**). After

isolating tiles that were uniformly differentially methylated, we found 1415 tiles (1030 genes) where injury-induced changes in DNA methylation were reversed by SAM treatment, while 64 tiles (47 genes) experiencing no reversal post SAM-treatment (**Figure 3C**). Of the 1451 reversing tiles, 1048 tiles (755 genes) are initially hypermethylated during the injury, and experience hypomethylation during SAM treatment, while 367 tiles (258 genes) are hypomethylated during injury and hypermethylated during SAM treatment (**Figure 3E**). Gene ontology analysis revealed that promoter regions that undergo a reversal after SAM treatment are enriched in domains of cell migration, cell signalling and communication, and actin cytoskeleton structure (**Figure 3D**). Promoter regions that did not reverse after SAM treatment did not associate with any gene ontology.



[**Figure 3:** *SAM Treatment is associated with the reversal of chronic pain induced DNA methylation*. A) 1526 tiles are differentially methylated in both Injury and SAM Treatment. B) Of those 1526 tiles, 1479 are uniformly differentially methylated where all tiles

associated to a single gene are all hypermethylated or hypomethylated. 47 tiles show variable differential methylation. C) 1415 tiles show a reversal in differential methylation from Injury (Sham-Veh vs SNI-Veh) to SAM Treatment (SNI-Veh to SNI-SAM), and 64 tiles experiencing no reversal. Side Column: Blue = reversal, red = no reversal. D) Top 15 gene ontologies associated with reversing genes. Displayed ontologies are filtered for a maximum size of 2000 genes and are from Biological Processes or Molecular Function domains. Listed are the number of differentially methylated genes / total number of genes in each ontology. E) Reversing tiles are predominantly hypermethylated by injury and then hypomethylated by SAM. Sham-Vehicle: n = 3, SNI-Vehicle: n = 4, SNI-SAM: n = 4. SAM: s-adenosyl methionine; DM: Differential methylation.]

3.3 SAM Treatment corrects SNI-induced differential methylation at key junctures in the Ras signalling pathway

The enriched gene ontologies that were influenced by nerve injury and reversed by SAM were predominantly in domains of cellular signal transduction, cell motility and locomotion, cytoskeletal and actin organization, and tissue development. The Ras signalling pathway (KEGG 04014) is involved in many of these domains, and key hubs were reversed of differential methylation after SAM treatment (**Figure 4A**). We detected 77 genes in the Ras signalling pathway that were differentially methylated in either Injury or the SAM treatment, which act on 39 different nodes in the Ras signalling pathway (**Figure 4B**). 12 nodes in the pathway display a reversal of differential methylation as a result of SAM treatment, including the key hub node of Ras and transduction nodes RhoA,

RIN1, and Ral. A single node can represent a number of genes which have the same or similar function within the pathway.

The classical transduction pathway for Ras signalling is for extracellular ligands such as growth factors (GF) to activate receptor linked tyrosine kinases (RTK). Activation of RTKs lead to binding of docking proteins such as Grb2 and SOS, and subsequent downstream activation of Ras proteins through GTP exchange. Ras proteins function as molecular switches for numerous downstream processes such as cell proliferation, differentiation, adhesion and migration, as well as regulating actin cytoskeletal structure. Our data shows differential methylation across the three major aspects of this pathway: extracellular signal transduction, Ras and Ras-related guanine exchange factors (GEF) and GTPase activating proteins (GAP), and downstream effectors.

At the level of extracellular transduction, we identified 18 different GFs and 12 different RTKs that undergo differential methylation either after injury or SAM treatment, with 5 GFs and 5 RTKs experiencing a SAM associated correction of injury differential methylation. GFs and RTKs were predominantly hypermethylated in injury and hypomethylated in SAM treatment, with a few exceptions (*Fgf15, Fgf2, Fgf22, Igf2, Fgfr4, Pdgfrb*) (**Figure 4C**). The downstream effectors of RTKs, *Grb2* and *SOS1*, were hypermethylated in injury and hypomethylated in SAM treatment respectively.

We identified three separate Ras genes which undergo differential methylation, *MRas, HRas*, and *RRas2*. *MRas* is hypermethylated in injury, and hypomethylated in SAM treatment (**Figure 4C**), while *HRas* and *RRas2* are only hypermethylated in injury or hypomethylated in SAM treatment respectively. Ras proteins are activated by GEFs,

which replace Ras-bound GDP with GTP, and inactivated by GAPs, which activates Ras GTPase activity and returns Ras to an inactive Ras-GDP state. We identified 2 differentially methylated RasGEFs, *Rasgrf1* and *Rasgrp2*, which are hypomethylated and hypermethylated respectively, both in the SAM treatment condition. We also identified a differentially methylated RasGAP, *Rasa1*, which is hypermethylated after injury.

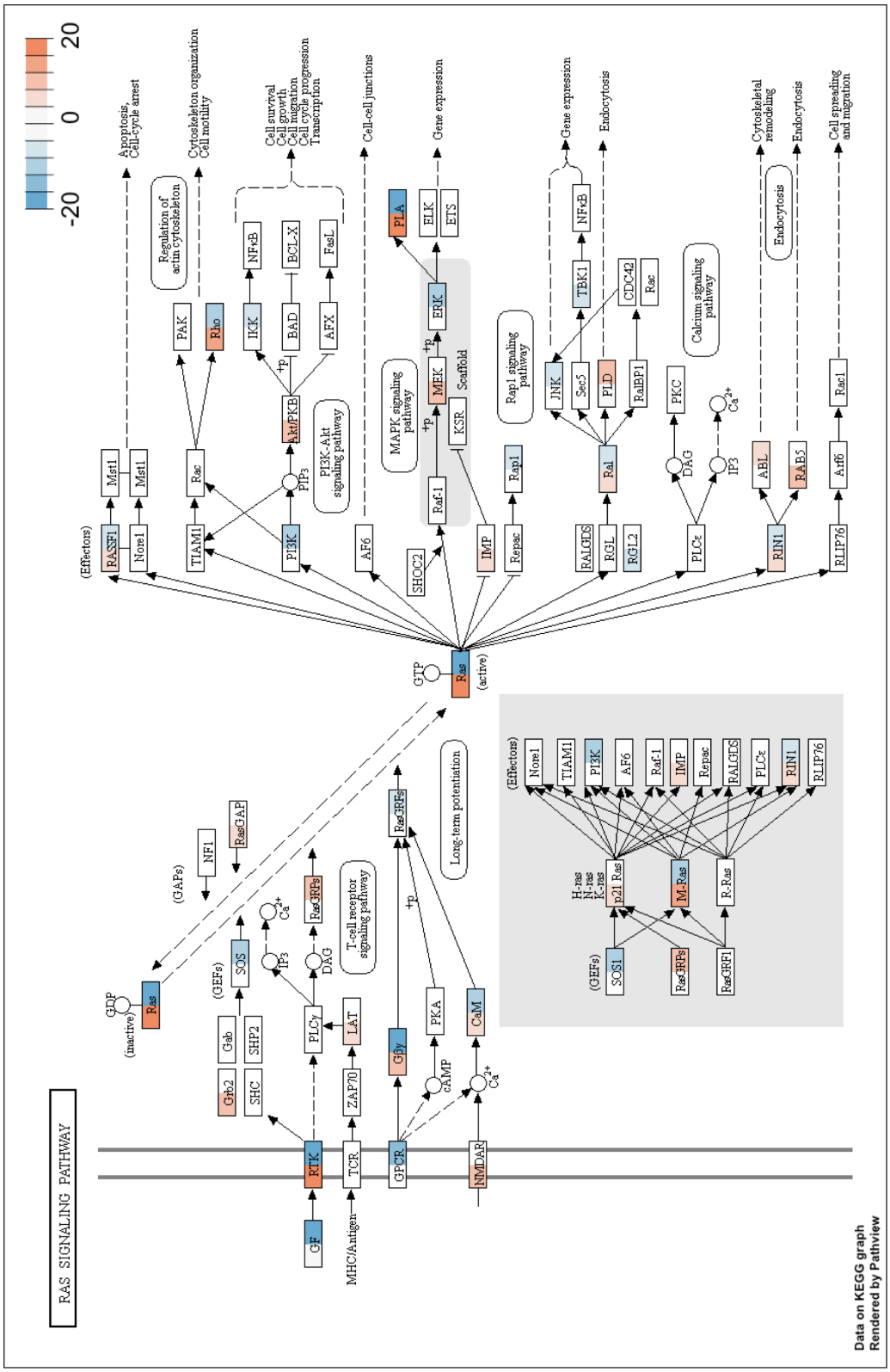
Ras proteins activate numerous effectors such as TIAM1, Rin1, Rgl, PI3K, Repac, and Raf-1 which in turn regulate downstream processes or cellular functions. A number of these effectors or their downstream targets were differentially methylated after injury or SAM treatment. Ras affects the MAPK/ERK signalling pathway, a major regulator of gene expression, through Raf-1 activity and both MEK gene *Map2k1* and ERK gene *Mapk3*, are hypermethylated after injury and hypomethylated after SAM treatment respectively. Other differentially methylated effectors or downstream targets involved in gene expression regulation include Ral gene *Ralb*, JNK gene *Mapk9,* and *Tbk1*.

Processes of cytoskeleton remodeling and cell motility are mediated through *Rin1* and TIAM1 / Rac in the Ras signalling pathway, with differential methylation of *Rin1,* and downstream Rho-related gene *4930544G11Rik* detected (**Figure 4C**). Other differentially methylated cytoskeletal structure or cell motility genes not shown include mDia gene *Diaph1,* myosin light chain genes *Myl2, Myl9, Myl10,* gelsolin genes *Gsn* and *Scin,* and ERM genes *Ezr* and *Rdx*.

Finally, Ras can affect the PI3K-AKT-mTOR signaling pathway, responsible for cell cycle regulation and proliferation. The PI3K gene *Pik3r2* and AKT gene *Akt1* are both

differentially methylated in the Ras signalling pathway, as well as non-Ras pathway PI3K genes *Pik3cg* and *Pik3r5*. Downstream of AKT, CREB genes *Atf6b, Creb1,* and *Creb5* are all hypomethylated after SAM treatment, while CREB gene *Creb3l4* is hypermethylated after injury. The mTOR signalling pathway is also affected, with Raptor gene *Rptor,* and Raptor stabilizing complex genes *Tel2* and *Tti1* showing injury related hypermethylation and SAM treatment related hypomethylation. Interestingly, Deptor gene *Deptor* is hypomethylated in both conditions. Downstream of mTOR activity, protein synthesis related genes *Eif4ebp1*, *Eif4e*, *Rps6kb2,* and *Eif4b* are all hypomethylated after SAM treatment, with only *Eif4b* showing injury related hypermethylation.

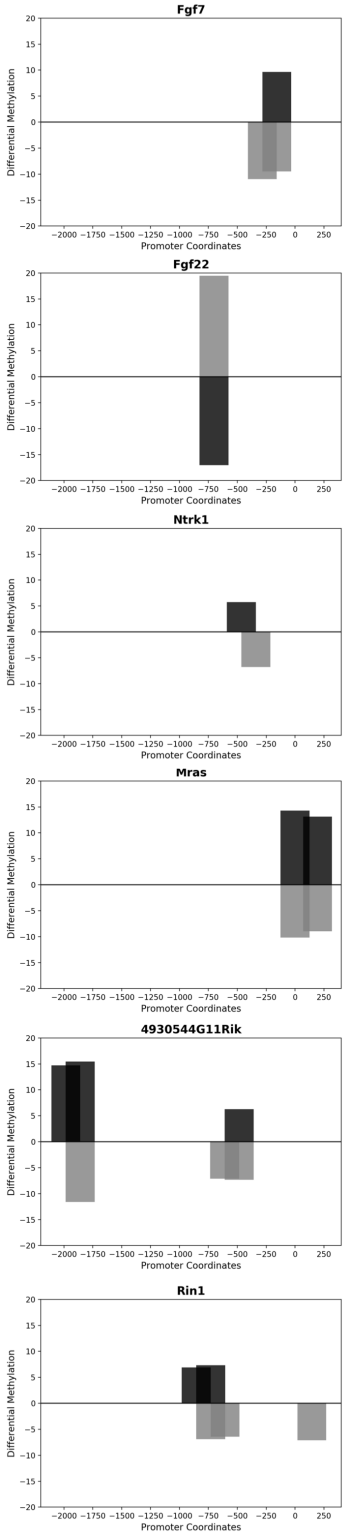
A)


RAS SIGNALING PATHWAY
-20
0
20
Data on KEGG graph
Rendered by Pathview

B)

KEGG Node	Gene	Injury DM	SAM Treatment DM
AKT/PKB	Akt1	11.89	NA
GF	Angpt4	NA	-8.73
	Csf1	9.81	-10.54
	Efna4	NA	9.95
	Egf	16.05	NA
	Fgf15	-5.73	NA
	Fgf17	7.94	-7.65
	Fgf2	-19.76	NA
	Fgf22	-17.02	19.46
	Fgf7	9.62	-10.23
	Fgf8	NA	-6.02
	Igf1	NA	-10.71
	Igf2	-6.79	NA
	Ntf3	5.29	-9.58
	Pdgfa	NA	-5.4
	Pdgfb	NA	11.07
	Pdgfc	NA	-8.81
	Pgf	NA	-6.38
	Vegfa	NA	-9.77
CaM	Calml4	7.45	-9.32
RTK	Egfr	NA	-9.08
	Fgfr1	5.32	-11.38
	Fgfr2	NA	8.74
	Fgfr3	13.14	-11.94
	Fgfr4	-11.49	NA
	Flt1	8.61	-8.81
	Flt3	NA	-6.41
	Kit	7.08	-7.5
	Ntrk1	5.75	-6.81
	Ntrk2	5.01	NA
	Pdgfrb	-8.62	NA
	Tek	NA	-10.67
NMDAR	Grin2b	8.81	NA
Ras/p21 Ras	Hras	7.82	NA
Ras/p21 Ras	Rras2	NA	-6.55
MEK	Map2k1	9.27	NA
ERK	Mapk3	NA	-9.68
Mras	Mras	13.73	-9.55
PI3K	Pik3r2	NA	-8.85
PLA	Pla1a	7.67	NA
	Pla2g12a	6.08	NA
	Pla2g1b	NA	11.88
	Pla2g2a	6.44	NA
	Pla2g2c	NA	-8.62
	Pla2g2e	-8.01	NA
	Pla2g2f	-11.27	-10.49
	Pla2g4b	8.36	-9.31
	Pla2g4d	28.2	-12.35
	Pla2g5	NA	-10.21
Ral	Ralb	5.2	-5.84
RasGAPs	Rasa1	7.91	NA
RasGRFs	Rasgrf2	NA	-5.87
RasGRPs	Rasgrp2	NA	9.94
Rho	4930544G11Rik	12.14	-8.69
RIN1	Rin1	7.12	-6.82

C)



[**Figure 4**: *SAM Treatment reverses Injury-induced differential methylation at crucial hubs in the Ras signalling pathway.* A) The Ras signalling pathway experiences differential methylation at multiple nodes. Left side: Injury, Right side: SAM Treatment. Scale bar: differential methylation. B) Nodes within the Ras signaling pathway can be expressed by multiple related genes. C) Location of differentially methylated regions within genes of interest. Black: Injury, grey: SAM treatment. SAM: s-adenosyl methionine. Pathway was rendered using Pathview [321]]

4. Discussion

We have previously demonstrated that SAM chronic treatment attenuates nerve injury-related mechanical sensitivity as well as injury-related cognitive deficit [234]. Given the difficulty of developing novel therapies against chronic pain, we explored the mechanisms underlying SAM-related attenuation to identify potential avenues of treatment. Our current study supports SAM's ability to reverse chronic pain-induced changes in PFC DNA methylation and examines those effects at the level of individual genes and gene pathways.

First, we confirmed previous findings of differential PFC methylation many months following nerve injury [22, 200, 313] and differential methylation in response to chronic systemic SAM administration [234]. We identified over 3500 differentially methylated genes after either injury or SAM treatment, indicating that both states are capable of inducing widespread PFC methylation changes. Second, we showed the reversal of injury-related differential methylation after SAM treatment concurrent with pain

attenuation. This is consistent with work from other domains where reduction of a disease state with treatment is capable of reversing methylation patterns [322, 323]. Finally, we found that these reversals occurred at a number of key junctures in the Ras signalling pathway. These reversals reflect a substantial reorganization of cellular functioning during injury and SAM treatment, and potentially influencing LTP and other pain-related functions. These changes and subsequent reversals of DNA methylation in pain relevant domains support the potential of targeting of epigenetic mechanisms to treat and alleviate chronic pain.

4.1 PFC Methylation Response to Injury and SAM

Both neuropathic pain and SAM treatment are capable of inducing widespread and highly significant changes in PFC methylation, with each condition inducing differential methylation in nearly 17% of the ~22,500 genes examined. We observed regions with differential methylation of up to 40% and an adjusted p-value of less than $1x10^{-7}$. In comparison, human fetal brain methylation during development changes by up to 80% per year while methylation change as a result of aging changes by 1% per year as a child or 0.01% as an adult [324]. These widespread changes demonstrate not only the global impact of chronic pain but also the responsivity of the PFC methylome to environmental states.

At 7 months post-injury, we observed a slight trend towards hypermethylation when comparing between Sham-Vehicle and SNI-Vehicle groups. This is consistent with previous observations of PFC hypermethylation during chronic pain at multiple time points

after SNI [313], or 3 weeks after spinal nerve ligation [236]. Injury induced hypermethylation would imply increased gene repression in response to injury. Indeed, in studies of PFC mRNA expression after injury, Alvarado et al. 2013 found decreases in mRNA expression in mouse PFC six months after SNI (278 upregulated genes to 367 downregulated genes)[22], and Descalzi et al. 2017 found similar results 2.5 months after SNI in mouse medial PFC (179 upregulated to 204 downregulated genes). This consistent trend across studies may indicate the promotion of hypermethylation in chronic pain, potential mechanisms include an increase of aging related methylation [325, 326]. While a hypermethylation trend may reveal how DNA methylation responds during chronic pain, both hypermethylated and hypomethylated genes must be considered when identifying disrupted functions.

We observed a trend towards hypomethylation following SAM treatment of SNI animals. This result is surprising, as SAM is the primary methyl donating substrate for DNA methyltransferases (DNMTs) and would therefore be expected to increase methylation. Indeed, we previously established that chronic administration of SAM significantly increases global methylation in PFC post-injury [234]. There are a number of explanations why systemic SAM treatment would decrease methylation in promoters while increasing global methylation. SAM is not only a methyl donor to DNMTs but is the primary methyl donor to most methyltransferase enzymes such as histone methyltransferases or catechol-O-methyltransferase [327-330]. Histone methylation at different histone tail positions can recruit chromatin modifying complexes and result in either open or closed chromatin conformation and corresponding changes in DNA

methylation [215]. Therefore increases in SAM availability could lead to altered histone methylation patterns with increased H3K4 or H3K36 methylation associated with open chromatin and hypomethylation and increased H3K9 or H3K27 methylation leading to closed chromatin and hypermethylation [215, 331]. Moreover, the SAM metabolite s-adenosylhomocysteine (SAH) is an inhibitor of most methyltransferases [332, 333], therefore increased administration of SAM may lead to an accumulation of SAH.

4.2 Differentially Methylated Functional Domains in Injury and SAM

Following nerve injury, differentially methylated genes are enriched for domains of intracellular signalling, cell motility and locomotion, cellular adhesion, and cytoskeletal formation. These domains confirm previous observations of differentially methylated functions in PFC after neuropathic injury [200, 313]. Following SAM treatment, differentially methylated genes are enriched in similar functional domains observed in injury, primarily those related to locomotion and cell motility, intracellular signalling and signal transduction, and cell adhesion. SAM treatment was also enriched for differentially methylated genes involved in tissue development, and cellular export. These enriched domains indicate different potential mechanisms involved in late-stage chronic pain and SAM treatment reversal.

The presence of similar differentially methylated functional domains following both injury and SAM treatment imply that similar mechanisms are involved in late stage chronic pain maintenance and recovery. In injury, 60-65% of differentially methylated genes within each ontology are hypermethylated, whereas in SAM treatment, 75-80% of differentially

methylated genes are hypomethylated. Thus functional pathways in injury may be slightly repressed overall. However it is important to consider what stage of a functional pathway is differentially methylated. For example, if the hypermethylated genes are concentrated in branches of the pathway that are largely inhibitory, then overall pathway activity would be potentiated. Similarly, while functional pathways are more disposed towards hypomethylation following SAM treatment, we cannot conclude the impact on overall activity of a pathway without considering the function of the individual genes.

4.3 Differential Methylation of the Ras Signalling Pathway

Intracellular signalling pathways are involved in a multitude of functions in chronic pain, however we examined the Ras signalling pathway in detail. The Ras-MAP kinase (MAPK) signalling pathway undergoes significant differential methylation following both injury and SAM treatment. Differential methylation of the Ras-signalling protein MRas, and MAP kinases MEK and ERK could potentially affect protein translation regulation [334]. Differential methylation of Rin1 and Rho family member 4930544G11Rik could affect actin cytoskeletal organization, cell migration, and synaptic plasticity [335-337]. Neuronal MAPK activity via the ERK1/2 branch in primary nociceptive afferents and spinal dorsal horn is required for the induction and maintenance of both peripheral and central sensitization [338, 339]. Astrocyte and microglial MAPK activity in the ERK1/2, p38, and JNK branches have also been observed in spinal cord after the onset of chronic pain [340-343]. In neurons, MAPK activity via Ras-ERK1/2 is necessary for the insertion of AMPA-R subunits during long term potentiation (LTP) [344]. Supraspinal MAPK pathway activation is also noted in amygdala, anterior cingulate cortex, and PFC after peripheral

injury [345-347], with neuronal phospho-ERK1/2 upregulation specifically noted in medial PFC [348].

4.4 PFC Methylation Reversal after SAM Treatment

Changes in DNA methylation in response to external stimuli are well established, and a number of studies have previously reported reversals in disease or condition related DNA methylation after successful treatment [322, 323, 349]. We are the first study to investigate epigenome-wide reversals in chronic pain DNA methylation after effective attenuation of pain. We demonstrate that an intervention which attenuates mechanical hypersensitivity after onset of neuropathic pain also induces the reversal of injury-driven changes in DNA methylation at hundreds of gene promoters. After identifying differentially methylated tiles that were present in both Injury and SAM treatment analyses, nearly all (1415/1479) tiles displayed a reversal in differential methylation. This is an incredible finding as it represents over 1000 genes changing towards an uninjured methylation status after a successful intervention. Proportionally, it represents ~5% of the mouse genome or ~25% of genes that were differentially methylated post-injury. These may be a critical subset of genes responsible for mediating chronic pain's impact upon the brain. Indeed, these genes are enriched in domains of intracellular signalling, actin and cytoskeletal structure, cell migration, and ion channel binding, which have been proposed to underlie chronic pain related decreases in grey matter and subsequent recovery after treatment in humans [118, 298, 350].

In this study, promoter methylation was typically increased by injury and decreased after treatment. However, SAM treatment in SNI animals typically did not fully reverse DNA methylation to levels matching those observed in control uninjured, vehicle-treated mice. Thus, while SAM treatment is capable of attenuating pain-related differential methylation, it was generally not sufficient to return the animals to the equivalent of a non-chronic pain state.

4.5 Limitations

When considering this study, a number of limitations must be considered. First, our results are exploratory. As a result, the group size of 3-4 animals is low and we selected a permissive adjusted p-value of 0.1 in order to reduce the likelihood of false negatives. Second, our study focused on promoter region methylation; methylation at distal enhancers and within the gene body is also known to play a role in regulating gene transcription [183, 295, 351]. While promoter region methylation is a dominant mechanism of DNA methylation regulation, there are a number of other mechanisms that influence gene transcription, translation, and ultimately expression. Third, the chronic systemic administration of SAM may affect the sensation of chronic pain via mechanisms unrelated to DNA methylation. As stated above, SAM also is a methyl donor for histone methyltransferases and COMT, which both have well-established impacts upon pain sensation. Fourth, our study contained males only therefore our conclusions do not account for sex differences in response to chronic pain. However, we recognize these limitations and believe our results provide an important first look into the plasticity of PFC DNA methylation after successful treatment for chronic pain.

5. Conclusions

Our findings provide first evidence for epigenome-wide reversal of pain-induced differential DNA methylation after treatment in an animal model of chronic pain. These changes primarily occurred in domains of intracellular signaling, cell motility and locomotion, and cytoskeletal structure, reflecting potential changes in translational control, astrocyte and microglial activity, and synaptic pruning and formation. DNA methylation has a clear relationship with chronic pain and may contribute to the cortical recovery observed after therapeutic interventions. These findings provide a crucial insight to the effect of chronic pain on the prefrontal cortex, and potentially reveals mechanisms of how the brain is able to recover.

Supplemental Figures

Supplemental Table 1 – Probe Bed File. Genomic coordinates for the bisulfite capture-sequencing probes

See Appendix 1 of Thesis

Supplemental Table 2 – Blacklist Bed File. Genomic coordinates for regions known to have anomalous, unstructured, and high signal/read counts in next gen sequencing

See Appendix 2 of Thesis

Chapter 4: DNA Methylation Response to Exercise Treatment of Chronic Pain

5.1. Preface

Exercise is a frequently recommended prescription for the relief of chronic pain, and in recent years non-pharmacological interventions have become increasingly recommended in lieu of pharmacological treatments when addressing chronic pain. Exercise effectively reduces pain sensitivity and improves cognitive functioning and PFC health. In particular, exercise can induce increases in brain volume in both healthy individuals and those suffering from chronic illnesses. Moreover, exercise also impacts DNA methylation in the brain. The previous manuscripts and other research has established the correlation between the development and treatment of chronic pain and altered PFC DNA methylation. However, it is unknown what effect treating chronic pain with a non-pharmacological exercise intervention will have upon PFC DNA methylation. Examining PFC DNA methylation in response to a non-pharmacological exercise intervention will broaden our understanding of the relationship between PFC DNA methylation and chronic pain, and clarify the potential of DNA methylation as a therapeutic target.

In this study, we hypothesized that access to voluntary running exercise would attenuate neuropathic pain in a mouse model, and counteract or reverse chronic pain associated changes in PFC DNA methylation.

5.2. Manuscript III:

Voluntary exercise attenuates chronic neuropathic pain and reverses nerve injury-induced modifications in DNA methylation in mouse frontal cortex.

Authors:

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Abstract:

Exercise is a commonly prescribed non-pharmacological intervention for chronic pain with demonstrated benefits in reducing pain and improving quality of life. Chronic pain is associated with reversible changes in cortical thickness and altered epigenetic regulation; exercise has been shown to impact both of these phenomena. We hypothesized that therapeutic exercise attenuates pain-related epigenetic modifications in the brain. To explore the epigenetic response to exercise in chronic pain, we provided voluntary access to home cage running wheels for 4 months, eight months after induction of neuropathic pain via Spared Nerve Injury (SNI) in male mice. Home cage running wheel exposure attenuated SNI-induced mechanical sensitivity. Epigenome-wide analysis of DNA methylation in prefrontal cortex (PFC) was employed to identify PFC epigenetic response and underlying mechanisms. Over 5000 differentially methylated regions were detected following both SNI and exercise intervention, representing nearly 4000 unique genes in each. Differentially methylated genes following both SNI and exercise intervention were significantly enriched in gene ontologies for ion transport and homeostasis, cell adhesion, and locomotion. SNI also resulted in enrichment for domains in cell death and actin cytoskeleton, while exercise also resulted in enrichment for domains in immune function and morphogenesis. 1199 differentially methylated regions, representing 856 genes, reversed their chronic pain-induced differential methylation as a result of voluntary running. These reversing genes were enriched in domains of vascular endothelial growth factor signalling, biological adhesion, and tissue development. We also found over 150 differentially methylated genes in SNI mice with known pain-related

functions, many of which were reversed by exercise. We demonstrate the effectiveness of a non-pharmacological intervention against chronic pain that reduced mechanical hypersensitivity and reversed many pain-driven changes in DNA methylation. These results underscore the role of DNA methylation in maintaining chronic pain and highlight underlying mechanisms and potential novel therapies to successful pain treatment.

1. Introduction

Exercise is a central component of many treatment plans for chronic pain, and is frequently recommended in advance of pharmacological interventions [137, 352]. Exercise can be effective against a number of chronic pain conditions, yielding effective reductions in pain sensitivity [136, 353-355]. Exercise also improves a number of chronic pain comorbidities such as physical functioning and conditioning [356-358], sleep and fatigue [359, 360], and mood disorders [361-363]. Importantly these benefits persist long after exercise has been stopped, providing long-term relief of symptoms, positive reinforcement to improve compliance, and a continuing method for individuals to manage their symptoms outside of clinical care [141, 364, 365].

Given the benefits, understanding the mechanisms of exercise-based treatments on chronic pain is crucial. In healthy individuals, exercise improves cognitive functioning and prefrontal cortex (PFC) health [366-369], two areas that are adversely affected by chronic pain. During chronic pain, the PFC undergoes a number of structural and anatomical changes that result in the loss of grey matter and cortical thickness, reorganization of synaptic connections, and changes in gene expression [21-23, 100, 104]. A number of human and animal studies have demonstrated the loss of PFC grey matter across different pain models and conditions [15-20, 82]. Interestingly, treatments that attenuate pain are capable of reversing this loss [24-26, 86, 115]. Chronic pain also affects PFC gene expression with transcriptome-wide changes in mRNA expression level detected in long-term neuropathic pain [22, 23]. The plasticity and reversibility of these

changes is not only encouraging with regard to effectively treating chronic pain, but suggests the involvement of epigenetic mechanisms.

Epigenetic regulation is a mechanism by which gene expression can be stably but flexibly controlled without modifying the underlying genetic sequence. The process of DNA methylation involves the covalent addition of a methyl residue to cytosine nucleotides. When it occurs in the promoter region of a gene, it commonly results in repression of gene expression via interference with general and specific transcription factors [243, 244]. Chronic pain development is associated with PFC DNA methylation changes in animal models of chronic pain [22, 200, 234, 313]. Studies examining promoter region DNA methylation found gene-specific changes in DNA methylation, which correlated to mRNA transcript levels [200], and that these changes showed dynamic patterns of regulation up to one year post-injury [313]. Moreover, successful attenuation of pain was found to reduce global PFC DNA methylation levels in the PFC [22, 234].

Given this profile of structural and functional changes, loss of PFC grey matter, and changes in gene expression and epigenetic regulatory pathways, aerobic exercise is particularly interesting as it impacts these mechanisms. Aerobic exercise induces increases in brain volume correlated to the level of physical fitness in both healthy individuals and patients suffering from chronic illnesses [370-373]. Aerobic exercise also impacts epigenetic regulation of the brain, causing differential DNA methylation and histone modification [374-377]. However, there has yet to be research on the response

of PFC DNA methylation to an aerobic exercise therapy provided in treatment of a long-term chronic pain.

To explore the impact of exercise upon long-term chronic pain, we provided aerobic intervention eight months after neuropathic injury and collected genome-wide PFC DNA methylation after four months. First, exercise intervention significantly reduced mechanical hypersensitivity when provided 8 months post-injury. Second, our results demonstrate corresponding strong and robust changes in PFC DNA methylation with 5251 differentially methylated regions in SNI and 6247 differentially methylated regions after exercise intervention. Differentially methylated genes in SNI mice were enriched in domains of Ion transport and homeostasis, cell adhesion, and locomotion and motility, while differentially methylated genes after Exercise Intervention were enriched in domains of ion transport and homeostasis, locomotion and motility, immune response, and morphogenesis. Finally, the exercise intervention induced the reversal of chronic pain related differential methylation of 1241 regions.

2. Materials and Methods

2.1 Animals

Male CD-1 mice (Charles River Laboratories, St-Constant, QC, Canada) were used in this study. Animals were received at 6-8 weeks of age and housed 3-4 per cage on a 12h light/dark cycle in a temperature controlled room in ventilated polycarbonate cages (Allentown, Allentown, NJ) with corncob bedding (7097, Teklad Corncob Bedding,

Envigo, UK) and cotton nesting squares for enrichment. Mice were given access to food (2092X Global Soy Protein-Free Extruded Rodent Diet, Irradiated) and water *ad libitum*. Animals were habituated to the housing conditions for at least one week prior to any experimental interventions.

All experiments were approved by the Animal Care Committee at McGill University, and conformed to the ethical guidelines of the Canadian Council on Animal Care and the guidelines of the Committee for Research and Ethical Issues of the International Association for the Study of Pain [253].

2.2 Neuropathic pain model: Spared Nerve Injury

Animals were randomly assigned to receive either spared nerve injury (SNI) or sham surgery. Nerve injury was induced using the Spared Nerve Injury model of neuropathic pain, as adapted for mice [254, 255] at 6 to 8 weeks of age. Under deep isoflurane anesthesia, an incision was made on the medial surface of the thigh, exposing the three branches of the sciatic nerve. SNI surgery consisted of ligation and transection of the left tibial and common peroneal branches of the sciatic nerve, while sparing the sural nerve. The tibial and common peroneal branches were tightly ligated with 4:0 silk (Ethicon) and sectioned distal to the ligation. Sham surgery consisted of exposing the nerve without damaging it.

2.3 Exercise Intervention: Running Wheels

Eight months after SNI or sham surgery, animals were randomly assigned to receive exercise intervention or control. Exercise intervention was provided for 4 months.

Exercise intervention consisted of a running wheel placed in the home cage which could be accessed *ad libitum*. The wheels consisted of a spinning saucer-like wheel mounted on a dome shaped hut for nesting (InnoDome™ and InnoWheel™, Bio-Serv, Flemington, NJ). Control animals received the same running wheel and hut but with a screw placed to prevent the wheel from spinning. Group sizes: Sham-Sedentary: n = 8, Sham-Running: n =17, SNI-Sedentary: n = 9, SNI-Sedentary: n = 9.

2.4 Behavioural assessment of mechanical sensitivity

Behavioral assessments were performed 8 months after SNI or sham surgery to acquire a baseline of neuropathic pain, and then animals were reassessed every month for the 4 months of intervention. After a 1 hour habituation period to the testing apparatus, von Frey filaments (Stoelting Co, Wood Dale, IL) were applied to the plantar surface of the hind paw until filaments were bent for either 3 seconds or hind paw withdrawal. Mechanical sensitivity was determined as the 50% withdrawal threshold using the up-down method [256]. The stimulus intensity ranged from 0.04 to 4.0 g, corresponding to filament numbers 2.44 to 4.56. The experimenter was blind to treatment group.

2.5 Isolation of prefrontal cortex, DNA capture, and bisulfite sequencing

Following completion of SAM treatment, mouse PFC was dissected following isoflurane anesthesia and decapitation. DNA methylation analysis group sizes: Sham-Sedentary: n = 4, Sham-Running: n = 3, SNI-Sedentary: n = 6, SNI-Running: n = 6. PFC was defined as a region with an anterior boundary of the frontal pole, approximately +3.00 Bregma, posterior boundary of approximately +1.00 Bregma, lateral boundaries of +1 mm from midline, and a ventral boundary wherein the olfactory bulb, caudate putamen, and

areas below the rhinal fissure and lateral ventricles were all removed [257]. This defined area isolates the prelimbic, orbital, and infralimbic cortices corresponding to the mouse medial PFC. Once dissected, tissue was homogenized and genomic DNA was extracted using the Qiagen DNeasy Blood and Tissue kit and protocol.

Genome-wide methylation analysis was performed using the Roche SeqCap Epi Developer M Enrichment system on bisulfite-treated DNA (Roche Nimblegen; WI, USA), with custom designed primers targeting promoter and enhancer regions of the genome. Probe design was based on the mm9 reference genome and associated H3K4me1 and H3K4me3 binding (probe BED file available in **Supplemental Table 1**). Briefly, 1 μg of genomic DNA per sample was fragmented into 200bp lengths, and adapter and index sequences were ligated to each end of the fragment according to the KAPA Library Preparation Kit protocol. Sample DNA was then bisulfite converted following the EZ DNA Methylation-Lightning Kit (Zymo Research; CA, USA). Sample DNA was then PCR amplified, hybridized with custom capture probes, and PCR amplified again in accordance with Roche SeqCap Epi system protocols [259]. Sample captured bisulfite-converted DNA sequencing was performed by Genome Quebec on the Illumina HiSeq 2500 following Illumina guidelines. Paired-end sequencing reads of 125bp in length were generated.

2.6 DNA methylation pre-processing

Capture sequencing data was pre-processed using the McGill University Genome Quebec Innovation Centre GenPipes Methyl-Seq Pipeline [260]. The pipeline proceeds through Trimmomatic, Bismark Align, Picard Deduplication, and Bismark Methylation Call

[261, 262]. Baseline pipeline parameters were set as a minimum sequence quality of PHRED score > 30, alignment reference genome was mm10 (GRCm38), and minimum read coverage per base was set at 10 reads. A detailed outline of the Methyl-Seq pipeline steps and process can be found at https://bitbucket.org/mugqic/genpipes. Before analysis, collected sequence data was filtered to remove a blacklist of regions identified to have anomalous, unstructured, and high signal/read counts in next gen sequencing [263]. The blacklist used was specific for mm10 and the BED file can be found in **Supplemental Table 2.**

2.7 Differential methylation analysis

Differential methylation analysis was performed using R and the MethylKit package [317]. For a CpG site to pass through to analysis, it was required to be sequenced to a minimum depth of at least 10 reads in each sample. Coverage values between samples were normalized using a scaling factor derived from differences between the median of coverage distributions. Tiling windows were used to summarize methylation information over the genome. Tiles were set to be 250 base pairs (bp) in length and advance in 125 bp steps. Methylated and unmethylated cytosine counts within each tile are summed to provide an overall methylation proportion within the tile. Only CpGs that were annotated to a promoter region, defined as 2000 bp upstream or 200 bp downstream from the transcription start site, were selected for analysis. MethylKit uses logistic regression to model a log odds ratio based on methylation proportion within each tile. Calculated p-values are adjusted to q-values using the SLIM method [318].

Tiles were defined as being differentially methylated between groups if the adjusted p-value was less than < 0.1 and had a difference in methylation $> 5\%$. While the selection of an FDR threshold of 0.1 carries greater risk of type I error, false positive, than the more typical threshold of 0.05, it is preferable for the exploratory purposes of this study. Differentially methylated tiles can be further divided into hypermethylated or hypomethylated. In comparisons between groups, the control group acts as the reference point, i.e. Control: Sham-Vehicle, Experimental: SNI-Vehicle. Therefore, if the experimental group tile methylation is 5% or larger than the control, the tile is considered to be hypermethylated, and if the treatment tile methylation is reduced by -5% or more compared to control, the tile is considered to be hypomethylated.

Tiles were annotated to their associated genes and genomic regions using the annotatePeaks function of the ChIPseeker [265] R package, using a TxDb object created from the Gencode "mmusculus_gene_ensembl" Biomart database. Each tile position was annotated and tracked individually throughout the analysis. For homology conversion, gene symbols from non-mouse species were converted to known mouse homologs based on the Mouse Genome Database (MGD) – Vertebrate Homology, Mouse Genome Informatics, The Jackson Laboratory, Bar Harbor, Maine [266].

To simplify analysis of genes that undergo reversals in differential methylation after exercise intervention in SNI, we isolated genes for uniform differential methylation. Uniform differential methylation occurs when all tiles annotated to a single gene are uniformly hypermethylated or hypomethylated. Variable differential methylation occurs

when the tiles annotated to a single gene are both hypermethylated and hypomethylated tiles, and removed from reversal analysis.

2.8 Statistical analysis

Two-way repeated measures ANOVA with Bonferroni post-hoc test was used to detect group differences in mechanical sensitivity using the von Frey behavioural assay. Pairwise comparisons of tiles between experimental groups utilized logistic regression to model the log-odds ratio of methylation proportion per tile. Analyses were corrected for multiple comparisons using the SLIM method [318]. The hypergeometric test was used to test for significant enrichment of pain-related genes and for significant enrichment of gene ontology domains.

2.9 Gene ontology analysis

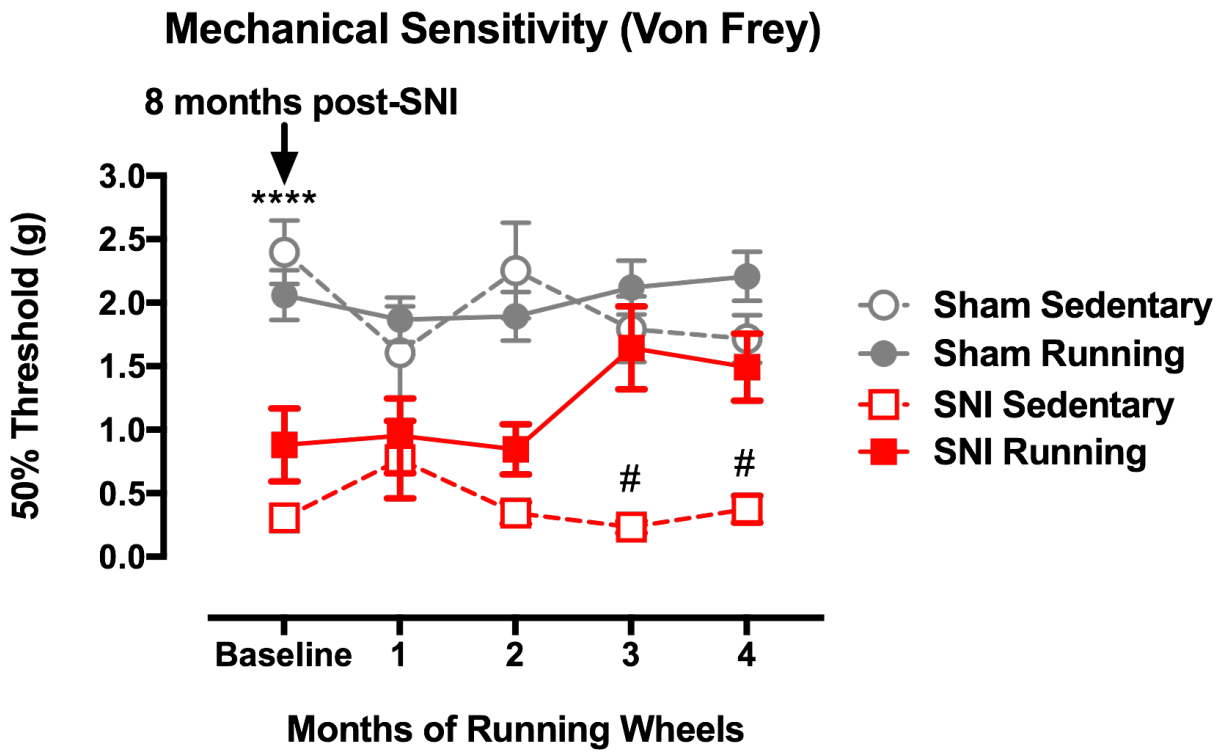
Differentially methylated genes identified were submitted to gProfiler [319], a web-based gene ontology tool. The GO Biological Processes and Molecular Function databases were selected as ontology databases. Ontology p-values were adjusted using the g:SCS correction for multiple comparisons [320] and an ontology was considered enriched at an adjusted p-value < 0.05. All analysed ontologies were limited to a maximum size of 2000 genes to increase function specificity. Term grouping was used to identify groups of ontologies by shared functional domains and areas using the following keywords or term names. Ions: *ions, cation, anion*; Immune: *immune, immuno-, cytokine, leukocyte, lymphocyte, bacteria, monocyte, T cell, B cell, defense, microglia, inflamm-*; Adhesion: *adhesion*; Locomotion: *locomot-, motil-, migration, -taxis*; Development and

Morphogenesis: *development, morphogenesis, -genesis, differentiation, generation, proliferation*; Cell Death: *death, apop-, necro-*; Actin Cytoskeleton: *actin, cytoskel-, supramolecular.*

3. Results

3.1 Spared Nerve Injury-induced mechanical sensitivity is attenuated by home cage running wheels.

We have previously demonstrated that SNI produces mechanical hypersensitivity at late stages of chronic pain [313]. At 8 months post-injury, animals that received SNI showed mechanical hypersensitivity in the ipsilateral hind paw compared to Sham animals (Two tailed Welch's t-test: Sham Animals (Sed + Run) vs SNI Animals (Sed + Run), $t_{39.34} = 7.04$, $p < 0.0001$) (**Figure 1**). At this time point, animals were provided with either running or control wheels. After three months, SNI and had access to running wheels reduced mechanical hypersensitivity compared to sedentary SNI mice (2-way repeated measures ANOVA, Bonferroni post-hoc: 3 month SNI-Run vs SNI-Sed, $t_{8.31} = 4.27$, $p = 0.014$; 4 month SNI-Run vs SNI-Sed, $t_{10.52} = 3.93$, $p = 0.015$). Therefore, long-term access to aerobic exercise can reduce neuropathic pain induced mechanical hypersensitivity.



[**Figure 1**: *Long-term access to home cage voluntary running wheels attenuates peripheral neuropathic pain*. 8 months post-SNI, *ad libitum* access to aerobic exercise in the form of running wheels can attenuate mechanical hypersensitivity after 3 months of exercise. Sham-Sedentary: n = 4, Sham-Running: n = 3, SNI-Sedentary: n = 6, SNI-Running: n = 6. # $p < 0.05$, SNI-Sed vs SNI-Run, 2-way repeated measures ANOVA with Bonferroni post-hoc test. **** $p < 0.0001$ Sham animals vs SNI animals, Two-tailed Welch's t-test. SNI: spared nerve injury]

3.2 Spared Nerve Injury and Exercise lead to extensive changes in PFC DNA methylation that affect multiple functional pathways

We have previously demonstrated changes in PFC promoter region methylation in response to SNI at multiple time points post-injury [313]. Here we examined global PFC promoter methylation post-injury and post-exercise to determine the effect of exercise on injury related changes in PFC promoter methylation.

Differentially methylated (DM) regions in the PFC were identified by bisulfite capture sequencing followed by comparison between Sham-Sedentary, SNI-Sedentary, and SNI-Running conditions. Tiles of 250 base pairs (bp) were used to subdivide the genome into analysis regions, followed by selection of tiles located within promoter regions of genes defined as -2000 to +200 from the transcription start site. Genes identified as differentially methylated underwent gene ontology analysis to identify affected functional pathways. We limited the discussed gene ontology size to a maximum of 2000 genes for better specificity of affected functions and pathways.

To observe the injury effect, SNI-Sedentary animals were compared against Sham-Sedentary animals 1 year post-injury and 4 months post-running wheels. We collected 203,354 tile regions covering 22,732 unique gene promoters. We identified 5251 differentially methylated tiles in total, with 2534 hypermethylated and 2717 hypomethylated, representing 1654 and 1798 unique genes respectively (**Figure 2A**). We detected a number of tiles that underwent robust differential methylation (adjusted p-value $< 1 \times 10^{-7}$ and absolute differential methylation > 10%): 56 hypermethylated tiles representing 37 unique genes, and 65 hypomethylated tiles representing 41 unique genes.

These robustly differentially methylated genes include interleukin 1 gene *Il1f8* (24.1% DM), toll-like receptor *Tlr6* (16.5% DM), and acid-sensing ion channel *Asic3* (-35.1% DM).

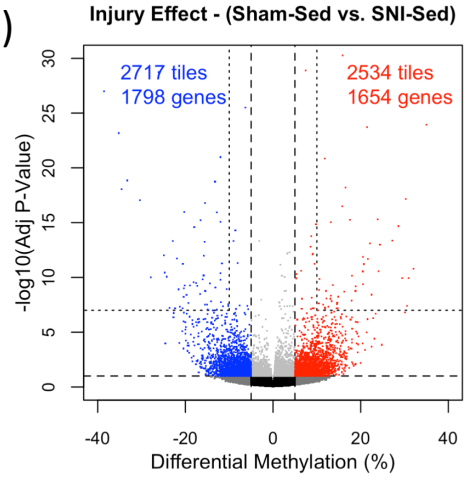
After submitting the identified differentially methylated genes to gProfiler, we identified 187 enriched gene ontologies in the domains of Biological Processes and Molecular Function. The top 15 enriched ontologies determined by adjusted p-value are involved in ion transport, cellular locomotion, cell morphogenesis, cell adhesion, and cytoskeletal structure (**Figure 2C**). Term grouping and hypergeometric testing was also used to identify functional domains were enriched by nerve injury. Gene ontologies related to ion transport, binding, and homeostasis were significantly enriched in Injury, with 44 related ontologies detected ($p = 3.56 \times 10^{-37}$). Other significantly enriched domains include locomotion and motility (15 ontologies detected, $p = 4.53 \times 10^{-7}$), adhesion (8 ontologies, $p = 8.79 \times 10^{-6}$), actin and cytoskeletal structure (9 ontologies, $p = 0.0034$), and cell death and apoptosis (7 ontologies, $p = 0.041$) were also detected. Morphogenesis and development (26 ontologies, $p = 0.12$) and immune and inflammation (3 ontologies, $p = 0.9$) were not significantly enriched (**Figure 2E**).

To observe the effect of exercise during neuropathic pain, we compared SNI-Running animals to SNI-Sedentary animals. We evaluated 179,769 tiling regions covering 22,338 unique gene promoters. We detected 6247 differentially methylated tiles in total, dividing into 2809 hypermethylated and 3438 hypomethylated tiles representing 1799 and 3014 unique genes respectively (**Figure 2B**). We identified 63 hypermethylated tiles and 86 hypomethylated tiles with a robust differential methylation (adjusted p-value $< 1 \times 10^{-7}$ and absolute differential methylation > 10%). These tiles represent 45 and 64 genes

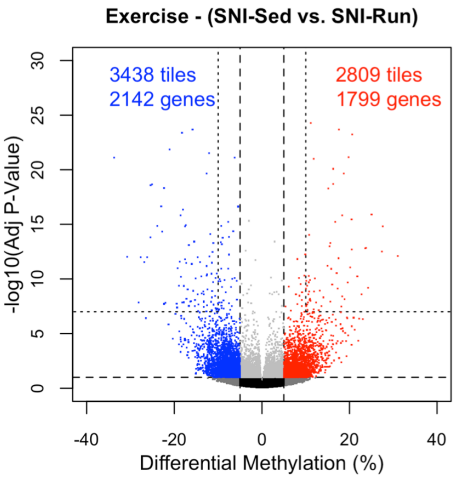
respectively and include the eukaryotic translation initiation factor 3 subunit *Eif3f* (-15.2% DM), interleukin gene *Il12a* (-12.6% DM), and toll like receptor *Tlr1* (-16.3% DM).

We identified 263 gene ontologies enriched for differentially methylated genes. The top 15 ontologies are predominantly associated with locomotion and cell motility, with additional enrichments involved in areas of tissue development, morphogenesis, and biological adhesion (**Figure 2C**). Term grouping and hypergeometric analysis determined identified functional domains enriched by exercise. Exercise resulted in significant enrichment in gene ontologies related to ion transport, homeostasis, and binding (37 ontologies, $p = 5.96 \times 10^{-23}$), locomotion (24 ontologies, $p = 2.71 \times 10^{-11}$), adhesion (15 ontologies, $p = 8.08 \times 10^{-11}$), immune system and inflammation (32 ontologies, $p = 1.01 \times 10^{-8}$), and morphogenesis and development (47 ontologies, $p = 8.02 \times 10^{-4}$). Cell death (8 ontologies, $p = 0.09$) and actin cytoskeleton (5 ontologies, $p = 0.11$) were not significantly enriched (**Figure 2E**).

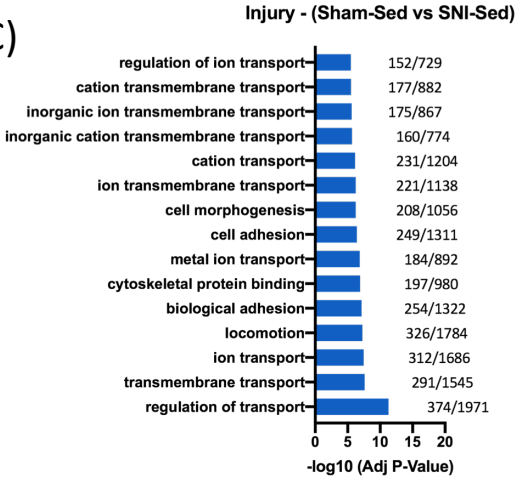
A)



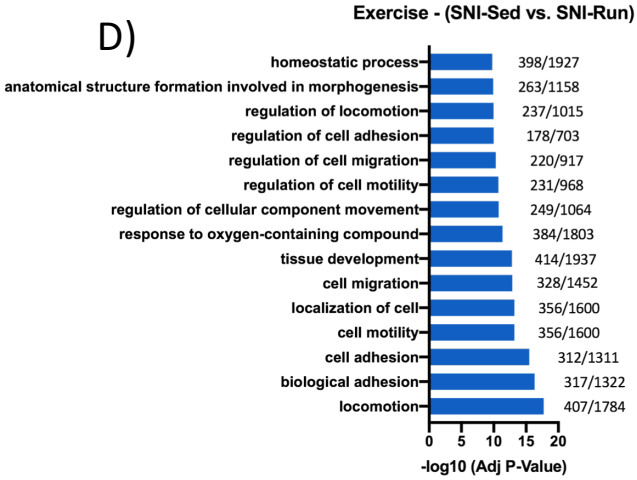
B)



C)



D)



E)

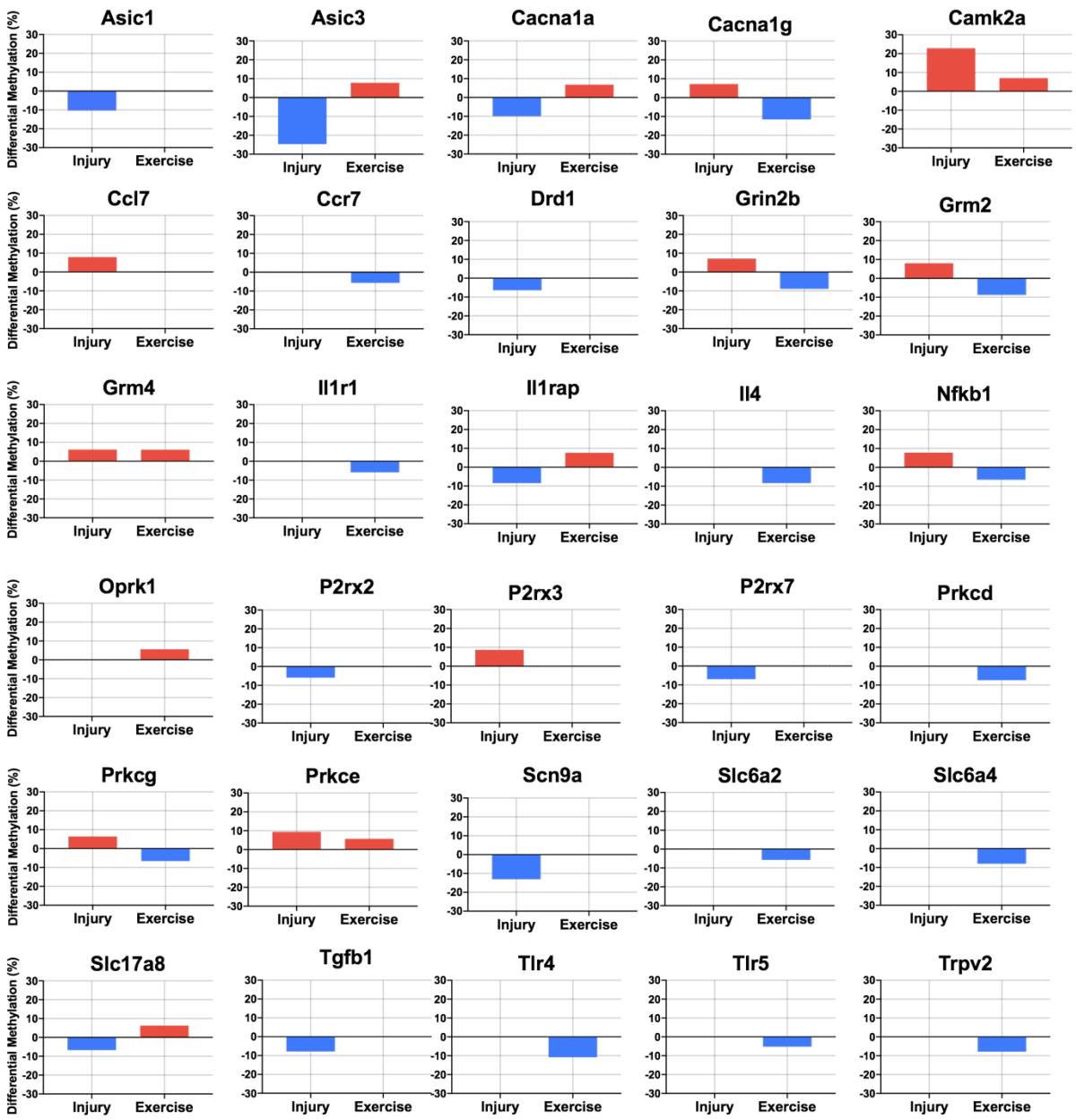
Gene Ontologies Per Domain in Injury and Exercise

Ontology Domains		Injury		Exercise	
Domain Names	Total Ontologies	Enrichment p-value	Ontologies Detected	Enrichment p-value	Ontologies Detected
Actin Cytoskeleton	260	1.34×10^{-4}	9	0.12	5
Adhesion	149	8.79×10^{-6}	8	8.08×10^{-11}	15
Cell Death	428	0.041	7	0.097	8
Immune	843	0.95	3	1.02×10^{-8}	32
Ion Transport	383	3.57×10^{-37}	44	5.96×10^{-23}	37
Locomotion	384	4.54×10^{-7}	15	2.71×10^{-11}	24
Morphogenesis	2378	0.12	26	8.03×10^{-4}	47

[**Figure 2**: *Injury and Exercise induce strong changes in PFC DNA methylation affecting multiple functional pathways and pain-related genes*. The magnitude and statistical significance of promoter region tile differential methylation during A) Injury and B) Exercise intervention. Tiles are displayed in terms of positive or negative methylation difference with control as the reference point compared to experimental, against –log10(adjusted p-value). Horizontal dashed line indicates an adjusted p-value threshold of 0.1 and vertical dashed line indicates methylation difference thresholds of 5% and -5%. Dotted lines encircle robust differentially methylated tiles with an adjusted p-value threshold of $1x10^{-7}$ and absolute differential methylation > 10%. Red: hypermethylated; blue: hypomethylated; dark grey: non-significant but with methylation differences of > 5%; light grey: significant but with methylation differences of < 5%, black = not different. The top 15 enriched gene ontologies for differentially methylated genes in C) Injury and D) Exercise. Displayed ontologies are filtered for a maximum size of 2000 genes and are from Biological Processes or Molecular Function domains. Listed are the number of differentially methylated genes / total number of genes in each ontology E) Enrichment of gene ontology domains in Injury and Exercise. Displayed are the total ontologies within the reference list, and the number of enriched ontologies detected in injury and exercise within each broadly described domain name. Hypergeometric test.]

3.3 Differential Methylation after Spared Nerve Injury and exercise affect pain-related genes

To identify differentially methylated genes with known roles in pain, we compared our datasets to curated lists of pain-related genes identified by Ultsch et al [271] and the Human Pain Genetics Database (HGPD) [272]. Differentially methylated pain-related genes were significantly enriched in SNI mice, with 110 identified from Ultsch list and 49 identified from the HPGD (Ultsch: $p = 1.2 \times 10^{-6}$; HPGD: $p = 0.053$. Hypergeometric Test). In the exercise condition, differentially methylated genes were significantly enriched for only Ultsch list pain genes, with 109 DM pain genes were identified, and 49 from the HPGD (Ultsch: $p = 0.0007$; HPGD: $p = 0.298$. Hypergeometric Test). Of the 110 DM Ultsch pain genes identified in SNI and 109 DM Ultsch pain genes identified after exercise, 49 genes are shared between the two conditions. Similarly, 49 genes from SNI and 49 genes from exercise were identified from the HGPD, with 22 genes common to both SNI and exercise. A number of pain related genes displayed reversals in differential methylation after treatment, such as *Asic3*, NFkB subunit *Nfkb1*, NMDA receptor subunit *Grin2b*, glutamate metabotropic receptor Grm2, and glutamate transporter *Slc6a4* (Figure 3.

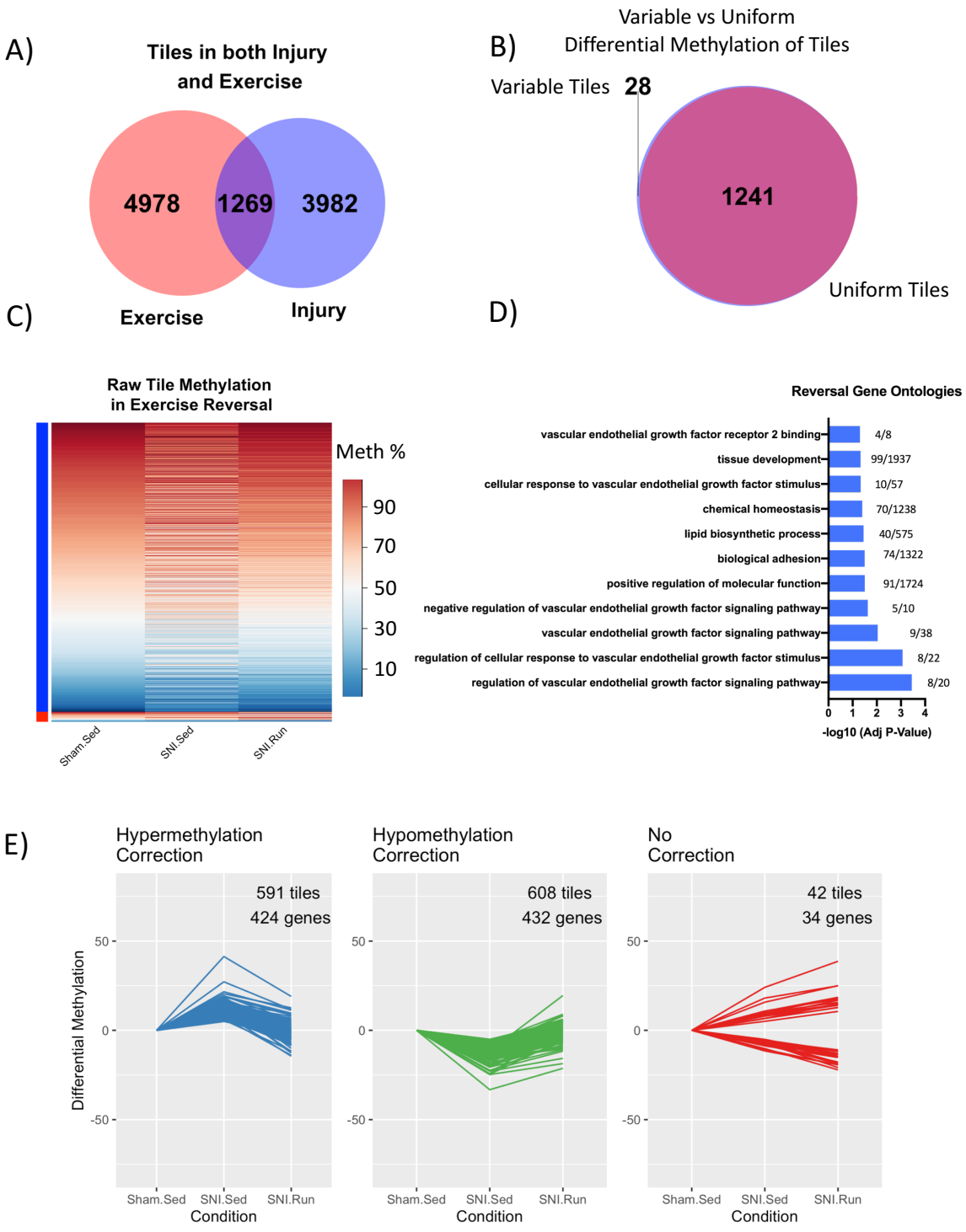


[**Figure 3**: *Spared Nerve Injury and Exercise affect pain-related gene methylation.* Differential methylation of 30 pain genes of interest where displayed differential methylation is the average of all identified tiles per gene. Pain genes have been previously identified by either Ultsch et al. 2013 [271] or the Human Pain Genetics Database [272].

Red indicates hypermethylation, blue indicates hypomethylation. Sham-Sedentary: n = 4, SNI-Sedentary: n = 6, SNI-Exercise: n = 6]

3.3 Exercise reverses spared nerve injury-induced differential methylation

To further understand the impact of Injury and Exercise upon PFC DNA methylation, we identified 1269 overlapping tile regions that undergo differential methylation both after Injury and after Exercise intervention (**Figure 4A**). Filtering for uniform differential methylation identified 1241 tiles, representing 890 genes, and 28 tiles representing 10 genes that experience variable differential methylation across their promoter regions (**Figure 4B**). After selecting only uniformly differentially methylated genes, we identified 1199 tiles (856 genes) that reverse their SNI-induced differential methylation after exercise treatment, with 42 tiles (34 genes) experiencing no reversal or increases in SNI-induced differential methylation as a result of exercise intervention (**Figure 4C**). Of the 1199 reversing tiles, 591 tiles (424 genes) are initially hypermethylated as a result of Injury, and experience hypomethylation during exercise intervention, while 608 tiles (432 genes) are hypomethylated during injury and hypermethylated during Exercise (**Figure 4E**). These reversal genes are enriched in ontologies predominantly associated with vascular endothelial growth factor (VEGF) activity, as well as tissue development and biological adhesion (**Figure 4D**). Differentially methylated genes associated with VEGF signalling include *Vegfa, Rela, Il12a, Il12b, Myo1c Ptp4a3, Smoc2, Xdh, Dab2ip,* and *Cadm4*. Promoter regions that did not reverse after exercise did not associate with any gene ontology.



[**Figure 4**: *Exercise intervention results in the reversal of chronic pain induced DNA methylation*. A) 1269 tiles are differentially methylated in both Injury and Exercise. B) Of

those 1269 tiles, 1241 are uniformly differentially methylated and 28 tiles show variable differential methylation. C) 1199 tiles show a reversal in differential methylation from Injury (Sham-Sed vs SNI-Sed) to Exercise intervention (SNI-Sed to SNI-Run), and 42 tiles do not undergo reversal. Side Column: Blue = reversal, red = no reversal. D) Gene ontologies associated with reversing genes. Displayed ontologies are filtered for a maximum size of 2000 genes and are from Biological Processes or Molecular Function domains. Listed are the number of differentially methylated genes / total number of genes in each ontology. E) The magnitude of differential methylation after injury, and reversal after Exercise intervention. Sham-Sedentary: n = 4, SNI-Sedentary: n = 6, SNI-Running: n = 6]

3.4 Nerve Injury and Exercise affect and reverse differential methylation at key junctions of the PI3K-Akt signalling pathway

To identify mechanisms affected by PFC DNA methylation in SNI and Exercise, we identified functional pathways that have high numbers of differentially methylated genes. From the KEGG database of biological pathways [378, 379], the PI3K-Akt signalling pathway contains 65 differentially methylated genes from Injury and 70 differentially methylated genes from Exercise, of which 26 are shared in both conditions (**Figure 5B**). 18 genes within the PI3K/Akt signalling pathway display a reversal of pain-induced differential methylation as a result of Exercise intervention.

The PI3K/AKT pathway is primarily involved in mediating neuronal survival in response to extracellular stimuli such as growth factors (GF), extracellular matrix (ECM) signalling, or response to pathogens or antigens. The PI3K/Akt pathway acts via

extracellular signals binding to receptor tyrosine kinases or G-protein coupled receptors, which stimulate phosphatidylinositol 3'-kinase (PI3K). PI3K catalyzes the production of second messenger molecule phosphatidylinositol-3,4,5-triphosphate (PIP3), which in turn subsequent activates Akt. Akt then mediates cellular functions like transcription, translation, proliferation, growth, and survival through phosphorylation of upstream substrates (**Figure 5A**).

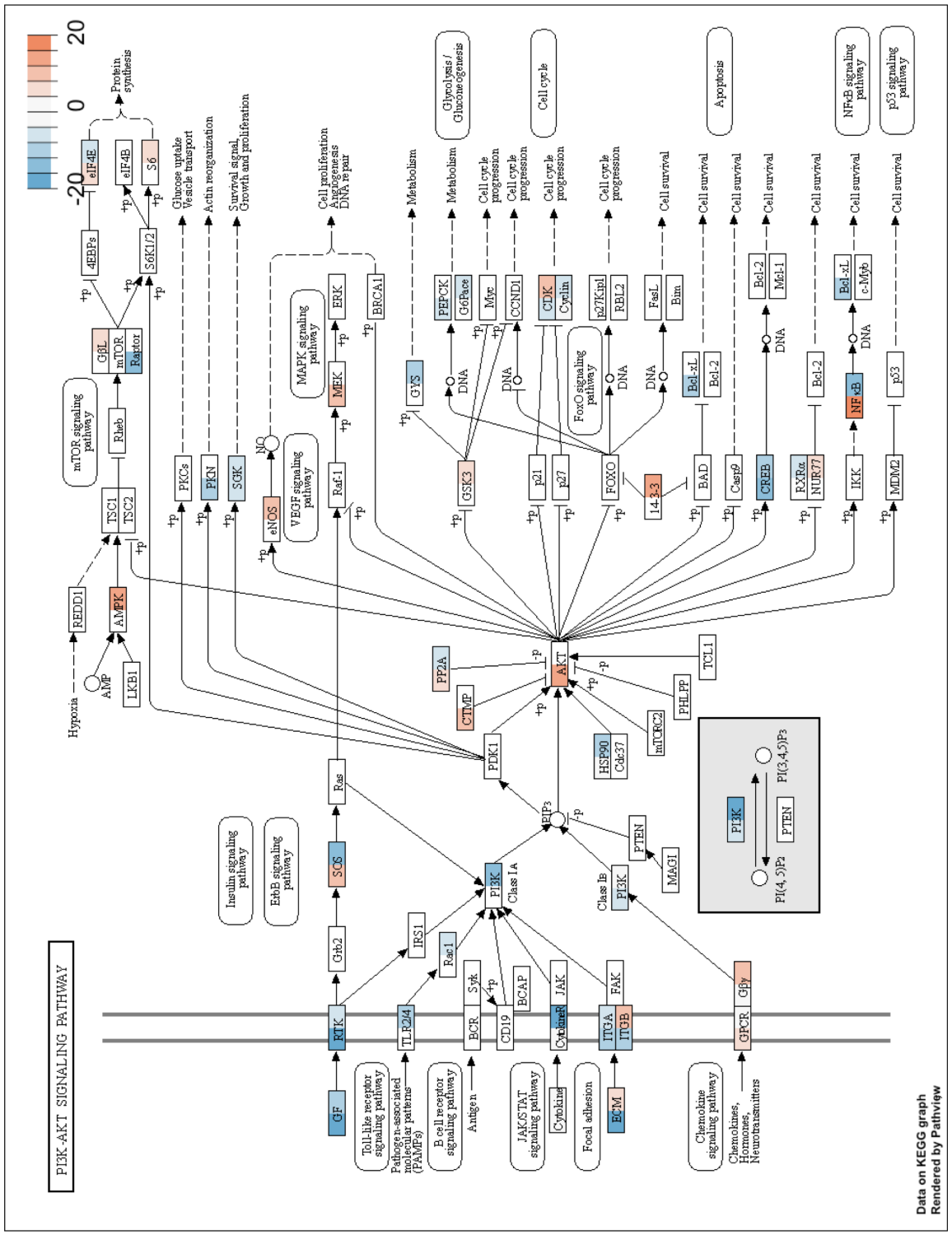
We identified 42 extracellular signalling molecules that experience differential methylation in either Injury or Exercise: 3 cytokines, 22 ECM molecules, and 17 GFs. The receptors of these extracellular signals are also affected, with 5 cytokine receptors, 7 integrins, 5 GPCRs, 6 receptor tyrosine kinases and the toll like receptor *Tlr4* experiencing differential methylation. A number of extracellular signals and their paired receptors were affected, including vascular endothelial growth factor *Vegfa*, fibroblast growth factors *Fgf7*, *Fgf8* and their receptors *Fgfr2*, *Fgfr3 [380],* neurotrophin *Ntf3* and its receptor *Ntrk2*, macrophage colony stimulating factor *Csf1* and *Csf1r*, granulocyte colony stimulating factor *Csf3* and *Csf3r*, and many collagens, fibronectins, and laminins which bind to integrins (ITGA and ITGB) (**Figure 5C**).

Downstream of the cell membrane receptors, intracellular signalling molecules activate PI3K. Integrins, cytokine receptors, RTKs, and TLRs send their downstream mediators FAK, JAK, Rac1, and IRS1 respectively to activate class IA PI3Ks, while GPCRs send $G\beta\gamma$ complex proteins to activate class IB PI3Ks. In our dataset, only the class IA PI3K gene *Pik3cd* was hypomethylated by exercise, along with its upstream regulator *Rac1*. The class IB PI3K stream was more heavily affected, with the only known

class IB PI3K *Pik3cg* and its two regulatory subunits *Pik3r5* and *Pik3r6* all experiencing differential methylation, as well as 5 different Gβγ complex genes (**Figure 5C**). Both class IA and IB PI3Ks catalyze the formation of PIP_3 which in turn serves to activate Akt, the main mediator of this pathway. The Akt gene *Akt2* is hypermethylated after Injury, and a number of its regulatory mediators are also affected in Injury and Exercise, including Akt repressor PP2A subunits *Ppp2r2d* and *Ppp2r3a*.

Finally, the phosphorylation of Akt triggers the activation of downstream pathways involved in cellular survival, metabolism, cell cycle progression, metabolism, and protein synthesis. A number of crucial mediators of cellular survival are differentially methylated, including the CREB genes *Creb5* and *Atf6b*, and the NFκB genes *Nfkb1* and *Rela* (**Figure 5C**). The anti-apoptotic gene *Bcl2l1* is also hypomethylated in response to injury. In cell cycle regulation, CDK genes *Cdk4* and *Cdk6* along with their cyclin regulators *Ccnd2* and *Ccnd3* are differentially methylated. Also, interesting to note are the differentially methylated genes in the mTOR signalling pathway. Two subunits of the mTOR complex, *Raptor* and *Mlst8*, are differentially methylated as well as the downstream targets of the mTOR complex, eukaryotic initiation factors *Eif4e* and *Eif4e2*, and ribosomal protein *Rps6*.

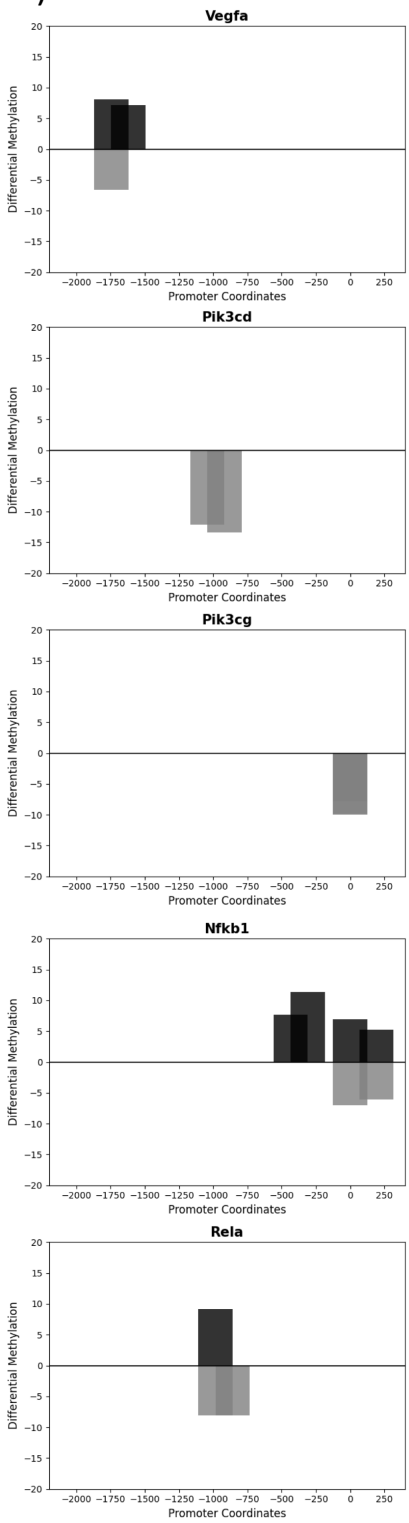
A)


PI3K-AKT SIGNALING PATHWAY
-20
0
20
Protein synthesis
Glucose uptake
Vesicle transport
Actin reorganization
Survival signal
Growth and proliferation
Cell proliferation
Angiogenesis
DNA repair
Metabolism
Glycolysis / Gluconeogenesis
Cell cycle progression
Cell cycle
Cell survival
Apoptosis
NFκB signaling pathway
p53 signaling pathway
Hypoxia
AMP
LKB1
AMPK
REDD1
mTOR signaling pathway
TSC1
TSC2
Rheb
GβL
mTOR
Raptor
4EBPs
eIF4E
eIF4B
S6K1/2
S6
PKCs
PKN
SGK
NO
eNOS
VEGF signaling pathway
MAPK signaling pathway
ERK
MEK
Raf-1
BRCA1
GYS
PEPCK
G6Pase
Myc
CCND1
CDK
Cyclin
p27Kipl
RBL2
FasL
Bim
Bcl-xL
Bcl-2
BAD
Casp9
CREB
Bcl-2
Mcl-1
FXRα
NUR77
Bcl-2
IKK
NF-κB
Bcl-xL
c-Myb
MDM2
p53
FoxO signaling pathway
FOXO
14-3-3
DNA
PP2A
CTMP
PDK1
AKT
PHLPP
TCL1
mTORC2
HSP90
Cdc37
PIP3
PTEN
MAGI
PI3K
Class IA
Class IB
PI3K
PTEN
PI(4,5)P2
PI(3,4,5)P3
Ras
SOS
Grb2
IRS1
Rac1
GF
RTK
TLR2/4
BCR
Syk
CD19
BCAP
CytokineR
JAK
ITGA
ITGB
FAK
GPCR
Gβγ
Insulin signaling pathway
ErbB signaling pathway
Toll-like receptor signaling pathway
Pathogen-associated molecular patterns (PAMPs)
B cell receptor signaling pathway
Antigen
JAK/STAT signaling pathway
Cytokine
Focal adhesion
ECM
Chemokine signaling pathway
Chemokines, Hormones Neurotransmitters
Data on KEGG graph
Rendered by Pathview

B)

KEGG Node	Gene	Injury DM	Exercise DM	KEGG Node	Gene	Injury DM	Exercise DM
14-3-3	Ywhah	NA	14.76	GF	Ereg	NA	-6.37
AKT	Akt2	12.17	NA		Fgf18	-9.79	NA
AMPK	Prkaa2	NA	12.94		Fgf20	NA	10.07
Bcl-xL	Bcl2l1	-8.87	NA		Fgf22	-15.89	NA
CDK	Cdk4	NA	-5.96		Fgf7	NA	6.91
	Cdk6	-7.17	14.1		Fgf8	8.86	NA
CREB	Atf6b	-6.24	-5.1		Hgf	-10.88	-8.8
	Creb5	-7.65	-5.13		Ntf3	NA	-9.01
CTMP	Them4	10.16	NA		Pdgfa	NA	5.71
Cyclin	Ccnd2	6.27	-5.85		Pdgfb	-7.72	NA
	Ccnd3	-6.65	NA		Pgf	-7.24	-5.77
Cytokine	Csf3	8.03	NA		Vegfa	7.62	-6.6
	Il4	NA	-8.3	GPCR	Chrm1	-6.48	NA
	Il7	-5.56	6.22		F2r	8.59	NA
CytokineR	Csf3r	6.75	-8.15		Lpar2	5.88	NA
	Il2rb	NA	-6.68		Lpar3	NA	7.18
	Il6ra	-10.68	-5.8		Lpar5	NA	-9.2
	Prlr	NA	-5.9	GSK3	Gsk3b	NA	7.38
ECM	Chad	NA	5.94	GYS	Gys2	NA	-9.17
	Col1a2	-6.6	NA	HSP90	Hsp90ab1	12.1	-9.7
	Col2a1	-8.18	-5.03		Hsp90b1	-11.09	NA
	Col4a1	-6.97	-6.51	ITGA	Itga11	-6.54	NA
	Col6a2	-6.93	NA		Itga2b	6.73	NA
	Col6a3	NA	7.85		Itga3	NA	8.34
	Col6a6	-6.61	NA		Itga4	NA	-7.25
	Col9a1	-7.34	NA		Itga6	NA	-5.39
	Col9a3	5.58	NA		Itga9	-10.13	NA
	Fn1	7.32	-5.62	ITGB	Itgb7	-9.17	8.27
	Ibsp	NA	5.59	MEK	Map2k1	11.1	NA
	Lama3	17.16	-10.29	NFkB	Nfkb1	7.8	-6.54
	Lama5	10.7	-12.32		Rela	9.18	-8.13
	Lamb3	NA	5.98	NUR77	Nr4a1	NA	7.34
	Lamc1	NA	13.08	PEPCK	Pck1	-6.33	NA
	Lamc2	10.97	NA	PI3K-IA	Pik3cd	NA	-12.74
	Reln	-9.23	NA	PI3K-IB	Pik3cg	NA	-9.21
	Spp1	-8.1	NA		Pik3r5	-7.53	NA
	Thbs2	-11.39	NA		Pik3r6	NA	5.72
	Thbs3	-7.38	5.64	PKN	Pkn1	-8.76	NA
	Vtn	NA	6.55	PP2A	Ppp2r2d	7.31	NA
	Vwf	7.9	-6.14		Ppp2r3a	NA	-6.13
eIF4E	Eif4e	7.64	NA	Rac1	Rac1	NA	-7.19
	Eif4e2	NA	-6.59	Raptor	Rptor	-12.3	NA
eNOS	Nos3	NA	10.36	S6	Rps6	NA	5.57
G6Pace	G6pc3	NA	-5.85	RTK	Csf1r	-6.13	NA
GBL	Mlst8	NA	5.89		Fgfr2	-8.24	10.46
GBy	Gnb1	NA	-14.68		Fgfr3	NA	-7.59
	Gnb4	-8.84	9.22		Met	11.44	-7.44
	Gnb5	NA	5.84		Ngfr	-9.74	NA
	Gng11	NA	8.3		Ntrk2	-6.56	NA
	Gngt1	7.71	NA	RXRa	Rxra	NA	-5.28
GF	Angpt1	NA	-5.14	SGK	Sgk1	-6.83	-7.09
	Angpt2	NA	10.41	SOS	Sos1	NA	-7.64
	Csf1	5.71	NA		Sos2	11.11	-7.07
	Efna2	6.96	NA	TLR2/4	Tlr4	NA	-10.79
	Efna3	-9.6	NA				

C)



[**Figure 5**: *Injury and Exercise affect multiple nodes throughout the PI3K-AKT signalling pathway.* A) The PI3K-AKT signalling pathway experiences differential methylation at multiple nodes. Left side: Injury, Right side: exercise. Scale bar: differential methylation. B) Nodes within the PI3K-AKT signaling pathway can be expressed by multiple related genes. Red: Hypermethylation, Blue: Hypomethylation, Grey: No differentially methylated tiles were detected. Pathway was rendered using Pathview [321]. C) Each differentially methylated region for select genes of interest relative to transcription start site located at promoter coordinate 0. Black bars: Injury. Grey bars: Exercise.]

4. Discussion

Given the difficulty of developing novel pharmacological interventions and the complexity and diversity of chronic pain-related mechanisms, our study sought to explore other therapeutic avenues and identify their impact upon PFC functioning. Increased physical activity is commonly recommended and prescribed for chronic pain amongst clinicians and physiotherapists, with demonstrated efficacy in ameliorating reported pain. While previous work shows aerobic exercise can induce epigenetic changes and attenuate grey matter loss, there has yet to be any work exploring the effects of aerobic exercise on PFC DNA methylation in subjects with long-term chronic pain. Our study provides evidence that aerobic exercise induces epigenetic changes in PFC during chronic pain, affecting a number of functional pathways and reversing hundreds of pain-related changes in DNA methylation.

Here we demonstrate that non-pharmacological therapeutic intervention can attenuate long-term peripheral neuropathic pain and mediate epigenetic changes in PFC. First, by providing SNI animals access to voluntary running exercise, we can attenuate mechanical hypersensitivity 8 months after onset of neuropathic pain. These results are in line with previous findings from human and animal studies [136, 381]. Second, we show that voluntary exercise can alter PFC promoter DNA methylation of thousands of genes after animals have experienced a long-term neuropathic pain. This is the first study to demonstrate genome-wide changes in PFC methylation after exercise, and is supported by work in hippocampus or on single genes [382, 383]. Third, these changes occur in a number of pain-relevant functional domains such as ion transport and homeostasis, immune functioning, and cytoskeletal structure. Finally, many of these exercise-related changes reverse the effects of chronic peripheral injury on DNA methylation. This implies that treatment reverses disease pathology at the epigenetic level and is supported by other work examining addiction and post-traumatic stress [322, 323]. Finally, the PI3K-Akt signalling pathway is heavily affected by injury and exercise, with many downstream implications for cellular survival, neurogenesis, learning and memory, and protein expression.

4.1 PFC DNA Methylation in Response to Injury and Exercise

PFC DNA methylation is dramatically altered after long-term neuropathic pain and treatment of that pain with increased physical activity. At one year post-injury, we identified over 5000 differentially methylated regions affecting nearly 3500 genes, representing a substantial portion of the genome undergoing some degree of altered

methylation. Even isolating for genes that undergo a substantial change with an adjusted p-value of $< 1x10^{-7}$ and absolute differential methylation > 10%, we still identified over 70 genes that show a strong change as a result of injury. This result is mirrored after the exercise intervention, with nearly 6500 differentially methylated tiles representing almost 4000 genes, and over 100 genes going through robust differential methylation. While some of these widespread alterations in DNA methylation may not translate to meaningful changes in gene expression, a substantial proportion of the genome has been impacted by and is responsive to long-term injury and its therapeutic intervention.

To determine what molecular and cellular functions may be regulated by DNA methylation, we turned to gene ontology analysis. We identified a number of broad functional domains that were affected by injury or exercise or both, such as ion transport and homeostasis, cellular adhesion, locomotion and motility, and immune function. These broad functional domains were identified by grouping gene ontologies by similar function.

Ontologies related to ion transport, homeostasis, and binding were heavily enriched in both injury and exercise ontologies, with 44 and 39 ontologies detected respectively, and accounting for 8 of the top 15 gene ontologies in Injury. Ontologies related to calcium ion transport and homeostasis genes were affected in particular by injury and exercise. A number of genes involved in regulating Ca^{2+} concentration and activity are differentially methylated, potentially affecting their expression and the regulation of Ca^{2+} in the cortex. The influx and homeostasis of Ca^{2+} is crucial for triggering neurotransmitter release, mediating synaptic plasticity, and controlling cell survival and apoptosis [384-386]. In DRG sensory neurons, peripheral neuropathy reduced cytosolic

concentrations of Ca^{2+} [387, 388] and caused a loss of inward Ca^{2+} current, in particular through T-type Ca^{2+} channels [389, 390], which lead to increased neuronal hyperexcitability. In SNI mice, cytosolic Ca^{2+} concentration is potentially reduced after the hypomethylation and subsequent increased expression of calcium pump SERCA (*Atp2a3*), which moves calcium from cytosol into the ER, and the hypermethylation of the sodium/calcium exchanger *Slc8a2*, which moves calcium out of the mitochondria into the cytosol. Calcium influx through T-Type calcium ion channel *Cacna1g* may also be reduced as a result of hypermethylation in injury. Conversely, exercise may increase cytosolic Ca^{2+} concentration by increasing expression of ER Ca^{2+} exporters: IP3 receptors (*Itpr1, Itpr2*) and ryanodine receptor (*Ryr2*), all of which are hypomethylated in the exercise group. *Slc8a2* also reverses its differential methylation and becomes hypomethylated, potentially increasing the export of Ca^{2+} from the mitochondria. Finally, the T-type calcium channel *Cacna1g* also reverses to hypomethylation, potentially increasing influx of calcium. Interestingly, restoring inward Ca^{2+} current reduced neuronal hyperexcitability [391]. Changes of internal calcium concentration and calcium influx can also affect long term potentiation (LTP) and synaptic plasticity.

Synaptic plasticity is a hallmark of chronic pain, with changes in glutamate transmission and cortical excitation noted amongst chronic pain patients and experimental models [51, 392]. LTP proceeds through an early transient phase mediated by PKC and CaMKII and the insertion of new AMPARs into the post-synaptic membrane, and a late persistent phase involving the growth of a new dendritic spine mediated by the MAPK signalling pathway. First, multiple NMDA receptor subunits (*Grin2b, Grin2c, Grin2d*)

that are required for the calcium influx to initiate LTP are hypermethylated in injury and hypomethylated in exercise. The key early LTP genes CaMKII (*Camk2a*) and calmodulins 1 and 2 (*Calm1, Calm2*) are hypermethylated by both injury and exercise. Therefore, early phase LTP may be repressed in both conditions. However, late phase LTP may be repressed in injury and promoted by exercise. PKCζ (*Prkcz*), required for late phase maintenance, and the synaptic structure mediator *Rac1* are both hypomethylated by exercise. Rac1 is essential for regulating synaptic growth and plasticity and Rac1 inhibition induces significant deficits in LTP and can reduce neuropathic pain 1 month after injury [276, 393]. An interesting future direction would be to explore if the hypomethylated Rac1 observed was to promote LTP as an adaptive response to exercise, causing the attenuation of pain. These observations concur with previous work showing exercise induces changes in mRNA expression of genes associated with neuronal activity, synaptic structure, and plasticity [394].

Further work is needed to explore the relationship of DNA methylation and calcium regulation as a number of other Ca^{2+} ion channels (*Cacna1s, Cacna1d, Cacna1a, P2rx1, P2rx2, P2rx3, P2rx7*), Ca^{2+} transporters (*Atp2b1, Slc25a4*), and Ca^{2+} mediators (*Stim1, Orai3, Adcy3, Adcy7, Adcy8*) are also differentially methylated in injury and exercise. Other studies have shown interactions between nuclear calcium signalling and histone deacetylase activity [395, 396] and this interplay may help mediate DNA methylation responses to chronic pain.

Another functional domain that was regulated by both injury and exercise was immune response and inflammation. Interestingly, only 3 immune related gene ontologies were detected in injury, while 32 immune related gene ontologies were detected in exercise. Immune and inflammation ontologies in exercise were also predominantly hypomethylated, potentially indicating the activation and increased expression of immune related genes and domains in exercise. Chronic exercise is already known to counteract chronic inflammation in the brain by decreasing pro-inflammatory M1 microglia and the expression of proinflammatory cytokines [397, 398]. Here, chronic exercise may be increasing anti-inflammatory responses in PFC by upregulating production of anti-inflammatory cytokines and promoting M2 microglia proliferation and migration to the PFC. Indeed, the M2 microglia inducing *Il4* was hypomethylated by exercise along with the M2 microglia secreted anti-inflammatory *Ccl22*. Despite these anti-inflammatory indicators, the immune response of the brain after injury and exercise is not clear. A number of pro-inflammatory interleukins (*Il1f6, Il12a, Il12b, Il17f, Il20*) are hypomethylated by exercise indicating a pro-inflammatory response. Both Injury and Exercise comparisons show an enrichment of locomotion and cell adhesion ontologies potentially representing the invasion and activation of microglia. Given the involvement of immune factors in multiple systems and the existence of microglia on a pro-inflammatory and anti-inflammatory continuum, the contribution of inflammatory processes to the therapeutic benefits of exercise against late-stage chronic pain is complex and requires further investigation.

4.2 PFC Methylation Reversal after Exercise

Environmental and external factors are capable of affecting cortical DNA methylation and this methylation is plastic, with a number of studies successfully reversing disease or condition related DNA methylation after intervention [322, 323, 349]. We are the first study to investigate the effect of exercise on chronic pain-induced changes in DNA methylation, and we demonstrate not only widespread changes after exercise but also the reversal of chronic pain related DNA methylation at hundreds of positions. We identified 1269 differentially methylated regions that are shared between injury and exercise, of which 1199 undergo a reversal in differential methylation. Said differently, nearly 20% of differentially methylated genes identified in injury reverse their differential methylation after an exercise intervention that successfully attenuated pain.

How this reversal occurs is still unknown, however any widespread changes in DNA methylation must come about through the activity of methylating DNMTs, demethylating TET enzymes, and the appropriate histone modifications that ensure the same genetic regions are available to be modified. Previous work has found decreases in DNMT expression and histone deacetylase (HDAC) activity and increases in histone acetylase (HAT) in hippocampus and frontal cortex after treadmill or running wheel [374, 399, 400]. Swimming also increased H3K9 and H3K14 acetylation in hippocampus of mice, both strong histone markers of active promoters [401, 402]. Decreases in DNMT and HDAC activity combined with an increase in histone acetylation and HAT activity would favour demethylation and an open chromatin environment, implying that the genome is in a state of plasticity and methylation changes can more readily occur.

However even though the genome may be in an open state, one of the key questions that must be answered is how specific genes and sequences are targeted for differential methylation and why certain sequences are available for reversal while others are resistant to intervention.

4.3 Impact of Injury and Exercise on PI3K-Akt Pathway

For a closer examination of one of the affected signalling pathways in injury and exercise, we selected the PI3K-Akt pathway. Increased expression and phosphorylation of PI3K and Akt in dorsal root ganglia and spinal cord is associated with increased pain sensation, and the inhibition of PI3K successfully reduces pain [403, 404]. PI3K/Akt signalling contributes to central sensitization in the spinal cord, mediates microglia and astrocyte reactivity, and regulates neuronal survival [405-408]. In our dataset, the class IA PI3Kδ (*Pik3cd*) is hypomethylated in exercise. The class IA PI3Ks are primarily activated by upstream receptor tyrosine kinases and growth factors. In particular, the growth factor VEGF (*Vegfa*) was hypermethylated in injury and hypomethylated in exercise, and VEGF related ontologies were significantly enriched among reversal genes. VEGF activity via PI3K signalling increases neurogenesis and induces synaptic remodelling through regulation of NMDA receptor 2B subunits (*Grin2b*), which is hypomethylated in exercise as well [409, 410]. Increased expression of VEGF is also responsible for promoting angiogenesis, hypothesized to improve cognition and brain health through increased perfusion [411, 412]. Downstream of VEGF and PI3K, two forms of the small GTPase Rac (*Rac1, Rac2*) were also hypomethylated in exercise. Rac signalling induces vascular permeability and is required for the stabilization of actin

filaments during LTP synapse formation [413, 414]. Thus in exercise, VEGF may mediate a pro-recovery response through the PI3K/Akt pathway, resulting in novel synaptic plasticity, angiogenesis and the potential invasion of circulating immune cells resulting in PFC signalling undergoing pain attenuating adaptation. The differential methylation of these genes may reflect a more persistent change in expression and a transition to a new brain state.

4.4 Limitations

A number of limitations must be considered regarding our results and conclusions. First, our results require further validation and follow up studies to examine the downstream impact of the differential methylation observed. While promoter region methylation is a strong regulatory mechanism of gene expression, other mechanisms can influence gene transcription, translation, and ultimately expression. Second, given our group sizes of 3-6 and a permissive adjusted p-value of 0.1, there is a greater risk of false positives. The permissive adjusted p-value was selected in order to maximize the sensitivity of our analysis, in line with the exploratory nature of our study. Third, our study focused on promoter region methylation, however non-promoter DNA methylation can also have impacts upon gene transcription with methylation at distal enhancers and within the gene body capable of regulating gene transcription [183, 295, 351]. Fourth, we were unable to validate that each mouse in our running paradigm ran the same amount and therefore received the same "dosage" of exercise. We wished to avoid potential confounds of forced running paradigms, such as stress-induced analgesia, in favour of voluntary and *ad libitum* exercise. Fifth, our study contained male animals only therefore

our conclusions do not account for sex differences in response to chronic pain. We recognize these limitations but we also believe our results provide novel and relevant insight to PFC DNA methylation response during chronic pain and its successful treatment.

5. Conclusions

Our findings provide first evidence for reversal of chronic pain-induced epigenome-wide changes in DNA methylation as a result of therapeutic exercise. The widespread involvement of differentially methylated gene involved in calcium signalling, LTP, and immune responses in the PFC may provide new insights to how these processes are regulated in response to injury and recovery. While the responsiveness of DNA methylation to intervention is well-established, we also demonstrate that exercise can reverse DNA methylation on a large scale after long-term chronic pain. This implicates DNA methylation as a contributor to the cortical recovery observed in human patients after successful therapeutic intervention. These findings are a promising insight to the responsiveness of prefrontal cortex to non-pharmacological intervention, and a foundation for further research into more effective treatments against chronic pain.

Supplemental Figures

Supplemental Table 1 – Probe Bed File. Genomic coordinates for the bisulfite capture-sequencing probes

See Appendix 1 of Thesis

Supplemental Table 2 – Blacklist Bed File. Genomic coordinates for regions known to have anomalous, unstructured, and high signal/read counts in next gen sequencing

See Appendix 2 of Thesis

Chapter 5: Conclusions

6.1. Summary

Chronic pain is a leading cause of disability and reduced quality of life, and remains a difficult disease to treat and manage. This thesis explored the contribution of DNA methylation as a regulatory mechanism in maintaining chronic pain and in mediating therapeutic interventions. We hypothesized that PFC DNA methylation would undergo significant changes in response to both chronic pain onset and to successful pain reducing therapies.

Our first study characterized the progression of DNA methylation changes in the brain at four time points along chronic pain development and maintenance. We found robust differential methylation of hundreds of genes at one day, two weeks, six months, and one year post-injury. This study was the first to show rapid changes in PFC DNA methylation one day after injury and the first to explore PFC DNA methylation one year after injury. Moreover, differentially methylated genes displayed time dependent dynamic patterns of methylation across the time course, with many pain related genes only being differentially methylated at specific time points. This work demonstrated that peripheral neuropathic pain induces changes in PFC DNA methylation that evolve as pain becomes increasingly chronic.

Having identified a clear and dynamic relationship between DNA methylation and chronic pain, we investigated PFC DNA methylation response to interventions. We previously demonstrated chronic systemic SAM administration attenuates chronic pain [234]. Our second study examined the effect of this successful intervention upon PFC

DNA methylation. Chronic SAM administration induced widespread differential methylation and we identified potential underlying mechanisms contributing to SAM's action in alleviating chronic pain.

Following pre-clinical evidence and clinical reports [136], we next investigated the efficacy of voluntary exercise in reducing chronic pain. We confirmed that voluntary running exercise successfully attenuates chronic pain and demonstrate widespread changes in DNA methylation. This successful intervention one year after injury is the first to explore PFC DNA methylation response to and recovery from chronic pain at such a late time point. This work contributes to a rapidly growing literature on the relationship of epigenetics, exercise, and chronic pain and is the first to investigate PFC DNA methylation in a successful exercise-based intervention.

The results of our two intervention studies demonstrate that successfully attenuating pain is reflected in the PFC methylation state through a reversal of pain-related differential methylation. The direct reversal in DNA methylation of a subpopulation of genes after reduction of a disease state has been demonstrated in other fields, however this is the first evidence in the field of chronic pain.

6.2. Discussion

Exploring PFC DNA methylation in response to chronic pain provides two forms of insight: first, by revealing an important regulatory process mediating the functional and structural changes seen in PFC during chronic pain, and second, by identifying functional pathways and domains affected by chronic pain.

Previous research provided an excellent foundation for the DNA methylation changes we could expect in response to chronic pain. Nearly all experiments examining DNA methylation in pain-related structures during chronic pain clearly show widespread changes. These changes are observed to occur rapidly [235, 236], but are also maintained during later stages of chronic pain [200].

6.2.1. **Dynamics of PFC DNA Hypermethylation and Hypomethylation**

The results from all three experiments within this thesis clearly describe malleable, responsive, and dynamic changes in DNA methylation as chronic pain develops, consolidates, and is treated. Our time course study revealed differential methylation at every time point. Differential PFC methylation was skewed towards hypermethylation at each time point and in the SAM study control group, a result that has been noted in previous studies [236]. This hypermethylation presents an interesting contrast to our previous research, with PFC hypomethylation observed using the same pain model at similar time points [233, 234]. This discrepancy can be explained by the difference in techniques and is revealing about the response of PFC DNA methylation. Gregoire et al. 2016 and Tajerian et al. 2013 measured global methylation using methods that do not account for genomic location [233, 234]. In contrast, our analysis was targeted and limited to gene promoter regions, thus implying chronic pain induces a global hypomethylation with site-specific hypermethylation. This dual profile of methylation changes is a common hallmark in cancer, with site-specific hypermethylation of tumor suppressor genes and hypomethylation of centromeric repeated elements or long and short interspersed repeat

elements (LINE or SINE) [415-417]. Moreover, the specific genes and repeated elements that are differentially methylated vary depending on the cancer subtype, implying a functional role for both in cancer development [418].

The global hypomethylation observed in cancer predominantly occurs at centromeric satellite DNA, LINEs, and SINEs. Hypomethylation in these regions lead to chromatin instability as large segments of heterochromatin are demethylated and released from being sequestered at the nuclear membrane. In cancer, this results in increased risk of DNA strand breakage and recombination events. The disruption of chromatin structure also interferes with enhancer-promoter interaction and can move actively transcribed genes to the nuclear periphery resulting in their repression [419]. Another proposed effect of centromeric hypomethylation is the release of sequestered DNMTs and MBDs that were engaged in repressing these non-coding regions [418]. The release of DNMTs and MBDs would induce widespread hypermethylation at available sites throughout the genome. These mechanisms are currently only hypothesised to occur in chronic pain, however the similarity of global hypomethylation between cancer and chronic pain encourages further investigation.

In contrast to global hypomethylation, hypermethylation in cancer almost universally targets CpG islands. Cancer-related hypermethylation has characteristic profiles associated with the specific cancer subtypes and has a high concordance with genetic alterations, disease risk, and outcomes [420]. It is unclear if this characteristic profile is causal or simply correlated, however these profiles are most likely the result of a specific mechanism or environmental cue that causes their development. Cancer

research has observed that hypermethylated regions are associated a simultaneous facultative heterochromatin histone mark, H3K27me3 [421-423], and active promoter mark, H3K4me3 [424, 425]. The combination of the repressive H3K27me3 and active H3K4me3 marks is known as a bivalent promoter or poised promoter. They are common during development as genes in embryonic stem cells await the appropriate environmental signal to initiate transcription. However, it has been recently proposed that bivalent domains may also exist in adult tissues as a mechanism to tightly regulate tissue specific genes [426, 427] as the conversion of H3K27me3 to H3K27 acetylation serves to activate promoters [428]. Indeed, the hypermethylation of bivalent promoters has also been observed as blood, brain, kidney, and skeletal muscle tissue ages [429, 430].

Pain-related hypermethylation could be targeted in chronic pain via a similar bivalent promoter-based mechanism. EZH2 is the HMT responsible for methylating and marking H3K27 methylation as part of the Polycomb repressive complexes 2 and 3 [431]. EZH2 is also required for DNMT binding and DNA methylation at EZH2-targeted promoters [432]. EZH2 is elevated in spinal cord after peripheral nerve injury in both neurons and microglia and when EZH2 activity is inhibited, thermal and mechanical hyperalgesia are attenuated [433]. Thus pain-related hypermethylation may be mediated by EZH2-bound DNMT directed towards H3K27me3 marked gene promoters. Hypermethylation at H3K27me3 marked gene promoters may push these promoters to a more repressed epigenetic state, leading to cellular dysfunction or abnormal function. This mechanism may be particularly relevant in sustaining microglial inflammatory states. EZH2 expression is much higher in microglia than in neurons during chronic pain [433],

and EZH2 H3K27 methylating activity promotes a pro-inflammatory M1 phenotype and represses an anti-inflammatory M2 phenotype [434].

Finally, while we noted a predominant skew towards hypermethylated genes, we must also address the significant number of hypomethylated genes observed at all time points during the chronic pain time course. In contrast to the relationship between hypermethylation and bivalent promoters in cancer and aging, hypomethylation is associated with a number of different histone marks. In cancer, hypomethylation is observed at the constitutive heterochromatin H3K9me3 marks, perhaps in correlation to the global hypomethylation at centromeres discussed above. In contrast, hypomethylation in aging occurs in a tissue dependent manner, primarily at the active enhancer mark of H3K4me1 but can also occur at H3K4me3 marks. The site selection for hypomethylation in aging appears to be closely related to transcription factor binding [435]. Given that we detected hypomethylation in promoter regions in our studies, it is unlikely that hypomethylation in chronic pain follows a cancer-like mechanism and may be similarly dependent on transcription factor targeting. Transcription factors are known to prevent *de novo* DNA methylation by sterically interfering with DNMT binding and by recruitment of TETs [436-438]. Thus, hypomethylation in chronic pain may be guided by transcription factor binding at gene promoter regions. Further research is required to match hypomethylated pain-related promoters with transcription factor binding sites and histone marks, and determine the mechanism of hypomethylation targeting in chronic pain.

In summary, three mechanisms of differential methylation may explain the methylation profiles observed in chronic pain. The hypermethylation and hypomethylation seen at each time point might be the result of time point specific profiles of vulnerable or available DNA regions. Pain-related hypermethylation may be targeted by bivalent promoters in the PFC, with tissue specific profiles dictating which genes are affected. Pain-related hypomethylation may occur via transcription factor binding to prevent methylation in response to chronic pain or by actively promoting demethylation via recruitment of TET, again with tissue specific binding patterns dictating affected genes. Centromeric hypomethylation may contribute to cellular dysregulation by disrupting enhancer-promoter interactions and inappropriately repressing genes. It is likely that much of the observed differential methylation is irrelevant to actually mediating chronic pain changes. Many of the changes may be non-specific, non-targeted collateral effects of the reaction to chronic pain. Similar dynamics are seen in cancer and development [418, 439].

6.2.2. **Impact of PFC DNA Methylation on Synaptic Plasticity**

Our studies reveal widespread changes in DNA methylation during the time course of chronic pain development and in response to intervention. As mentioned during the introduction, most forms of chronic pain present with synaptic plasticity in the form of peripheral or central sensitization. Among our studies, functional domains related to the actin cytoskeleton and ion channels and transport are particularly enriched for differentially methylated genes and are related to synaptic plasticity. The involvement of

DNA methylation in these functions may imply an overarching mechanism regulating multiple cellular systems at once, and a potential therapeutic avenue to simultaneously target multiple dysregulated systems.

Synaptic plasticity is one of the predominant proposed mechanisms that mediate chronic pain in PFC. Indeed, previous research has observed changes in synaptic formation and density, neurotransmitter production and release, and post-synaptic receptors [350, 440, 441]. These processes are affected by differentially methylated pathways throughout the chronic pain time course and during interventions.

Actin and cytoskeleton formation, organization, and regulation are some of the key elements that regulate synaptic formation and density. Actin formation and stabilization is a dynamically regulated process that requires frequent expression of necessary proteins. The regulation of actin assembly and stabilization is crucial in both LTP and long term depression (LTD), and affects the growth or loss of dendritic synapses [442]. The Ras and PI3K signalling pathways are involved in mediating synaptic structure and trafficking of AMPA receptors and both hyper- or hypoactivity of these signalling pathways impairs synaptic plasticity [443]. The actin cytoskeleton is relevant during chronic pain, as a foundation for synaptic plasticity but also to mediate intracellular signalling cascades [275, 298, 444]. Across the chronic pain time course, gene ontologies for the actin cytoskeleton are enriched for differentially methylated genes, potentially reflecting a dysregulation of normal cellular architecture as chronic pain develops. The Ras and PI3K-Akt signalling pathways are differentially methylated during chronic pain and undergo reversals after intervention. Differential methylation of these pathways could result in the abnormal

regulation and expression of the actin cytoskeleton and affect normal synaptic transmission.

In addition to the actin cytoskeleton, the glutamatergic AMPA and NMDA receptors are also differentially methylated. AMPA and NMDA receptors are a crucial element in synaptic plasticity, required for the influx of calcium that triggers either LTP or LTD [445]. Both receptors have a well-characterized role in chronic pain and have been previously investigated as analgesic targets [446-448]. AMPA receptor subunits *Gria2* and *Gria1* are hypermethylated at 6 months post-injury and in the injury group of the SAM experiment respectively. NMDA receptor subunits are differentially methylated at 6 months post-injury and following both SAM and exercise interventions. Specifically, the NMDA receptor subunit *Grin1* is hypomethylated 6 months post-injury, while *Grin2b, Grin2c,* and *Grin2d* were all hypermethylated after injury and hypomethylated after intervention in the intervention studies. This methylation profile of AMPA and NMDA receptors may indicate a preference for LTD in the PFC during the later stages of chronic pain. LTP and LTD rely on similar molecular mechanisms but differ through the amplitude of pre-synaptic signalling and post-synaptic potentials. High frequency or high amplitude pre-synaptic glutamate release that induces large excitatory post-synaptic potentials favour LTP, while low frequency but prolonged glutamate release that results in modest post-synaptic depolarization favours LTD [445]. Hypermethylation of AMPA and NMDA receptor subunits would imply reduced expression, potentially indicating smaller excitatory post-synaptic potentials after injury. Subsequent hypomethylation of NMDA receptor subunits after intervention may indicate increased expression of NMDA receptors and promotion

of LTP. Increased LTP could contribute to the increase in cortical grey matter observed in human patients after successful pain attenuation.

Changes in synapse signalling and structure are well-established responses to chronic pain occurring at every level of pain transmission. Targeting DNA methylation is a novel potential therapeutic approach to reversing maladaptive changes in these functions during chronic pain. The reversal of injury-induced changes in DNA methylation by both a pharmacological and a non-pharmacological intervention, long after the establishment of chronic pain, support this conclusion.

6.2.3. **Limitations**

When considering the results of this thesis and their implications for pain research, a number of limitations must be kept in mind. First, across all three experiments only male mice were used to explore the relationship between PFC DNA methylation and chronic pain. Sexual dimorphism in pain sensitivity has been well established in both human populations and animal models. Pain is more frequently reported by women than men, and several common chronic pain conditions are more prevalent in women [449]. There is also evidence for morphine to be moderately more efficacious in women than men in clinical and experimental studies, though the evidence is less clear for other μ-opioid and κ-opioid receptor acting compounds [450].

Animal models of chronic pain have also revealed robust sex differences in pain sensitivity and biological response with female mice showing greater pain behaviour than their male counterparts [451, 452]. Differences in immune cell activity have been proposed to mediate some proportion of the observed dimorphism [294, 453, 454]. Of

particular relevance to this thesis, a study of mouse medial PFC in SNI found a greater deficit in cognitive flexibility coupled with a loss of parvalbumin expression and decrease in axon initial segment length in layer 5/6 of the infralimbic cortex in males. In contrast, female mice had less impairment and no changes in parvalbumin expression or axon initial segment length [115]. This difference in behaviour and cellular response highlights the clear sexual dimorphism in pain sensitivity and pathobiology between males and females. By collecting only male PFC, the data we present here represents the male PFC DNA methylation response with associated functional domains. However, there are likely to be female specific differential methylation that must be examined to fully understand the relationship between PFC DNA methylation and chronic pain.

Another limitation of this thesis is the use of only one pain model across all three manuscripts. The spared nerve injury model of neuropathic pain produces a persistent and robust peripheral neuropathy, which was preferable to ensure a reliable and consistent pain presentation across all test animals. However, this model does not reflect the clinical presentation or prevalence of chronic pain disorders observed in human populations. In human pain populations, individuals presenting with neuropathic characteristics represent ~20% of all chronic pain sufferers [455-457], and direct nerve damage only accounts for 4% of reported chronic pain [7]. By contrast, rheumatoid and osteoarthritis account for nearly 40% of reported chronic pain, with herniated and deteriorating discs representing an additional 15%. While these conditions underlie the vast majority of chronic pain, their complexity is not represented by our model.

A number of animal models exist to model these more common causes of chronic pain. To model arthritic chronic pain, intra-articular injection of collagen antibodies, collagen, or adjuvants such as Complete Freund's Adjuvant will generally produce an inflammatory response and pain behaviours for 1-2 weeks [458]. Models of discogenic back pain commonly consist of traumatic puncture or damage to lumbar discs, or transgenic knockout induced disc degeneration such as SPARC-null mice [459]. However traumatic puncture of the disc does not always result in discogenic pain, and the transgenic knockout of the SPARC gene could have unforeseen effects upon genetic or epigenetic regulation. Thus, while other pain models may have greater clinical validity and relevance, the SNI model was chosen to produce a reliable and consistent chronic pain phenotype to evaluate PFC DNA methylation across subjects.

6.3. Future Directions

There are a number of questions that require additional investigation to further the work accomplished in this thesis.

1. *To what extent do the observed changes in DNA methylation translate into changes in gene transcription and protein expression?*

There is a clear impact of chronic pain upon PFC DNA methylation. However, previous research has demonstrated that not all changes in DNA methylation translate into meaningful changes in gene transcription and protein expression. Performing follow up RNA-sequencing on the same tissue from which this dataset was derived will help connect DNA methylation changes to potential changes in phenotype. Measurement of

protein expression will provide further insights into the functional outcome of altered DNA methylation.

2. *Which transcription factors are predominantly affected by the observed DNA methylation?*

When DNA methylation occurs in promoters, it can interfere with transcription factor binding as a mechanism for repressing gene expression. Understanding which transcription factors are primarily affected and if their binding sites are altered across all genes or a subset of genes would provide insight to which upstream regulatory pathways are repressed or potentiated and how that affects downstream gene transcription. This could be achieved by identifying the DNA sequence surrounding or proximal to differentially methylated positions and cross-referencing to transcription factor binding motif databases such as JASPAR or ENCODE.

3. *How do changes in PFC DNA methylation relate to observed pain-related behaviours?*

In humans and animal subjects, chronic pain is associated with a number of supraspinally-mediated comorbidities including anxiety, depression, and cognitive decline. Previous research has successfully correlated DNA methylation changes to measures of pain sensitivity [200], however no one has yet investigated their correlation to affective-cognitive processes in the context of chronic pain. Correlating DNA methylation to affective-cognitive dimensions of chronic pain would provide insights to underlying mechanisms, and if compared to DNA methylation correlations with pain sensitivity, may allow us to separate sensory from affective-cognitive mechanisms.

4. *What are the cell-type specific DNA methylation changes?*

Each cell type has its own profile of DNA methylation in accordance with its developmental pathway and current cellular activity. Neurons, microglia, and astrocytes all have well-established and separate contributions to the development and maintenance of chronic pain. Performing fluorescence-activated cell sorting (FACS) before analyzing DNA methylation would allow for cell-type specific methylation profiles to be developed and provide greater insight to cell type response to chronic pain.

5. *Do other pain conditions present with overlapping changes in DNA methylation in PFC?*

Previous studies have demonstrated that different chronic pain syndromes have region-specific patterns of brain activation [460]. As a central integrator of ascending nociceptive input, cognitive and affective responses to pain, and descending modulation, the PFC response to different pain models may vary as well. Utilizing different animal models such as chronic constriction injury, which produces a chronic resolving neuropathy, or induction of chronic inflammatory pain through the destruction of tissues surrounding a joint, may reveal different PFC methylation responses. Understanding commonalities and differences across types of pain will provide insights into the generalizability of these findings and to the potential therapeutic implications.

6.4. Contribution to the Scientific Literature

By examining the relationship between chronic pain and PFC DNA methylation, the work in this thesis consists of several novel contributions to the field of pain research. The significance and impact of these contributions have been discussed in context of the

existing knowledge in the manuscripts and discussion above. They are concisely summarized here:

1. PFC DNA methylation undergoes dynamic and robust changes across the time course of chronic neuropathic pain onset, development, and maintenance, suggesting a time-dependent regulation of gene expression. This study was also the first to show rapid changes in PFC DNA methylation one day after injury.

Topham, L., Gregoire, S., Kang, H., Salmon-Divon, M., Lax, E., Millecamps, M., Szyf, M., & Stone, L. S. (2020). The transition from acute to chronic pain: dynamic epigenetic reprogramming of the mouse prefrontal cortex up to 1 year after nerve injury. *Pain*, *161*(10), 2394–2409.

2. Chronic SAM treatment associated with successful pain attenuation induces changes in PFC DNA methylation at thousands of gene promoters.

Topham, L., Gregoire, S., Kang, H., Salmon-Divon, M., Lax, E., Millecamps, M., Szyf, M., & Stone, L. S. Attenuation of neuropathic pain by SAM is associated with genome-wide reversals of nerve injury induced changes in DNA methylation. *In preparation*

3. Long-term running exercise associated with successful pain attenuation induces changes in PFC DNA methylation at thousands of gene promoters.

Topham, L., Gregoire, S., Kang, H., Salmon-Divon, M., Lax, E., Millecamps, M., Szyf, M., & Stone, L. S. Attenuation of neuropathic pain through voluntary exercise is associated with genome-wide reversals of nerve injury induced changes in DNA methylation. *In preparation*

4. Successful attenuation of neuropathic pain by either SAM treatment or exercise causes a reversal in DNA methylation, correcting pain-induced DNA methylation changes. While this is consistent with work from other domains, we were the first to demonstrate it in a model of chronic pain.

Topham, L., Gregoire, S., Kang, H., Salmon-Divon, M., Lax, E., Millecamps, M., Szyf, M., & Stone, L. S. Attenuation of neuropathic pain by SAM is associated with genome-wide reversals of nerve injury induced changes in DNA methylation. *In preparation*

Topham, L., Gregoire, S., Kang, H., Salmon-Divon, M., Lax, E., Millecamps, M., Szyf, M., & Stone, L. S. Attenuation of neuropathic pain through voluntary exercise is associated with genome-wide reversals of nerve injury induced changes in DNA methylation. *In preparation*

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8.2 Supplemental Tables

Appendix 1

Probe Bed File. Genomic coordinates for the bisulfite capture-sequencing probes

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Appendix 2

Blacklist Bed File. Genomic coordinates for regions known to have anomalous, unstructured, and high signal/read counts in next gen sequencing

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chr11   3198630  3199440
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Appendix 3

Manuscript I: All differentially methylated CpGs and annotated genes identified

geneId	SYMBOL	FDR	DiffMeth	Timepoint
ENSMUSG00000045382	Cxcr4	0.001688827	-41.47582511	D1
ENSMUSG00000070645	Ren1	0.065936369	31.33012821	D1
ENSMUSG00000041577	Prelp	0.039934062	34.21064917	D1
ENSMUSG00000026411	Tmem9	0.089247273	-28.03923324	D1
ENSMUSG00000026479	Lamc2	0.08643574	34.93093522	D1
ENSMUSG00000100221	4930532M18Rik	0.032984078	-34.31364871	D1
ENSMUSG00000056708	Ier5	1.08E-05	-49.96768283	D1
ENSMUSG00000026470	Stx6	9.63E-06	-56.70652877	D1
ENSMUSG00000033684	Qsox1	0.029109334	33.67880486	D1
ENSMUSG00000026466	Tor1aip1	0.039773233	18.05132503	D1
ENSMUSG00000050565	Tor1aip2	0.005457363	49.51505017	D1
ENSMUSG00000101768	NA	0.096590058	23.23051948	D1
ENSMUSG00000103225	NA	0.046842556	-30.25803867	D1
ENSMUSG00000058267	Mrps14	0.080802783	41.15465127	D1
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ENSMUSG00000037499	Nenf	0.00162993	-41.12428634	D1
ENSMUSG00000026637	NA	0.012559273	-33.19569923	D1
ENSMUSG00000026094	Stk17b	6.82E-09	43.0952381	D1
ENSMUSG00000049439	Cyp20a1	0.001673387	38.20059922	D1
ENSMUSG00000102549	NA	1.37E-05	45.02459958	D1
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ENSMUSG00000070031	Sp140	0.000942957	-26.95669571	D1
ENSMUSG00000098634	Mir8096	0.07973354	-25.26467216	D1
ENSMUSG00000098634	Mir8096	0.013242118	-29.08649245	D1
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ENSMUSG00000026271	Gpr35	0.020523108	-39.59623323	D1
ENSMUSG00000037542	Aldh8a1	0.005910155	28.13383619	D1
ENSMUSG00000111368	NA	0.096091794	-21.43712769	D1
ENSMUSG00000075184	F830002L21Rik	0.008358321	-23.17447264	D1
ENSMUSG00000061759	Armt1	0.003693388	28.83247744	D1
ENSMUSG00000020250	Txnrd1	0.082442242	-24.5471968	D1
ENSMUSG00000048981	Krt31	0.055963051	19.46608947	D1
ENSMUSG00000003518	Dusp3	0.000127138	-46.89166702	D1
ENSMUSG00000020930	Ccdc103	0.011126904	33.68818799	D1

ENSMUSG00000075510	Fam187a	0.053606151	32.66145728	D1
ENSMUSG00000034714	Ttyh2	0.022123987	35.86088619	D1
ENSMUSG00000033880	Lgals3bp	0.027117135	-14.31245016	D1
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ENSMUSG00000025137	Pcyt2	3.39E-05	35.40774889	D1
ENSMUSG00000097062	NA	0.001676968	39.32924563	D1
ENSMUSG00000084822	NA	0.00434204	30.02329567	D1
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ENSMUSG00000032878	Ccdc85a	1.29E-05	51.61764706	D1
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ENSMUSG00000065539	Mir216a	1.25E-07	38.13485146	D1
ENSMUSG00000085893	NA	3.35E-06	48.40063803	D1
ENSMUSG00000020458	Rtn4	7.36E-05	45.83047161	D1
ENSMUSG00000020297	Nsg2	0.002735898	-24.25925926	D1
ENSMUSG00000078924	Gm12169	0.002594279	16.26552795	D1
ENSMUSG00000059864	Olfr1393	0.038648134	33.14465403	D1
ENSMUSG00000063386	Olfr1387	5.32E-11	42.67001115	D1
ENSMUSG00000036620	Mgat4b	0.000358108	28.77648667	D1
ENSMUSG00000052642	4930504O13Rik	0.029482075	-27.16964286	D1
ENSMUSG00000108265	Olfr318	0.000448675	34.01686549	D1
ENSMUSG00000108265	Olfr318	0.021390839	28.85450876	D1
ENSMUSG00000107677	Olfr316	0.007662064	-38.01646627	D1
ENSMUSG00000107677	Olfr316	5.18E-09	-43.75238579	D1
ENSMUSG00000060808	B9d1os	0.006114256	-26.2829723	D1
ENSMUSG00000042377	Fam83g	6.88E-05	-28.70741577	D1
ENSMUSG00000004798	Ulk2	0.015255848	35.87301587	D1
ENSMUSG00000041073	Nacad	7.11E-09	-30.28299916	D1
ENSMUSG00000041073	Nacad	0.000919765	42.72178408	D1
ENSMUSG00000018554	Ybx2	0.013652037	-36.33241758	D1
ENSMUSG00000018565	Elp5	0.059443649	-41.27705628	D1
ENSMUSG00000000318	Clec10a	0.008433616	-39.46404984	D1
ENSMUSG00000087512	Gm11985	0.069360175	-25.96582339	D1
ENSMUSG00000017774	Myo1c	0.054504872	-29.54430438	D1
ENSMUSG00000069796	Gm11426	0.00100696	-35.89966965	D1
ENSMUSG00000069796	Gm11426	0.044693772	-24.83409183	D1
ENSMUSG00000020883	Fbxl20	0.002693643	-37.1969697	D1
ENSMUSG00000093176	Mir5119	0.001039287	-25.06339882	D1
ENSMUSG00000019312	Grb7	0.048814643	-23.35202936	D1
ENSMUSG00000038013	Wipf2	2.30E-08	-51.19103323	D1

ENSMUSG00000075570	Krt26	0.017031294	37.28889532	D1
ENSMUSG00000069718	Gm11563	2.34E-05	46.3343254	D1
ENSMUSG00000069717	Gm11568	0.075728989	23.24175904	D1
ENSMUSG00000070335	Krtap9-1	0.006566857	40.52531322	D1
ENSMUSG00000001175	Calm1	0.031240041	-38.40845429	D1
ENSMUSG00000021268	Meg3	0.071775382	-12.90322581	D1
ENSMUSG00000054309	Cpsf3	0.006533812	-30.52320587	D1
ENSMUSG00000070166	NA	0.011227165	-30.17216716	D1
ENSMUSG00000052593	Adam17	5.98E-06	26.25598086	D1
ENSMUSG00000061477	Rps7	4.14E-08	-33.44261574	D1
ENSMUSG00000020629	Adi1	0.038569462	-35.21465844	D1
ENSMUSG00000020628	Trappc12	0.075368346	-14.28812416	D1
ENSMUSG00000020628	Trappc12	0.050828521	-28.1688706	D1
ENSMUSG00000004698	Hdac9	0.050467952	-42.55681818	D1
ENSMUSG00000092305	Prps1l1	1.92E-06	-31.62878788	D1
ENSMUSG00000019256	Ahr	1.43E-07	42.63004157	D1
ENSMUSG00000019256	Ahr	0.001949344	32.26631654	D1
ENSMUSG00000036231	Agr3	0.008587298	41.36716289	D1
ENSMUSG00000055884	Fancm	0.005534294	11.6359447	D1
ENSMUSG00000059114	Lrrc74a	0.014682277	33.68614025	D1
ENSMUSG00000095025	NA	9.79E-06	-45.41053922	D1
ENSMUSG00000021428	Riok1	0.003958819	-36.19319406	D1
ENSMUSG00000044231	Nhlrc1	0.054421625	-35.43568833	D1
ENSMUSG00000114681	NA	1.22E-06	-51.49853801	D1
ENSMUSG00000021555	Naa35	0.013453686	32.43574056	D1
ENSMUSG00000044934	Zfp367	0.035451535	-12.3015873	D1
ENSMUSG00000044934	Zfp367	0.007896056	-15.68153832	D1
ENSMUSG00000021510	Zfp729a	0.002735898	26.67937665	D1
ENSMUSG00000022126	Acod1	0.004286676	-21.36591479	D1
ENSMUSG00000025555	Farp1	0.025863719	22.57575758	D1
ENSMUSG00000037697	Ddhd1	0.03336397	10.41666667	D1
ENSMUSG00000068506	Gm5800	0.099843236	9.25	D1
ENSMUSG00000072571	Tmem253	0.059269192	-12.5	D1
ENSMUSG00000077928	Mir208b	0.06735446	11.02352352	D1
ENSMUSG00000040721	Zfhx2	0.054891712	11.9047619	D1
ENSMUSG00000022208	Jph4	5.74E-07	-38.57744108	D1
ENSMUSG00000022214	Dcaf11	5.28E-10	39.76328012	D1
ENSMUSG00000002325	Irf9	0.001542785	-40.87599945	D1
ENSMUSG00000048279	Sacs	0.090798451	-27.92607374	D1
ENSMUSG00000048279	Sacs	4.21E-07	23.10606061	D1
ENSMUSG00000089531	NA	0.007038643	-30.99229356	D1
ENSMUSG00000022090	Pdlim2	0.089247273	-33.65761689	D1
ENSMUSG00000033470	Cysltr2	0.001436454	-41.02698628	D1

ENSMUSG00000033470	Cysltr2	4.16E-11	-56.92766997	D1
ENSMUSG00000033470	Cysltr2	1.15E-08	-62.19114219	D1
ENSMUSG00000022105	Rb1	3.19E-05	-44.72373188	D1
ENSMUSG00000022070	Bora	0.071283951	-29.29923086	D1
ENSMUSG00000100172	NA	0.019479478	-34.74175741	D1
ENSMUSG00000000530	Acvrl1	0.0989798	-15.97222222	D1
ENSMUSG00000115520	NA	0.000942957	-28.1641604	D1
ENSMUSG00000100127	Gsdmcl-ps	0.039921344	-27.84590611	D1
ENSMUSG00000063354	Slc39a4	0.009132368	-30.46481971	D1
ENSMUSG00000033565	Rbfox2	7.77E-05	-22.32142857	D1
ENSMUSG00000022391	Rangap1	0.001942919	-37.83730159	D1
ENSMUSG00000068105	Tnfrsf13c	0.008501938	-24.81601732	D1
ENSMUSG00000049687	Fam109b	1.63E-09	-38.17599068	D1
ENSMUSG00000076395	NA	7.11E-09	-35.85408685	D1
ENSMUSG00000041852	Tcf20	2.13E-07	-34.35069444	D1
ENSMUSG00000058099	Nfam1	0.006340607	-32.03209147	D1
ENSMUSG00000022387	Brd1	0.004802514	30.9085213	D1
ENSMUSG00000091680	Klhdc7b	0.059310733	27.30383651	D1
ENSMUSG00000055022	Cntn1	6.61E-11	-59.23177273	D1
ENSMUSG00000038084	Opa1	0.032288924	22.11538462	D1
ENSMUSG00000022848	Dirc2	0.035401037	-10.59743954	D1
ENSMUSG00000049436	Upk1b	0.009988705	-18.75	D1
ENSMUSG00000091945	Vmn2r114	0.016761754	-20.95011258	D1
ENSMUSG00000048731	Ggnbp1	0.001061898	-26.23106061	D1
ENSMUSG00000062753	AI413582	0.001114252	-43.93092105	D1
ENSMUSG00000067203	NA	1.91E-06	-25.2759346	D1
ENSMUSG00000092512	NA	0.000205702	-25.85164835	D1
ENSMUSG00000061232	H2-K1	0.021532599	-10.17870422	D1
ENSMUSG00000098197	BC051537	2.35E-05	-17.76315789	D1
ENSMUSG00000098197	BC051537	1.36E-15	-49.21699738	D1
ENSMUSG00000092618	Btnl6	3.16E-06	-27.76144645	D1
ENSMUSG00000040482	Dxo	0.007454505	-22.2826087	D1
ENSMUSG00000007029	Vars	0.009666386	-27.4517368	D1
ENSMUSG00000007029	Vars	0.001130007	-18.67074275	D1
ENSMUSG00000007039	Ddah2	0.050206796	-32.44927458	D1
ENSMUSG00000035929	H2-Q4	0.010051619	23.34917409	D1
ENSMUSG00000035929	H2-Q4	4.84E-09	-24.90188574	D1
ENSMUSG00000093921	NA	0.047756106	-29.53431373	D1
ENSMUSG00000077931	Mir877	0.006566857	-36.37123746	D1
ENSMUSG00000037334	H2-M1	0.033837283	-21.13891011	D1
ENSMUSG00000098178	NA	0.063791144	7.99746653	D1
ENSMUSG00000098178	NA	0.091027721	7.832092422	D1
ENSMUSG00000098178	NA	0.075824161	6.723720227	D1

ENSMUSG00000098178	NA	0.03930705	7.049150154	D1
ENSMUSG00000117272	NA	0.000280389	36.53681087	D1
ENSMUSG00000023961	Enpp4	0.002093759	31.67629896	D1
ENSMUSG00000040327	Cul9	0.092237313	28.63607618	D1
ENSMUSG00000023993	Treml1	0.005306014	-40.32381222	D1
ENSMUSG00000023995	Tspo2	0.082712358	-36.6624687	D1
ENSMUSG00000043592	Unc5cl	7.43E-06	-44.57720588	D1
ENSMUSG00000043592	Unc5cl	4.79E-06	-48.77638033	D1
ENSMUSG00000097095	NA	0.000132916	20.65217391	D1
ENSMUSG00000091504	Vmn2r118	0.000177093	25.86206897	D1
ENSMUSG00000096965	3300005D01Rik	0.038749188	-33.43559411	D1
ENSMUSG00000071322	Tcp10a	0.000124249	-32.90627918	D1
ENSMUSG00000024066	Xdh	6.07E-05	43.58045478	D1
ENSMUSG00000033107	Rnf125	0.031723319	-26.7900782	D1
ENSMUSG00000098607	Mir6360	0.047717391	30.64285714	D1
ENSMUSG00000024376	Epb41l4a	0.00029736	20.58189655	D1
ENSMUSG00000012282	Wnt8a	1.22E-06	41.84149184	D1
ENSMUSG00000024370	Cdc23	7.03E-09	47.06834961	D1
ENSMUSG00000024370	Cdc23	6.90E-08	43.75	D1
ENSMUSG00000051439	Cd14	8.06E-05	25	D1
ENSMUSG00000024456	Diaph1	0.016803491	21.94910353	D1
ENSMUSG00000098608	Mir6981	0.00655392	19.79166667	D1
ENSMUSG00000085289	NA	0.019921461	-27.8612013	D1
ENSMUSG00000102047	2010010A06Rik	0.000358108	-31.8125	D1
ENSMUSG00000024552	Slc14a2	0.097478706	-32.33081584	D1
ENSMUSG00000098363	Mir6993	6.41E-09	54.20565165	D1
ENSMUSG00000098363	Mir6993	1.52E-09	52.06785543	D1
ENSMUSG00000098363	Mir6993	1.76E-12	51.96428571	D1
ENSMUSG00000036372	Tmem258	4.60E-07	52.06196581	D1
ENSMUSG00000024731	Ms4a10	2.49E-08	56.13357843	D1
ENSMUSG00000067571	Ms4a15	5.06E-08	50.98684925	D1
ENSMUSG00000024694	Keg1	0.037678513	-34.39964866	D1
ENSMUSG00000059105	Olfr1504	0.010051619	40.44117647	D1
ENSMUSG00000053279	Aldh1a1	0.035837461	32.15890523	D1
ENSMUSG00000053536	Cstf2t	0.009146276	19.25009999	D1
ENSMUSG00000035783	Acta2	0.076362775	11.25	D1
ENSMUSG00000025014	Dntt	0.001833406	44.81669663	D1
ENSMUSG00000055523	Gucy2g	0.03655099	-37.43235665	D1
ENSMUSG00000097785	B230217O12Rik	0.077952295	-33.32148829	D1
ENSMUSG00000040901	Kcnk18	3.19E-05	-44.02832951	D1
ENSMUSG00000071640	NA	0.025482917	-31.4788153	D1
ENSMUSG00000055312	Them7	0.000692852	-44.13636364	D1
ENSMUSG00000063751	Platr8	0.039475618	-30.03246753	D1

ENSMUSG00000096566	Olfr1306	0.094553521	-29.7826087	D1
ENSMUSG00000086221	4930412B13Rik	0.002791771	-35.28676489	D1
ENSMUSG00000027298	Tyro3	0.008358321	45.99206349	D1
ENSMUSG00000033902	Mapkbp1	4.16E-11	-60.18981019	D1
ENSMUSG00000079110	Capn3	0.046512653	-37.51919983	D1
ENSMUSG00000079110	Capn3	0.006340607	-42.70512821	D1
ENSMUSG00000074884	Serf2	0.017294148	21.15989703	D1
ENSMUSG00000026730	Pter	1.14E-06	-55.4918774	D1
ENSMUSG00000087115	Pcsk2os2	0.007021778	38.94486216	D1
ENSMUSG00000037307	Banf2	1.04E-11	46.77578617	D1
ENSMUSG00000037307	Banf2	1.14E-09	48.52941176	D1
ENSMUSG00000027429	Sec23b	3.01E-15	-72.0599285	D1
ENSMUSG00000027429	Sec23b	4.49E-11	-57.14435154	D1
ENSMUSG00000074754	Smim26	1.02E-19	68.83333333	D1
ENSMUSG00000055177	Cstl1	0.001917003	-30.12425803	D1
ENSMUSG00000027484	Bpifa5	0.000118681	-34.97738176	D1
ENSMUSG00000038523	1700003F12Rik	0.046318001	42.56960299	D1
ENSMUSG00000027598	Itch	0.001336619	28.04473304	D1
ENSMUSG00000038312	Edem2	0.013121979	29.41979659	D1
ENSMUSG00000074649	BC029722	0.004743469	25.03409091	D1
ENSMUSG00000038241	Cep250	0.001275366	20.97222222	D1
ENSMUSG00000074646	6430550D23Rik	3.97E-06	38.39364035	D1
ENSMUSG00000074646	6430550D23Rik	0.027117135	20.30750047	D1
ENSMUSG00000027642	Rpn2	0.013537501	-32.48917749	D1
ENSMUSG00000027650	Tti1	0.003078068	-41.49955437	D1
ENSMUSG00000044405	Adig	0.021532599	35.76010101	D1
ENSMUSG00000027654	Fam83d	0.01320344	-26.78571429	D1
ENSMUSG00000051769	Wfdc15a	1.14E-05	-52.51196172	D1
ENSMUSG00000050383	Svs3b	5.69E-06	52.32905983	D1
ENSMUSG00000027551	Zfp64	0.062662646	20.84677419	D1
ENSMUSG00000087382	Ctcflos	0.041656568	26.92945762	D1
ENSMUSG00000056115	Tas2r134	0.018551182	34.45277149	D1
ENSMUSG00000075141	Olfr1160	0.003067503	-32.8030303	D1
ENSMUSG00000088639	Mir1955	0.000146077	-34.86663739	D1
ENSMUSG00000091575	2010016I18Rik	0.084340796	36.70896695	D1
ENSMUSG00000028159	Dapp1	1.41E-05	-30.15625	D1
ENSMUSG00000049349	Gm5105	0.00655392	-38.02197802	D1
ENSMUSG00000049349	Gm5105	0.0147706	31.70535106	D1
ENSMUSG00000027708	Dcun1d1	0.014454853	-11.71875	D1
ENSMUSG00000104586	NA	0.096980078	14.88882634	D1
ENSMUSG00000036353	P2ry12	0.001571681	26.7166077	D1
ENSMUSG00000049013	Prss48	6.92E-05	46.06112054	D1
ENSMUSG00000015854	Cd5l	0.000215655	33.5797491	D1

ENSMUSG00000074489	Bglap3	0.000677687	-30.20199536	D1
ENSMUSG00000074489	Bglap3	0.071283951	-29.90211426	D1
ENSMUSG00000050092	Sprr2b	0.001336619	-35.11616743	D1
ENSMUSG00000042212	Sprr2d	0.000827167	-28.74080882	D1
ENSMUSG00000028528	Dnajc6	2.67E-05	-39.38994045	D1
ENSMUSG00000028528	Dnajc6	0.090279271	-29.72170599	D1
ENSMUSG00000033985	Tesk2	0.000111547	41.5625	D1
ENSMUSG00000028687	Mutyh	0.026359036	-40.98285082	D1
ENSMUSG00000033379	Atp6v0b	0.007038643	32.52966545	D1
ENSMUSG00000032870	Smap2	0.030991965	35.69791325	D1
ENSMUSG00000028649	Macf1	0.060943679	14.86437843	D1
ENSMUSG00000028876	Epha10	0.067346904	24.59232072	D1
ENSMUSG00000028936	Rpl22	0.029889024	29.95630637	D1
ENSMUSG00000029064	Gnb1	0.000195504	-42.97063081	D1
ENSMUSG00000073680	Tmem88b	0.028025085	27.58516845	D1
ENSMUSG00000029071	Dvl1	0.02594613	33.6802744	D1
ENSMUSG00000051557	Pusl1	0.018353173	33.8631048	D1
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ENSMUSG00000110404	Rnf223	0.001064472	-29.84334293	D1
ENSMUSG00000028280	Gabrr1	0.06068008	17.5	D1
ENSMUSG00000028232	Tmem68	0.003828047	31.40661499	D1
ENSMUSG00000035539	Ccdc180	0.055596562	15.97947875	D1
ENSMUSG00000039740	Alg2	0.054553167	-26.45968727	D1
ENSMUSG00000066324	Impad1	0.001375031	36.45289855	D1
ENSMUSG00000085108	Saxo1os	0.028292171	-35.55363876	D1
ENSMUSG00000088958	Scarna8	0.000287715	-34.15178571	D1
ENSMUSG00000028573	Fggy	0.04438631	-23.48160661	D1
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ENSMUSG00000029504	Ddx51	0.000174952	27.92207792	D1
ENSMUSG00000029504	Ddx51	0.007486442	20	D1
ENSMUSG00000029504	Ddx51	1.14E-07	30.85284281	D1
ENSMUSG00000098656	Mir7028	0.002693643	-19.48701299	D1
ENSMUSG00000041827	Oasl1	0.000446002	35.13738215	D1
ENSMUSG00000029454	Mapkapk5	0.077952295	12.73996265	D1
ENSMUSG00000029458	Brap	0.085837618	22.74853801	D1
ENSMUSG00000085957	Syna	0.00943105	33.36585315	D1
ENSMUSG00000007987	Ift22	0.079356125	-9.298515105	D1
ENSMUSG00000001739	Cldn15	0.035480405	31.85076291	D1
ENSMUSG00000037364	Srrt	0.000376123	23.86363636	D1
ENSMUSG00000037364	Srrt	0.01539898	13.46153846	D1

ENSMUSG00000104752	Gm5565	0.000205702	7.989690722	D1
ENSMUSG00000096798	Gm6309	0.001058069	13.79032258	D1
ENSMUSG00000106680	NA	0.077952295	30.66132173	D1
ENSMUSG00000104950	NA	0.016419474	37.03500204	D1
ENSMUSG00000040351	Ankib1	0.002389355	41.36796305	D1
ENSMUSG00000098264	Mir6414	0.01539094	18.02380952	D1
ENSMUSG00000029086	Prom1	0.000107483	-30.18583917	D1
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ENSMUSG00000079666	1700015F17Rik	0.007934254	32.4645983	D1
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ENSMUSG00000029204	Rhoh	0.025102211	-17.66917293	D1
ENSMUSG00000070780	Rbm47	0.046500679	-21.57407407	D1
ENSMUSG00000054892	Txk	0.096998409	-30.39321789	D1
ENSMUSG00000054892	Txk	0.08511121	-26.73597025	D1
ENSMUSG00000029153	Ociad2	0.054432331	-22.06832298	D1
ENSMUSG00000036256	Igfbp7	6.92E-05	-46.75457365	D1
ENSMUSG00000047652	NA	0.009127747	-39.50534759	D1
ENSMUSG00000029413	Naaa	0.023941248	44.84848485	D1
ENSMUSG00000030127	Cops7a	0.027423389	-8.887520525	D1
ENSMUSG00000071112	Spx	0.037218941	33.20649938	D1
ENSMUSG00000032942	Ucp3	1.88E-10	-41.24338624	D1
ENSMUSG00000030888	Rrp8	0.027629149	29.31129043	D1
ENSMUSG00000099579	1700120K04Rik	0.053606151	30.40506267	D1
ENSMUSG00000030780	BC017158	6.07E-05	46.21212121	D1
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ENSMUSG00000041578	Crx	0.027158871	-40.81520946	D1
ENSMUSG00000074365	Crxos	0.059310733	-21.8157748	D1
ENSMUSG00000007209	Ceacam9	0.000280389	33.452731	D1
ENSMUSG00000040866	Rsph6a	0.055883411	40.36796537	D1
ENSMUSG00000090715	Vmn1r167	0.014451248	24.31979346	D1
ENSMUSG00000092456	V1rd19	7.17E-06	30.41941744	D1
ENSMUSG00000108430	NA	0.003047266	-12.5	D1
ENSMUSG00000084174	Sycn	0.068080962	-26.91045168	D1
ENSMUSG00000046056	Sbsn	0.000550998	13.70967742	D1
ENSMUSG00000030463	4933421I07Rik	1.57E-07	-41.31730536	D1
ENSMUSG00000030463	4933421I07Rik	0.001657294	-28.36360229	D1
ENSMUSG00000030463	4933421I07Rik	0.01111679	-29.27864522	D1
ENSMUSG00000108438	NA	1.22E-06	-50.39241102	D1
ENSMUSG00000108438	NA	4.03E-07	-50.81858116	D1
ENSMUSG00000063713	Klk1b24	3.86E-07	-40.38008813	D1
ENSMUSG00000063713	Klk1b24	3.33E-06	-51.29960317	D1
ENSMUSG00000038704	Aspdh	0.0545549	14.20454545	D1
ENSMUSG00000038695	Josd2	1.00E-06	23.63095238	D1

ENSMUSG00000109236	NA	1.62E-11	44.55739998	D1
ENSMUSG00000058743	Kcnj14	0.084624914	23.71904837	D1
ENSMUSG00000070551	Mrgprb5	0.023911127	-32.91765348	D1
ENSMUSG00000030737	Slco2b1	0.018462333	26.86983573	D1
ENSMUSG00000030737	Slco2b1	3.60E-07	-37.20588235	D1
ENSMUSG00000098560	NA	0.042992437	18.53603604	D1
ENSMUSG00000001995	Sipa1l2	4.10E-05	-30.68657635	D1
ENSMUSG00000060427	Zfp868	0.001014943	15	D1
ENSMUSG00000005481	Ddx39	2.58E-05	25.73246452	D1
ENSMUSG00000031659	Adcy7	0.004743469	40.91804331	D1
ENSMUSG00000031661	Nkd1	0.032984078	-19.56711496	D1
ENSMUSG00000071047	Ces1a	0.059310733	25.96351846	D1
ENSMUSG00000032534	Cep63	0.012143969	17.30392157	D1
ENSMUSG00000032534	Cep63	9.09E-08	38.75377074	D1
ENSMUSG00000032534	Cep63	2.31E-13	55.47619048	D1
ENSMUSG00000032547	Ryk	0.021862208	-43.07255245	D1
ENSMUSG00000032577	Mapkapk3	0.091431211	16.86516778	D1
ENSMUSG00000025650	Col7a1	0.037792906	33.76908971	D1
ENSMUSG00000111564	NA	0.004743469	29.35606061	D1
ENSMUSG00000057551	Zfp317	0.016629095	-15.32033776	D1
ENSMUSG00000047822	Angptl8	0.037792906	-25.11496451	D1
ENSMUSG00000032125	Robo4	0.068080962	-12.47311828	D1
ENSMUSG00000002031	Ift46	0.076447623	34.82465247	D1
ENSMUSG00000002031	Ift46	0.06068008	34.72086737	D1
ENSMUSG00000002031	Ift46	0.045971258	34.36771562	D1
ENSMUSG00000037129	Tmprss13	0.085837618	15.51282051	D1
ENSMUSG00000032030	Cul5	0.003092308	44.36559365	D1
ENSMUSG00000035200	Chrnb4	3.81E-05	-48.68347685	D1
ENSMUSG00000032327	Stra6	0.002088162	-25	D1
ENSMUSG00000032327	Stra6	0.037461918	-21.70262533	D1
ENSMUSG00000032401	Lctl	0.028217566	-28.08162268	D1
ENSMUSG00000032401	Lctl	0.030255085	-42.46794872	D1
ENSMUSG00000007656	Arpp19	0.041511365	-28.2391934	D1
ENSMUSG00000032192	Gnb5	5.81E-05	-38.56315253	D1
ENSMUSG00000037410	Tbc1d2b	2.09E-06	38.5410642	D1
ENSMUSG00000046242	1600029I14Rik	0.000447989	-33.98018648	D1
ENSMUSG00000009670	Tex11	0.00326433	-50	D1
ENSMUSG00000035299	Mid1	0.051176464	18.75729349	D1
ENSMUSG00000035299	Mid1	0.010773518	20.56067966	D1
ENSMUSG00000035299	Mid1	0.047404977	22.52390424	D1
ENSMUSG00000035299	Mid1	0.044715997	18.7011187	D1
ENSMUSG00000035299	Mid1	0.042992437	18.40645161	D1
ENSMUSG00000035299	Mid1	0.044982426	21.02715846	D1

ENSMUSG00000035299	Mid1	0.016629095	23.0935859	D1
ENSMUSG00000035299	Mid1	0.010051619	21.97269268	D1
ENSMUSG00000035299	Mid1	0.015141991	29.65342694	D1
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ENSMUSG00000035299	Mid1	0.014451248	32.12258256	D1
ENSMUSG00000035299	Mid1	0.074580095	28.90180228	D1
ENSMUSG00000086695	NA	0.02558524	41.60196687	D1
ENSMUSG00000086695	NA	0.085723151	37.04784799	D1
ENSMUSG00000086695	NA	0.013687739	42.35209235	D1
ENSMUSG00000086695	NA	0.059310733	31.85216544	D1
ENSMUSG00000026347	Tmem163	0.000360038	-40.58059931	W2
ENSMUSG00000102014	2900009J06Rik	8.53E-05	-38.41269841	W2
ENSMUSG00000099760	NA	0.00279835	35.49355281	W2
ENSMUSG00000099760	NA	6.53E-07	43.35515873	W2
ENSMUSG00000045382	Cxcr4	5.21E-05	42.68981197	W2
ENSMUSG00000097028	Ptgs2os	0.000272516	29.38029502	W2
ENSMUSG00000026483	Fam129a	1.13E-07	25.09752322	W2
ENSMUSG00000059503	Olfr248	0.003155122	8.890286366	W2
ENSMUSG00000097291	NA	0.000802955	-26.14594083	W2
ENSMUSG00000026048	Ercc5	0.003696369	28.33622475	W2
ENSMUSG00000099950	9130227L01Rik	0.099967455	20.67442188	W2
ENSMUSG00000051223	Bzw1	0.024404597	-26.69349559	W2
ENSMUSG00000026196	Bard1	0.03292629	-25.12493978	W2
ENSMUSG00000055322	Tns1	0.036342605	30.94558326	W2
ENSMUSG00000055322	Tns1	0.018523991	35.30281449	W2
ENSMUSG00000055322	Tns1	0.00125968	-30.12715927	W2
ENSMUSG00000064272	Gpbar1	0.001330288	30.11376953	W2
ENSMUSG00000033276	Stk36	0.001116634	-36.60265149	W2
ENSMUSG00000033257	Ttll4	0.043079618	-33.21262071	W2
ENSMUSG00000026253	Chrng	0.049989172	-22.60613133	W2
ENSMUSG00000070732	Rbm44	0.000258355	-15.4077723	W2
ENSMUSG00000034353	Ramp1	0.006958629	-14.70707071	W2
ENSMUSG00000073608	Gal3st2c	0.001262238	24.31979111	W2
ENSMUSG00000034764	NA	0.001799792	32.4626354	W2
ENSMUSG00000019853	Hebp2	0.085945646	25.03581295	W2
ENSMUSG00000019986	Ahi1	0.000802955	39.80986655	W2
ENSMUSG00000019986	Ahi1	5.55E-05	40.67954389	W2
ENSMUSG00000050844	1700020N01Rik	0.003376586	15.90909091	W2
ENSMUSG00000050844	1700020N01Rik	0.006804902	15	W2
ENSMUSG00000048981	Krt31	2.69E-10	40.41346771	W2
ENSMUSG00000017316	Ppy	0.002404959	-32.40511738	W2
ENSMUSG00000080694	NA	3.29E-07	-47.90639989	W2
ENSMUSG00000034714	Ttyh2	3.24E-06	40.80655456	W2

ENSMUSG00000020792	Exoc7	0.000155741	18.18452381	W2
ENSMUSG00000077604	Snord1b	1.41E-11	36.60714286	W2
ENSMUSG00000025579	Gaa	0.048145039	-19.30424133	W2
ENSMUSG00000020279	Il9r	0.002360312	-27.54007473	W2
ENSMUSG00000020289	Nprl3	0.072305532	-19.64682962	W2
ENSMUSG00000040350	Trim7	0.020740539	15.8859992	W2
ENSMUSG00000040350	Trim7	0.093380251	12.44017015	W2
ENSMUSG00000040350	Trim7	0.00308554	21.72651423	W2
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ENSMUSG00000108265	Olfr318	0.002857907	-13.27744879	W2
ENSMUSG00000060030	Olfr317	0.015081272	-15.54554836	W2
ENSMUSG00000048919	Olfr223	0.001138627	28.08488613	W2
ENSMUSG00000005417	Mprip	0.040619442	23.27171661	W2
ENSMUSG00000010122	Slc47a1	0.041300312	9.418060201	W2
ENSMUSG00000033196	Myh2	0.006117578	-28.28168671	W2
ENSMUSG00000093100	Mir3971	0.033809317	16.47692436	W2
ENSMUSG00000093100	Mir3971	1.18E-05	27.52122085	W2
ENSMUSG00000035385	Ccl2	0.038912634	-25.89862561	W2
ENSMUSG00000035373	Ccl7	0.00161393	-27.97523741	W2
ENSMUSG00000035373	Ccl7	3.63E-05	-34.42901562	W2
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ENSMUSG00000046010	Zfp830	0.092969369	-20.65627944	W2
ENSMUSG00000046010	Zfp830	0.097161257	-17.45104332	W2
ENSMUSG00000020692	Nle1	0.007269201	28.56316704	W2
ENSMUSG00000020866	Cacna1g	0.059141313	28.60837222	W2
ENSMUSG00000020866	Cacna1g	9.36E-07	41.51843264	W2
ENSMUSG00000010080	Epn3	1.02E-06	-31.23021182	W2
ENSMUSG00000010080	Epn3	6.31E-08	-43.2082549	W2
ENSMUSG00000038013	Wipf2	3.72E-06	-37.19164169	W2
ENSMUSG00000020914	Top2a	0.066190004	27.62122606	W2
ENSMUSG00000017607	Tns4	0.000127802	-43.14177946	W2
ENSMUSG00000060807	Serpina6	0.000141062	-24.52589808	W2
ENSMUSG00000021081	Serpina1f	0.072776386	24.34015847	W2
ENSMUSG00000085820	4933406K04Rik	0.044882195	-12.36918878	W2
ENSMUSG00000085641	4930465M20Rik	0.015984729	-28.60835092	W2
ENSMUSG00000058070	Eml1	0.006511943	20.95948058	W2
ENSMUSG00000060950	Trmt61a	0.00026989	-11.22916311	W2
ENSMUSG00000056553	Ptprn2	0.028210279	-30.06525422	W2
ENSMUSG00000020672	Sntg2	0.005830447	23.76811994	W2
ENSMUSG00000112708	NA	0.004939515	-33.44830985	W2
ENSMUSG00000007867	Ift43	0.001882023	26.37738078	W2
ENSMUSG00000021254	Gpatch2l	0.045140638	28.69725983	W2
ENSMUSG00000015533	Itga2	0.000151744	-15.85229692	W2

ENSMUSG00000114255	NA	0.072083844	29.7295865	W2
ENSMUSG00000021313	Ryr2	0.064035019	-15.98902187	W2
ENSMUSG00000041112	Elmo1	0.036799974	-28.92912435	W2
ENSMUSG00000050295	Foxc1	0.058074953	-5.032051282	W2
ENSMUSG00000045410	Akr1e1	0.001882023	21.04545166	W2
ENSMUSG00000045410	Akr1e1	0.003063331	17.77531058	W2
ENSMUSG00000094772	NA	0.014057842	23.91957613	W2
ENSMUSG00000074870	Cts3	2.45E-10	-47.57791144	W2
ENSMUSG00000074870	Cts3	8.65E-09	-41.05917874	W2
ENSMUSG00000074870	Cts3	4.64E-06	-33.32674331	W2
ENSMUSG00000069805	Fbp1	0.028989207	-21.83123249	W2
ENSMUSG00000069805	Fbp1	0.020200628	-28.81159702	W2
ENSMUSG00000097101	1810034E14Rik	0.024932062	28.17043363	W2
ENSMUSG00000059839	Zfp874b	3.63E-05	-40.01560939	W2
ENSMUSG00000021611	Tert	0.007267276	31.127285	W2
ENSMUSG00000021549	Rasa1	0.00750925	14.08029879	W2
ENSMUSG00000058571	Gpc6	3.46E-15	-64.75815851	W2
ENSMUSG00000115016	AA536875	7.69E-07	35.02993207	W2
ENSMUSG00000072707	Olfr31	0.001262238	36.77872079	W2
ENSMUSG00000105635	NA	0.003243935	22.48067226	W2
ENSMUSG00000023243	Kcnk5	0.063587522	19.91245502	W2
ENSMUSG00000093081	Mir3075	0.000100758	31.92366949	W2
ENSMUSG00000071547	Nt5dc2	1.80E-06	-34.46531142	W2
ENSMUSG00000065481	Mir346	0.000553402	-27.90491308	W2
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ENSMUSG00000037697	Ddhd1	0.086189058	7.638888889	W2
ENSMUSG00000072575	Eddm3b	0.043079618	-22.29381953	W2
ENSMUSG00000059606	Rnase2b	0.017369136	13.52136752	W2
ENSMUSG00000000606	Vmn2r88	0.000802727	-25.19749364	W2
ENSMUSG00000022090	Pdlim2	0.012682154	19.42344498	W2
ENSMUSG00000093550	Higd1c	0.000518978	-29.42426459	W2
ENSMUSG00000093550	Higd1c	0.077694857	-29.40083844	W2
ENSMUSG00000058354	Krt6a	0.001073391	-17.64770193	W2
ENSMUSG00000058794	Nfe2	0.007269201	-31.30506411	W2
ENSMUSG00000022314	Rad21	0.041511647	13.82131757	W2
ENSMUSG00000098631	Mir6957	0.041025033	16.10414296	W2
ENSMUSG00000068099	1500009C09Rik	0.001307105	-15.18640351	W2
ENSMUSG00000049687	Fam109b	0.002791835	-9.656741108	W2
ENSMUSG00000076395	NA	8.43E-06	-13.73869261	W2
ENSMUSG00000116343	NA	0.001882023	16.32352941	W2
ENSMUSG00000037525	Bcdin3d	0.0010149	-35.89659275	W2
ENSMUSG00000037525	Bcdin3d	1.13E-05	-37.51208514	W2
ENSMUSG00000094430	Smbd1	0.006678231	25.88783442	W2

ENSMUSG00000022664	Slc35a5	4.52E-13	-36.59931078	W2
ENSMUSG00000052013	Btla	7.98E-11	-38.14183502	W2
ENSMUSG00000039763	Dnajc28	0.000566621	-23.4119224	W2
ENSMUSG00000061544	Zfp229	0.001267697	26.90871509	W2
ENSMUSG00000091945	Vmn2r114	0.004237021	26.61517307	W2
ENSMUSG00000091076	Vmn2r115	0.001901586	29.08499882	W2
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ENSMUSG00000062753	AI413582	0.004529764	-33.15338901	W2
ENSMUSG00000097217	NA	2.29E-08	24.86542443	W2
ENSMUSG00000079563	Pglyrp2	7.83E-05	35.37367479	W2
ENSMUSG00000067203	NA	0.000110945	19.48544231	W2
ENSMUSG00000073420	NA	3.69E-05	29.08424034	W2
ENSMUSG00000092618	Btnl6	1.88E-08	28.57750127	W2
ENSMUSG00000015468	Notch4	0.084997578	-26.46028155	W2
ENSMUSG00000073418	C4b	0.00494157	-23.43785472	W2
ENSMUSG00000073411	H2-D1	0.00534716	27.88187081	W2
ENSMUSG00000073411	H2-D1	0.027086969	16.54372105	W2
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ENSMUSG00000039269	2300002M23Rik	0.043148116	30.52929369	W2
ENSMUSG00000093921	NA	0.008453213	-24.70855625	W2
ENSMUSG00000077931	Mir877	0.019011404	-26.81754073	W2
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ENSMUSG00000025431	Crisp1	0.006804902	26.69215896	W2
ENSMUSG00000023961	Enpp4	0.058074953	17.6503578	W2
ENSMUSG00000070209	NA	6.99E-05	28.23490215	W2
ENSMUSG00000047150	1700001C19Rik	0.034969682	-23.14692982	W2
ENSMUSG00000117399	NA	2.23E-05	-32.30107855	W2
ENSMUSG00000071856	Mcc	0.089104626	-20.4186114	W2
ENSMUSG00000054072	Iigp1	0.099874351	-26.80330903	W2
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ENSMUSG00000032735	Ablim3	1.51E-05	-37.91119872	W2
ENSMUSG00000098366	Mir145b	0.000411976	-33.67209951	W2
ENSMUSG00000035765	Dym	0.000464192	28.05439211	W2
ENSMUSG00000102047	2010010A06Rik	0.018502335	27.38129002	W2
ENSMUSG00000024827	Gldc	0.035381068	-12.11868054	W2
ENSMUSG00000024771	Lipk	0.000102196	31.31168696	W2
ENSMUSG00000024907	Gal	0.025930189	25.91787233	W2
ENSMUSG00000055491	Pprc1	0.000112531	-16.29352279	W2
ENSMUSG00000055491	Pprc1	7.03E-05	-15.47149684	W2
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ENSMUSG00000042694	Stn1	0.091149097	-20.44376112	W2
ENSMUSG00000024975	Pdcd4	3.24E-06	-23.55581963	W2
ENSMUSG00000024976	Shoc2	9.16E-05	-15.52795031	W2

ENSMUSG00000082934	NA	5.86E-06	-42.5763289	W2
ENSMUSG00000055312	Them7	1.41E-08	-46.31061495	W2
ENSMUSG00000055312	Them7	0.001250765	34.93273863	W2
ENSMUSG00000086221	4930412B13Rik	0.006055096	26.02750748	W2
ENSMUSG00000079110	Capn3	0.000269525	18.49477683	W2
ENSMUSG00000027288	Zfp106	0.012083221	-24.83751044	W2
ENSMUSG00000038312	Edem2	1.02E-06	-21.71057328	W2
ENSMUSG00000074649	BC029722	1.49E-07	-20.79661162	W2
ENSMUSG00000038241	Cep250	0.000322858	-23.1351527	W2
ENSMUSG00000038241	Cep250	2.10E-06	-16.64318378	W2
ENSMUSG00000074646	6430550D23Rik	9.36E-07	-28.81313131	W2
ENSMUSG00000074646	6430550D23Rik	4.00E-07	-27.61752137	W2
ENSMUSG00000074646	6430550D23Rik	1.30E-07	-29.52850877	W2
ENSMUSG00000027624	Epb41l1	6.17E-05	-18.68253968	W2
ENSMUSG00000074628	Tldc2	0.001573164	22.7452776	W2
ENSMUSG00000084113	NA	0.000641942	16.57206991	W2
ENSMUSG00000037820	Tgm2	0.000418885	18.85278396	W2
ENSMUSG00000027670	Ocstamp	0.018502335	-25.67381216	W2
ENSMUSG00000082641	NA	6.76E-05	-31.0688808	W2
ENSMUSG00000026740	Dnajc1	0.081217417	28.33149049	W2
ENSMUSG00000035772	Mrps2	0.097693788	7.732980084	W2
ENSMUSG00000043102	Qrfp	0.009723821	27.54752734	W2
ENSMUSG00000001855	Nup214	0.049243904	24.02960014	W2
ENSMUSG00000009566	Fpgs	6.02E-07	34.92097199	W2
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ENSMUSG00000053746	Ptrh1	0.00182253	31.09539843	W2
ENSMUSG00000041921	Metap1d	0.072040922	-17.67676768	W2
ENSMUSG00000006494	Pdk1	1.03E-10	-49.34126984	W2
ENSMUSG00000028159	Dapp1	1.88E-08	-21.67343977	W2
ENSMUSG00000049349	Gm5105	0.034990381	22.05847566	W2
ENSMUSG00000027550	Lrrcc1	3.19E-06	31.87619896	W2
ENSMUSG00000028188	Spata1	0.058594638	-23.09395644	W2
ENSMUSG00000005034	Prkacb	0.013569165	7.268518519	W2
ENSMUSG00000048581	E130311K13Rik	0.001673614	-28.89243329	W2
ENSMUSG00000027788	Otol1	0.037936543	-28.2137642	W2
ENSMUSG00000088484	NA	4.45E-05	-31.48888845	W2
ENSMUSG00000028011	Tdo2	0.004179993	-25.10683761	W2
ENSMUSG00000101334	1700028M03Rik	3.12E-06	37.98843851	W2
ENSMUSG00000041842	Fhdc1	0.006706974	36.29187505	W2
ENSMUSG00000027927	Lelp1	0.00014867	-16.8942577	W2
ENSMUSG00000042212	Sprr2d	1.43E-05	-26.58080808	W2
ENSMUSG00000042212	Sprr2d	3.61E-10	-20.73311106	W2
ENSMUSG00000055030	Sprr2e	2.37E-07	-27.36111111	W2

ENSMUSG00000045539	Sprr3	1.66E-06	-18.75034705	W2
ENSMUSG00000074433	Lce3e	0.015745036	28.96701338	W2
ENSMUSG00000005779	Psmb4	3.63E-05	-29.90503459	W2
ENSMUSG00000087660	NA	3.07E-05	-32.35724477	W2
ENSMUSG00000019338	Zfp687	0.048850686	-13.68951103	W2
ENSMUSG00000038298	Pdzk1	0.099967455	-16.71516755	W2
ENSMUSG00000034919	Ttc22	0.000518978	20.67307692	W2
ENSMUSG00000086080	1700123O12Rik	0.000777791	28.72315439	W2
ENSMUSG00000028702	Rad54l	0.01108887	37.80522161	W2
ENSMUSG00000028700	Pomgnt1	0.026260586	25.63993584	W2
ENSMUSG00000028692	Akr1a1	0.070702967	-22.55296991	W2
ENSMUSG00000028687	Mutyh	0.000802955	28.34928156	W2
ENSMUSG00000028677	Rnf220	0.013186607	21.88997821	W2
ENSMUSG00000033295	Ptprf	0.008579484	-24.49759391	W2
ENSMUSG00000033253	Szt2	0.037976777	24.89729225	W2
ENSMUSG00000006392	Med8	0.018502335	27.11106405	W2
ENSMUSG00000006390	Elovl1	5.31E-07	-23.86695906	W2
ENSMUSG00000042616	Oscp1	0.00465654	10.68578256	W2
ENSMUSG00000042616	Oscp1	0.023847214	12.63338085	W2
ENSMUSG00000042616	Oscp1	1.18E-05	12.75532263	W2
ENSMUSG00000042616	Oscp1	0.001000175	9.834390416	W2
ENSMUSG00000042616	Oscp1	0.000411976	12.21468074	W2
ENSMUSG00000042616	Oscp1	0.029382162	9.871031746	W2
ENSMUSG00000042616	Oscp1	0.000100538	13.9668616	W2
ENSMUSG00000042616	Oscp1	0.01616783	10.06944444	W2
ENSMUSG00000042616	Oscp1	0.017391213	10.12196545	W2
ENSMUSG00000028779	Pef1	0.000803359	33.80217985	W2
ENSMUSG00000028776	Tinagl1	0.002546612	31.25789847	W2
ENSMUSG00000023232	Serinc2	0.072776386	30.05673907	W2
ENSMUSG00000078532	Nkain1	8.61E-08	39.36090462	W2
ENSMUSG00000078532	Nkain1	0.00070486	31.38001983	W2
ENSMUSG00000048003	Catsper4	0.000288515	-27.45690035	W2
ENSMUSG00000052912	Smarca5-ps	0.043959669	-28.05520058	W2
ENSMUSG00000041616	Nppa	0.091149097	13.62535613	W2
ENSMUSG00000065549	Mir200b	0.0097584	-26.42443908	W2
ENSMUSG00000110404	Rnf223	0.000679803	-35.85672408	W2
ENSMUSG00000028458	Tesk1	2.79E-12	-27.93637292	W2
ENSMUSG00000028458	Tesk1	1.41E-08	-24.64627897	W2
ENSMUSG00000028467	Gba2	0.004818619	-38.80224414	W2
ENSMUSG00000071001	Hrct1	0.029727427	-27.91666667	W2
ENSMUSG00000071000	Olfr155	0.024932062	-25.82425563	W2
ENSMUSG00000092677	Mir5106	0.011699315	31.16539771	W2
ENSMUSG00000041261	Car8	0.068387916	-21.10320557	W2

ENSMUSG00000085108	Saxo1os	4.42E-05	-33.71657754	W2
ENSMUSG00000050640	Tmem150c	0.023847214	25.52692723	W2
ENSMUSG00000029430	Ran	5.34E-07	26.2962963	W2
ENSMUSG00000019054	Fis1	0.097063594	15.30835767	W2
ENSMUSG00000095040	1700001J03Rik	0.025015334	9.285714286	W2
ENSMUSG00000029647	Pan3	0.027867731	-23.02105978	W2
ENSMUSG00000086494	2210417A02Rik	2.42E-08	-37.11836004	W2
ENSMUSG00000107313	NA	0.018906603	32.72253128	W2
ENSMUSG00000038181	Chpf2	0.00308554	-33.36958044	W2
ENSMUSG00000038044	Cct8l1	1.16E-05	31.14610517	W2
ENSMUSG00000029182	1700001C02Rik	0.000856285	30.63082421	W2
ENSMUSG00000098830	Mir7024	0.008560064	15.92362486	W2
ENSMUSG00000029082	Bst1	3.72E-06	-37.34572617	W2
ENSMUSG00000029086	Prom1	2.51E-08	-36.23025303	W2
ENSMUSG00000029086	Prom1	2.51E-06	35.45835428	W2
ENSMUSG00000015806	Qdpr	0.073718131	-18.00043659	W2
ENSMUSG00000015879	Fam184b	0.036544997	-18.53126189	W2
ENSMUSG00000029089	Pacrgl	0.0062294	-26.17434853	W2
ENSMUSG00000029089	Pacrgl	0.000524134	-20.07488261	W2
ENSMUSG00000052295	8030423F21Rik	0.009373635	-21.05666006	W2
ENSMUSG00000029204	Rhoh	0.015745036	27.90020899	W2
ENSMUSG00000070780	Rbm47	0.068587553	23.09912606	W2
ENSMUSG00000036256	Igfbp7	0.008330015	31.68110509	W2
ENSMUSG00000029381	Shroom3	0.040625374	13.50241546	W2
ENSMUSG00000057604	Lmcd1	2.77E-05	29.62690331	W2
ENSMUSG00000057604	Lmcd1	6.99E-05	26.44650843	W2
ENSMUSG00000094626	Tmem121b	0.007067375	-30.54459064	W2
ENSMUSG00000004902	Slc25a18	0.073927389	19.01515152	W2
ENSMUSG00000004902	Slc25a18	0.00182253	23.37417618	W2
ENSMUSG00000051586	Mical3	4.20E-09	33.75518926	W2
ENSMUSG00000051586	Mical3	0.000602782	21.93325193	W2
ENSMUSG00000086527	NA	4.94E-08	-48.66666667	W2
ENSMUSG00000030107	Usp18	0.00019323	27.94444444	W2
ENSMUSG00000106580	Mir7231	0.011883262	-29.1357443	W2
ENSMUSG00000030127	Cops7a	0.000814587	-9.057971014	W2
ENSMUSG00000079304	Tex52	0.001046441	34.17844257	W2
ENSMUSG00000041791	Capza3	8.81E-05	-37.56477591	W2
ENSMUSG00000030231	Plekha5	0.000281254	41.45450383	W2
ENSMUSG00000107456	Gm10400	5.82E-05	37.26698269	W2
ENSMUSG00000030259	Rassf8	0.019494748	31.35862816	W2
ENSMUSG00000108161	NA	1.41E-07	31.42391479	W2
ENSMUSG00000085600	E330012B07Rik	1.18E-05	-18.59567901	W2
ENSMUSG00000072660	NA	5.49E-11	-40.47274363	W2

ENSMUSG00000097716	1700026J14Rik	0.004750178	10.63492063	W2
ENSMUSG00000009281	Rarres2	0.001000175	12.54372814	W2
ENSMUSG00000052730	Gm5111	2.22E-05	18.91260252	W2
ENSMUSG00000052730	Gm5111	0.003705105	14.13426884	W2
ENSMUSG00000052730	Gm5111	0.000281254	12.62345679	W2
ENSMUSG00000007216	Zfp775	0.001138627	17.15686275	W2
ENSMUSG00000047867	Gimap6	0.001137393	14.09029014	W2
ENSMUSG00000108130	NA	0.007752555	15.12820513	W2
ENSMUSG00000054422	Fabp1	0.001400237	-30.55848989	W2
ENSMUSG00000055027	Smyd1	0.000320246	-25.94819328	W2
ENSMUSG00000055027	Smyd1	0.015081272	-28.75679983	W2
ENSMUSG00000107397	NA	0.0153881	26.91798942	W2
ENSMUSG00000032942	Ucp3	0.014235391	10.86956522	W2
ENSMUSG00000057596	Trim30d	0.006678231	23.5796623	W2
ENSMUSG00000030929	Eri2	0.017469195	25.33475783	W2
ENSMUSG00000030929	Eri2	0.060841339	22.51105512	W2
ENSMUSG00000045733	Sprn	0.001952354	25.46963271	W2
ENSMUSG00000003549	Ercc1	0.021931013	-28.19610113	W2
ENSMUSG00000062300	Nectin2	0.045904793	25.57417004	W2
ENSMUSG00000053964	Lgals4	0.029626165	29.05110649	W2
ENSMUSG00000063808	Gpatch1	0.096659906	16.84267859	W2
ENSMUSG00000030463	4933421I07Rik	0.004459828	29.65298582	W2
ENSMUSG00000108438	NA	0.000747511	26.57977269	W2
ENSMUSG00000108438	NA	5.55E-05	28.82796814	W2
ENSMUSG00000063713	Klk1b24	1.66E-06	31.77479291	W2
ENSMUSG00000063713	Klk1b24	9.45E-05	40.08564642	W2
ENSMUSG00000109236	NA	0.084997578	-14.79832428	W2
ENSMUSG00000092953	NA	0.000455612	-31.53485007	W2
ENSMUSG00000066850	Vmn1r65	0.006804902	22.50901876	W2
ENSMUSG00000066850	Vmn1r65	5.86E-08	25.33583301	W2
ENSMUSG00000096228	Olfr5	0.098796803	13.28205256	W2
ENSMUSG00000048067	Olfr1349	1.24E-08	47.87007285	W2
ENSMUSG00000030606	Hapln3	0.001307105	15.83850932	W2
ENSMUSG00000030737	Slco2b1	0.003328457	12.80193237	W2
ENSMUSG00000031502	Col4a1	0.07934164	10.74206495	W2
ENSMUSG00000057116	AF366264	0.060077169	19.19144823	W2
ENSMUSG00000039478	Micu3	0.065899987	31.74082496	W2
ENSMUSG00000011832	Evi5l	0.000679803	-27.80499503	W2
ENSMUSG00000025519	Tktl2	0.004608477	34.9765508	W2
ENSMUSG00000031620	Iqcm	0.005932712	-17.59190914	W2
ENSMUSG00000097882	0610038B21Rik	0.004717713	-28.92214196	W2
ENSMUSG00000037022	Mmaa	0.008174835	27.65149185	W2
ENSMUSG00000031709	Tbc1d9	0.007870779	23.18026759	W2

ENSMUSG00000003808	Farsa	0.004425285	14.20454545	W2
ENSMUSG00000003808	Farsa	0.02136734	11.17216117	W2
ENSMUSG00000003824	Syce2	0.02564631	-34.98784841	W2
ENSMUSG00000053693	Mast1	0.001427567	13.40626966	W2
ENSMUSG00000051952	Olfr371	6.72E-16	43.39866146	W2
ENSMUSG00000031697	Orc6	0.000679803	12.87326708	W2
ENSMUSG00000077393	NA	0.081217417	17.37982415	W2
ENSMUSG00000032572	Col6a4	0.000756786	-36.82176752	W2
ENSMUSG00000032596	Uba7	0.032460996	21.29393413	W2
ENSMUSG00000047257	Prss45	4.81E-05	28.04919101	W2
ENSMUSG00000032500	Dclk3	0.085945646	-19.19642857	W2
ENSMUSG00000087038	2900079G21Rik	0.011125641	28.41441847	W2
ENSMUSG00000053820	Bcl2a1c	0.069084997	-20.67989002	W2
ENSMUSG00000111564	NA	0.0153881	-26.50958848	W2
ENSMUSG00000056880	Gadl1	0.027867731	-24.88109925	W2
ENSMUSG00000056880	Gadl1	0.072992813	-24.00032838	W2
ENSMUSG00000056880	Gadl1	0.033809317	-27.29516796	W2
ENSMUSG00000039115	Itga9	0.004818619	23.2742674	W2
ENSMUSG00000034533	Scn10a	7.40E-05	37.68941162	W2
ENSMUSG00000032518	Rpsa	0.010385437	-10.84859585	W2
ENSMUSG00000111498	NA	4.20E-11	51.49429002	W2
ENSMUSG00000047508	Mbd3l2	1.88E-08	43.71321371	W2
ENSMUSG00000004099	Dnmt1	0.001137393	22.78186275	W2
ENSMUSG00000096472	Cdkn2d	0.000162342	34.97995791	W2
ENSMUSG00000096472	Cdkn2d	0.000294965	31.86386104	W2
ENSMUSG00000047822	Angptl8	0.023440631	27.23342585	W2
ENSMUSG00000110526	Olfr151	0.084997578	-21.20159933	W2
ENSMUSG00000066749	Olfr877	0.010349274	-11.18881119	W2
ENSMUSG00000049313	Sorl1	0.01123077	-25.63042971	W2
ENSMUSG00000085831	1700003G13Rik	0.003502189	17.7672622	W2
ENSMUSG00000037801	Iqch	0.097693788	15.06341569	W2
ENSMUSG00000032418	Me1	0.021581764	-14.04761905	W2
ENSMUSG00000095654	Plscr5	0.000741712	-33.45376023	W2
ENSMUSG00000032377	Plscr4	0.011676922	-22.20588235	W2
ENSMUSG00000040433	Zbtb38	0.069669718	-31.31034285	W2
ENSMUSG00000095872	Gm15128	0.035454078	25.58287663	W2
ENSMUSG00000025917	Cops5	0.058664874	14.84470653	M6
ENSMUSG00000025917	Cops5	0.074700967	14.45807894	M6
ENSMUSG00000025917	Cops5	0.055116731	14.88510206	M6
ENSMUSG00000025917	Cops5	0.016598916	11.1797164	M6
ENSMUSG00000026327	Serpinb11	0.006292895	-20.96180651	M6
ENSMUSG00000025938	Slco5a1	5.71E-07	38.53264791	M6
ENSMUSG00000025938	Slco5a1	2.79E-08	30.3558521	M6

ENSMUSG00000042207	Kdm5b	0.023670109	-18.00224767	M6
ENSMUSG00000026414	Tnnt2	8.64E-08	39.41487706	M6
ENSMUSG00000026414	Tnnt2	0.02132242	-31.28886416	M6
ENSMUSG00000026414	Tnnt2	0.000156465	30.97158397	M6
ENSMUSG00000026411	Tmem9	0.037135744	14.96757898	M6
ENSMUSG00000097113	Gm19705	0.003043947	-21.05890339	M6
ENSMUSG00000097448	NA	0.088963016	-21.94508658	M6
ENSMUSG00000100954	NA	0.016148909	6.018518519	M6
ENSMUSG00000026483	Fam129a	0.002490787	8.352490421	M6
ENSMUSG00000055547	Apobec4	0.010654905	-15.26763167	M6
ENSMUSG00000042772	Smg7	0.017781144	-25.64550265	M6
ENSMUSG00000056708	Ier5	0.009771837	25.71339716	M6
ENSMUSG00000026470	Stx6	0.000418803	27.85293622	M6
ENSMUSG00000050565	Tor1aip2	0.043976741	-20.05291005	M6
ENSMUSG00000050565	Tor1aip2	0.012753448	-20.76614358	M6
ENSMUSG00000050565	Tor1aip2	0.029182843	-25.28224294	M6
ENSMUSG00000050565	Tor1aip2	0.079289433	-23.82941582	M6
ENSMUSG00000050565	Tor1aip2	0.008318595	-24.2651916	M6
ENSMUSG00000026589	Sec16b	7.03E-06	23.18613485	M6
ENSMUSG00000026701	Prdx6	0.059222793	17.14767469	M6
ENSMUSG00000026584	Scyl3	5.66E-06	-24.82830554	M6
ENSMUSG00000073489	Ifi204	0.007630427	-22.29934754	M6
ENSMUSG00000059371	Olfr427	0.009792596	-28.10187757	M6
ENSMUSG00000055033	Olfr420	1.99E-05	-29.57760343	M6
ENSMUSG00000055033	Olfr420	0.026737252	-23.82967878	M6
ENSMUSG00000026532	Spta1	0.000693324	-25.62738436	M6
ENSMUSG00000055214	Pld5	0.032489781	-8.612040134	M6
ENSMUSG00000057335	Cep170	0.003241691	-26.85898873	M6
ENSMUSG00000015962	1700016C15Rik	0.01123288	-30.21856214	M6
ENSMUSG00000015962	1700016C15Rik	0.001615001	-25.5216333	M6
ENSMUSG00000026489	Coq8a	0.078157198	20.23790537	M6
ENSMUSG00000102923	NA	0.020598209	16.39698045	M6
ENSMUSG00000092578	4930488B22Rik	0.085214256	24.53176453	M6
ENSMUSG00000103478	NA	0.02170564	-14.0376677	M6
ENSMUSG00000103478	NA	1.55E-07	-39.94517544	M6
ENSMUSG00000039318	Rab3gap2	0.033887194	-10.11126599	M6
ENSMUSG00000077571	Snora36b	3.20E-06	-39.47619048	M6
ENSMUSG00000077571	Snora36b	0.039291795	-22.86874781	M6
ENSMUSG00000077571	Snora36b	0.066877815	-16.81205664	M6
ENSMUSG00000066595	Flvcr1	3.32E-05	39.85782677	M6
ENSMUSG00000026627	Tmem206	0.002005114	32.72793727	M6
ENSMUSG00000026156	B3gat2	0.012287907	-26.28741359	M6
ENSMUSG00000050217	Lgsn	0.002803872	26.72885809	M6

ENSMUSG00000026058	Khdrbs2	1.33E-07	37.03749465	M6
ENSMUSG00000091318	Gm5415	2.28E-26	63.16549829	M6
ENSMUSG00000091318	Gm5415	1.10E-17	65.56412789	M6
ENSMUSG00000102917	NA	7.28E-08	48.07174503	M6
ENSMUSG00000042215	Bag2	4.45E-05	41.35706903	M6
ENSMUSG00000026131	Dst	2.91E-09	45.06950203	M6
ENSMUSG00000026131	Dst	0.002260969	32.56558083	M6
ENSMUSG00000026124	Cfc1	0.008184337	15.32186949	M6
ENSMUSG00000037470	Uggt1	0.033270801	15.29917184	M6
ENSMUSG00000037447	Arid5a	4.98E-08	-41.62355229	M6
ENSMUSG00000037447	Arid5a	0.073926574	-15.0897413	M6
ENSMUSG00000067653	Ankrd23	2.48E-08	-36.47803409	M6
ENSMUSG00000046337	Fam178b	0.07424616	6.37100894	M6
ENSMUSG00000026117	Zap70	0.000637429	-29.63749618	M6
ENSMUSG00000026116	Tmem131	0.010876601	19.11568062	M6
ENSMUSG00000026112	Coa5	0.01824979	17.8407935	M6
ENSMUSG00000026078	Pdcl3	0.042267637	28.74083977	M6
ENSMUSG00000026078	Pdcl3	1.38E-10	43.8540039	M6
ENSMUSG00000057173	Rfx8	0.056663848	-12.25490196	M6
ENSMUSG00000026074	Map4k4	6.52E-10	50.93307342	M6
ENSMUSG00000079588	Tmem182	5.83E-05	34.50055062	M6
ENSMUSG00000025995	Wdr75	0.080214962	-11.55245955	M6
ENSMUSG00000051223	Bzw1	6.42E-06	30.12397077	M6
ENSMUSG00000102549	NA	0.067197984	-27.47146658	M6
ENSMUSG00000026196	Bard1	0.003576839	-26.31553539	M6
ENSMUSG00000026192	Atic	1.00E-08	-42.23179812	M6
ENSMUSG00000026192	Atic	0.002426361	-34.81992574	M6
ENSMUSG00000026193	Fn1	0.000103286	-37.18684291	M6
ENSMUSG00000101848	4933417E11Rik	0.042890433	-23.17111234	M6
ENSMUSG00000101968	1700027A15Rik	0.020277308	-20.62309109	M6
ENSMUSG00000101968	1700027A15Rik	0.010171683	20.40378594	M6
ENSMUSG00000006576	Slc4a3	0.077037022	17.26703308	M6
ENSMUSG00000038608	Dock10	0.010508244	-23.12572386	M6
ENSMUSG00000098797	Mir6344	0.00263571	32.86549589	M6
ENSMUSG00000100217	9930111H07Rik	0.008007937	-19.29672667	M6
ENSMUSG00000100217	9930111H07Rik	0.059283048	-15.61111111	M6
ENSMUSG00000055866	Per2	0.043665303	16.74934886	M6
ENSMUSG00000034292	Traf3ip1	0.002392641	17.86884336	M6
ENSMUSG00000112429	NA	0.099408872	-10.72068128	M6
ENSMUSG00000071392	Ect2l	0.027187382	-23.63747364	M6
ENSMUSG00000059554	Ccdc28a	0.030973757	18.31137636	M6
ENSMUSG00000019853	Hebp2	7.16E-11	39.08393588	M6
ENSMUSG00000071369	Map3k5	0.016760545	-31.01255689	M6

ENSMUSG00000071369	Map3k5	9.36E-06	-41.34067808	M6
ENSMUSG00000091618	H60c	0.010294465	-28.7019643	M6
ENSMUSG00000019826	Zbtb24	0.057851133	22.48351227	M6
ENSMUSG00000019763	Rmnd1	0.00037342	-15.01207729	M6
ENSMUSG00000019763	Rmnd1	2.99E-08	-23.07491582	M6
ENSMUSG00000061759	Armt1	0.000748371	-27.65733976	M6
ENSMUSG00000019767	Ccdc170	5.77E-05	-17.49597424	M6
ENSMUSG00000019856	Fam184a	0.021418538	10.78574953	M6
ENSMUSG00000019796	Lrp11	0.033635895	15.5329831	M6
ENSMUSG00000001120	Pcbp3	1.95E-06	-43.70546464	M6
ENSMUSG00000112612	NA	0.045009306	-22.43925205	M6
ENSMUSG00000112612	NA	3.72E-07	-32.75661403	M6
ENSMUSG00000009293	Ube2g2	0.03013137	-17.79803376	M6
ENSMUSG00000009293	Ube2g2	0.000245336	-35.93531066	M6
ENSMUSG00000009293	Ube2g2	7.72E-06	-29.29444301	M6
ENSMUSG00000096380	Gm19668	0.086686569	-10.9743175	M6
ENSMUSG00000046841	Ckap4	0.029910645	-18.93854771	M6
ENSMUSG00000020037	Rfx4	0.034928001	-21.25843265	M6
ENSMUSG00000020023	Tmcc3	0.069677263	-16.293607	M6
ENSMUSG00000020911	Krt19	6.12E-08	51.60195628	M6
ENSMUSG00000086347	NA	0.002686255	-36.82445272	M6
ENSMUSG00000065251	NA	0.007084677	-31.35436417	M6
ENSMUSG00000003518	Dusp3	1.46E-06	-31.97534029	M6
ENSMUSG00000078640	Gm11627	0.005202413	-24.80558647	M6
ENSMUSG00000078640	Gm11627	4.60E-05	-32.71203697	M6
ENSMUSG00000080694	NA	4.78E-09	41.77849224	M6
ENSMUSG00000020690	Efcab3	0.055716636	23.35567344	M6
ENSMUSG00000020690	Efcab3	0.005065655	28.7520832	M6
ENSMUSG00000099125	NA	0.089736087	-12.97979798	M6
ENSMUSG00000020599	Rgs9	0.000202093	-34.04606409	M6
ENSMUSG00000099630	1700096J18Rik	0.009055431	-36.04280807	M6
ENSMUSG00000018861	Fdxr	0.000266509	16.10567211	M6
ENSMUSG00000020737	Jpt1	0.045564939	7.575757576	M6
ENSMUSG00000089476	NA	0.049340284	6.921218878	M6
ENSMUSG00000089476	NA	0.073836301	5.555555556	M6
ENSMUSG00000020792	Exoc7	0.007106741	8.356869184	M6
ENSMUSG00000061878	Sphk1	0.000725717	-24.82176037	M6
ENSMUSG00000020802	Ube2o	0.005973941	-27.77777778	M6
ENSMUSG00000077604	Snord1b	2.23E-16	-42.93793794	M6
ENSMUSG00000098704	Mir6934	0.008962017	21.08453025	M6
ENSMUSG00000013483	Card14	0.030726858	19.3363767	M6
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ENSMUSG00000039908	Slc26a11	0.015258392	21.28136741	M6

ENSMUSG00000025371	Chmp6	0.048887545	13.18402894	M6
ENSMUSG00000039781	Cep131	0.023593641	15.57379539	M6
ENSMUSG00000025384	Faap100	0.001901457	17.55082972	M6
ENSMUSG00000039703	Nploc4	0.030496407	15.5376648	M6
ENSMUSG00000039703	Nploc4	0.002027335	12.17916523	M6
ENSMUSG00000039670	Oxld1	0.00520618	13.93487323	M6
ENSMUSG00000039670	Oxld1	5.15E-05	18.17898111	M6
ENSMUSG00000057594	Arl16	4.90E-05	23.70228825	M6
ENSMUSG00000057594	Arl16	0.00151397	14.56380739	M6
ENSMUSG00000039640	Mrpl12	0.000645181	15.2498974	M6
ENSMUSG00000039640	Mrpl12	0.079726941	21.0810971	M6
ENSMUSG00000025129	Ppp1r27	0.026413674	19.93095385	M6
ENSMUSG00000048445	Ccdc57	0.073825833	-15.90913473	M6
ENSMUSG00000020173	Cobl	0.000216493	-31.80354676	M6
ENSMUSG00000085561	1700046C09Rik	0.000214839	44.46744882	M6
ENSMUSG00000045671	Spred2	0.005132192	29.47041955	M6
ENSMUSG00000020458	Rtn4	0.0091139	27.32128805	M6
ENSMUSG00000020297	Nsg2	0.000296938	-12.09677419	M6
ENSMUSG00000020287	Mpg	0.003730926	23.3381792	M6
ENSMUSG00000020289	Nprl3	0.013246383	21.62988978	M6
ENSMUSG00000020289	Nprl3	6.07E-05	26.55006362	M6
ENSMUSG00000004296	Il12b	0.031164481	14.36174459	M6
ENSMUSG00000078924	Gm12169	0.023593641	17.16931217	M6
ENSMUSG00000009073	Nf2	0.065555465	15.70156695	M6
ENSMUSG00000009073	Nf2	0.082145118	18.80962747	M6
ENSMUSG00000098296	Mir6918	0.016046524	34.07836496	M6
ENSMUSG00000020358	Hnrnpab	0.005015273	-7.269021739	M6
ENSMUSG00000036391	Sec24a	0.012368311	-12.25490196	M6
ENSMUSG00000086493	NA	0.000364619	33.21694505	M6
ENSMUSG00000083175	NA	0.003314795	30.22723475	M6
ENSMUSG00000000782	Tcf7	0.067123105	30.17585336	M6
ENSMUSG00000080951	NA	0.074590056	26.54210687	M6
ENSMUSG00000087668	Gm11186	5.99E-06	35.47381133	M6
ENSMUSG00000020361	Hspa4	1.02E-06	34.83599149	M6
ENSMUSG00000105908	Mir6920	0.000161189	37.52640197	M6
ENSMUSG00000086789	Lyrm7os	0.001544718	34.64755639	M6
ENSMUSG00000020482	Ccdc117	0.031050426	-15.05149385	M6
ENSMUSG00000020482	Ccdc117	0.033313874	-14.22701826	M6
ENSMUSG00000020474	Polm	0.020856489	-28.2568438	M6
ENSMUSG00000020469	Myl7	0.005894462	23.63060953	M6
ENSMUSG00000072893	4933439C10Rik	0.038888811	22.4152098	M6
ENSMUSG00000059610	Olfr222	0.001474813	18.71309716	M6
ENSMUSG00000088950	NA	0.07029594	22.81529141	M6

ENSMUSG00000088950	NA	0.000214141	-25.99548666	M6
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ENSMUSG00000085551	1810063I02Rik	0.0293449	13.88988817	M6
ENSMUSG00000000301	Pemt	0.037629063	13.24464096	M6
ENSMUSG00000000301	Pemt	0.066877815	21.03683199	M6
ENSMUSG00000020538	Srebf1	0.075728661	14.19823232	M6
ENSMUSG00000042678	Myo15	0.057630656	-5.544548045	M6
ENSMUSG00000010142	Tnfrsf13b	0.042932515	15.65868144	M6
ENSMUSG00000069855	Slc47a2	0.031000632	14.76087794	M6
ENSMUSG00000020801	Med31	0.000428289	25.41250267	M6
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ENSMUSG00000038217	Tlcd2	0.003063535	-25.34617194	M6
ENSMUSG00000000631	Myo18a	0.003951741	19.62666593	M6
ENSMUSG00000065401	Mir144	0.065821413	17.91929121	M6
ENSMUSG00000017428	Psmd11	8.68E-06	40.49274799	M6
ENSMUSG00000017428	Psmd11	5.62E-06	31.86753876	M6
ENSMUSG00000035385	Ccl2	0.095331057	21.18377397	M6
ENSMUSG00000035373	Ccl7	0.024424029	20.91233245	M6
ENSMUSG00000035373	Ccl7	0.001173791	28.0016801	M6
ENSMUSG00000010342	Tex14	6.55E-07	-14.44821518	M6
ENSMUSG00000020857	Nme2	0.004465842	21.54782079	M6
ENSMUSG00000010080	Epn3	0.082145118	10.3171963	M6
ENSMUSG00000038721	Hoxb7	0.066206184	-9.281858272	M6
ENSMUSG00000048763	Hoxb3	0.074397738	-6.049240188	M6
ENSMUSG00000018669	Cdk5rap3	0.085063952	21.54768842	M6
ENSMUSG00000069717	Gm11568	0.025224898	17.24472366	M6
ENSMUSG00000070335	Krtap9-1	0.019530055	23.70514564	M6
ENSMUSG00000021185	Dglucy	0.000277247	-14.55992844	M6
ENSMUSG00000092054	Kif4-ps	0.00166184	-14.36026936	M6
ENSMUSG00000021101	NA	1.22E-09	-43.79396067	M6
ENSMUSG00000000701	Tcl1b5	3.19E-08	41.33169376	M6
ENSMUSG00000113535	NA	0.056428616	23.48941697	M6
ENSMUSG00000085820	4933406K04Rik	0.091109492	-16.90784926	M6
ENSMUSG00000021266	Wars	0.040319889	-14.70943913	M6
ENSMUSG00000040867	Begain	5.05E-05	-30.02972758	M6
ENSMUSG00000018707	Dync1h1	0.050586442	25.13071895	M6
ENSMUSG00000043945	Adam6a	9.58E-07	-34.1448735	M6
ENSMUSG00000102524	NA	0.062995156	-25.42644738	M6
ENSMUSG00000056553	Ptprn2	1.21E-07	-45.03523851	M6
ENSMUSG00000056553	Ptprn2	1.78E-05	-39.38792103	M6
ENSMUSG00000056553	Ptprn2	0.00014082	-33.30598956	M6
ENSMUSG00000101930	Gm5441	7.12E-07	43.47273097	M6
ENSMUSG00000101930	Gm5441	1.23E-05	34.37273676	M6

ENSMUSG00000020636	Allc	0.083295325	15.768728	M6
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ENSMUSG00000061477	Rps7	0.000161885	-26.37474079	M6
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ENSMUSG00000020573	Pik3cg	0.02627802	28.84460756	M6
ENSMUSG00000035860	Cdhr3	0.00958206	23.6708904	M6
ENSMUSG00000092305	Prps1l1	0.014582	6.451612903	M6
ENSMUSG00000092305	Prps1l1	0.011592048	7.692307692	M6
ENSMUSG00000061603	Akap6	0.028241324	9.420289855	M6
ENSMUSG00000112821	1700104L18Rik	0.050326529	22.86691087	M6
ENSMUSG00000045440	Insm2	0.049523047	-7.675279632	M6
ENSMUSG00000020993	Trappc6b	2.71E-07	30.40903541	M6
ENSMUSG00000020993	Trappc6b	0.000137493	29.78792089	M6
ENSMUSG00000034912	Mdga2	0.087621576	-29.17443667	M6
ENSMUSG00000113786	NA	0.063667251	22.08464738	M6
ENSMUSG00000021068	Nin	0.02354973	-32.4059738	M6
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ENSMUSG00000021068	Nin	0.000177574	-21.82780183	M6
ENSMUSG00000113694	NA	0.085063952	-22.34581552	M6
ENSMUSG00000021094	Dhrs7	0.058230754	-18.84145229	M6
ENSMUSG00000063450	Syne2	2.26E-10	38.79298942	M6
ENSMUSG00000021114	Atp6v1d	0.017840239	-8.641975309	M6
ENSMUSG00000021222	Dcaf4	0.055827729	13.83613493	M6
ENSMUSG00000042284	Itga1	0.092871831	25.57602213	M6
ENSMUSG00000113960	4933412O06Rik	0.02483945	20.11407292	M6
ENSMUSG00000041112	Elmo1	8.31E-13	35.00875418	M6
ENSMUSG00000099611	Vmn1r189	3.14E-05	26.03437674	M6
ENSMUSG00000021420	Fars2	0.089852655	-6.944444444	M6
ENSMUSG00000021420	Fars2	0.059819117	-7.512626263	M6
ENSMUSG00000039087	Rreb1	0.035690959	-24.28064743	M6
ENSMUSG00000099269	Calm5	0.069401865	10.41272651	M6
ENSMUSG00000021360	Gcnt2	0.06143802	-18.38622291	M6
ENSMUSG00000021363	Mak	0.001505238	-22.74072184	M6
ENSMUSG00000089815	Gm5083	0.010383027	22.77179039	M6
ENSMUSG00000000253	Gmpr	0.008962017	22.21256005	M6
ENSMUSG00000114681	NA	0.055471508	22.5945819	M6
ENSMUSG00000060176	Kif27	0.07029594	25.95174278	M6
ENSMUSG00000114531	A530065N20Rik	0.030463554	14.9912602	M6
ENSMUSG00000074870	Cts3	0.000771051	10.29616378	M6
ENSMUSG00000069805	Fbp1	0.000415186	11.85185185	M6
ENSMUSG00000069805	Fbp1	0.088575767	12.78919543	M6
ENSMUSG00000092103	Gm17039	0.042932515	21.93396177	M6
ENSMUSG00000021608	Lpcat1	0.000815014	-34.52189249	M6

ENSMUSG00000033991	Ttc37	0.000935461	32.92523149	M6
ENSMUSG00000033991	Ttc37	0.030959976	27.5725775	M6
ENSMUSG00000114900	NA	0.091889474	10	M6
ENSMUSG00000114382	Gm4814	0.091779801	24.6319397	M6
ENSMUSG00000021675	F2rl2	0.069659192	-27.99422799	M6
ENSMUSG00000021675	F2rl2	5.22E-06	29.43386785	M6
ENSMUSG00000021676	Iqgap2	0.001544718	32.02184182	M6
ENSMUSG00000046159	Chrm3	0.001089759	-33.28952496	M6
ENSMUSG00000022126	Acod1	5.71E-12	32.63006993	M6
ENSMUSG00000115515	NA	0.097350903	12.11056173	M6
ENSMUSG00000098433	Mir6391	0.000571795	-21.71717172	M6
ENSMUSG00000025555	Farp1	2.57E-07	-23.26923077	M6
ENSMUSG00000041703	Zic5	0.025207425	35.51441614	M6
ENSMUSG00000115016	AA536875	5.47E-15	42.49559415	M6
ENSMUSG00000042567	Nek10	0.002634381	-13.31484348	M6
ENSMUSG00000023243	Kcnk5	0.000459973	-24.79739602	M6
ENSMUSG00000021819	Zswim8	7.37E-06	-43.92857143	M6
ENSMUSG00000021797	9230112D13Rik	0.011910301	27.03043343	M6
ENSMUSG00000021798	Ldb3	0.064426568	27.08430639	M6
ENSMUSG00000065481	Mir346	0.001007944	24.86882989	M6
ENSMUSG00000021790	Dydc1	3.87E-08	-35.67334817	M6
ENSMUSG00000037697	Ddhd1	1.40E-06	-14.77272727	M6
ENSMUSG00000044285	NA	0.003089329	7.87037037	M6
ENSMUSG00000072575	Eddm3b	0.023592851	-18.72771968	M6
ENSMUSG00000035896	Rnase1	5.36E-11	21.5959596	M6
ENSMUSG00000059606	Rnase2b	0.001722883	15.22533023	M6
ENSMUSG00000072571	Tmem253	0.026302741	9.104414261	M6
ENSMUSG00000093044	Snord8	3.08E-06	26.61928651	M6
ENSMUSG00000000958	Slc7a7	0.00106985	8.536585366	M6
ENSMUSG00000040770	Il25	0.033170719	-10.86143111	M6
ENSMUSG00000002325	Irf9	9.32E-10	41.45785405	M6
ENSMUSG00000021933	Gucy1b2	8.05E-05	-9.148550725	M6
ENSMUSG00000075572	Defb43	5.22E-06	-17.55952381	M6
ENSMUSG00000075571	Defb30	0.03143654	9.75992409	M6
ENSMUSG00000014453	Blk	0.067775502	17.756022	M6
ENSMUSG00000022097	Sftpc	0.037194537	-20.27845707	M6
ENSMUSG00000022102	Dok2	0.00070452	27.21960735	M6
ENSMUSG00000068015	Lrch1	0.012994718	25.78667685	M6
ENSMUSG00000022000	Zc3h13	0.07029594	24.68436107	M6
ENSMUSG00000071262	Zfp957	0.020052486	23.43502954	M6
ENSMUSG00000022018	Rgcc	3.49E-06	23.56361069	M6
ENSMUSG00000022070	Bora	0.089738285	15.08563695	M6
ENSMUSG00000023031	Cela1	0.032380521	-17.16540404	M6

ENSMUSG00000058794	Nfe2	1.30E-05	27.87519147	M6
ENSMUSG00000058794	Nfe2	0.000213435	33.72835684	M6
ENSMUSG00000058794	Nfe2	1.29E-12	41.63634037	M6
ENSMUSG00000115474	4930430F21Rik	1.46E-06	-40.05001072	M6
ENSMUSG00000022257	Laptm4b	0.064426568	21.42022639	M6
ENSMUSG00000022257	Laptm4b	0.010412893	22.20739046	M6
ENSMUSG00000014313	Cox6c	0.039291795	-20.82813026	M6
ENSMUSG00000094112	9330182O14Rik	0.024712599	28.44619992	M6
ENSMUSG00000094112	9330182O14Rik	0.052176899	-17.55279503	M6
ENSMUSG00000038760	Trhr	0.003981227	-12.75957259	M6
ENSMUSG00000115654	Gm19303	0.025535748	-25.5402866	M6
ENSMUSG00000038622	Med30	0.058286714	18.56186688	M6
ENSMUSG00000053469	Tg	0.010095738	28.99140968	M6
ENSMUSG00000054263	Lifr	0.000464853	33.19149946	M6
ENSMUSG00000079020	Slc45a4	4.46E-05	-34.54944095	M6
ENSMUSG00000059895	Ptp4a3	0.064413485	-26.18926046	M6
ENSMUSG00000059895	Ptp4a3	0.000795596	-35.5151266	M6
ENSMUSG00000059895	Ptp4a3	0.000501768	-32.8636902	M6
ENSMUSG00000044361	BC024139	0.007631737	-33.23197269	M6
ENSMUSG00000093169	Mir3079	0.036518034	-33.65880684	M6
ENSMUSG00000022561	Gpaa1	2.41E-15	-57.66912141	M6
ENSMUSG00000022558	Mroh1	7.17E-12	-47.80179619	M6
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ENSMUSG00000022558	Mroh1	4.69E-15	-53.79315737	M6
ENSMUSG00000022560	Slc52a2	0.06143802	13.60036529	M6
ENSMUSG00000022550	Adck5	0.002882053	-30.56891041	M6
ENSMUSG00000034022	Cpsf1	0.005273764	-31.71988078	M6
ENSMUSG00000063354	Slc39a4	8.06E-07	30.41125541	M6
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ENSMUSG00000033576	Apol6	2.05E-09	-50.43619431	M6
ENSMUSG00000033576	Apol6	1.56E-10	-48.76652637	M6
ENSMUSG00000033565	Rbfox2	5.68E-17	48.90791689	M6
ENSMUSG00000071716	Apol7e	0.004581186	19.47698086	M6
ENSMUSG00000071716	Apol7e	0.003388168	21.6452983	M6
ENSMUSG00000062154	Tex33	0.000685782	24.58618515	M6
ENSMUSG00000022391	Rangap1	0.037454784	26.83191783	M6
ENSMUSG00000022390	Zc3h7b	0.000220615	-33.79302916	M6
ENSMUSG00000041852	Tcf20	0.00056068	8.742498636	M6
ENSMUSG00000058099	Nfam1	0.018718955	15.27777778	M6
ENSMUSG00000016664	Pacsin2	2.98E-06	19.41098455	M6
ENSMUSG00000078954	Arhgap8	0.090739837	12.71240809	M6
ENSMUSG00000116396	NA	0.077973198	13.5224118	M6
ENSMUSG00000022385	Gtse1	1.14E-08	28.14108168	M6

ENSMUSG00000022386	Trmu	0.001299593	27.68652916	M6
ENSMUSG00000035891	Cerk	0.001288287	26.86468989	M6
ENSMUSG00000035891	Cerk	0.011587609	29.79298479	M6
ENSMUSG00000023272	Creld2	0.027996703	14.30905696	M6
ENSMUSG00000036606	Plxnb2	4.33E-06	22.22222222	M6
ENSMUSG00000055022	Cntn1	0.038633969	19.67159278	M6
ENSMUSG00000049152	Ugt3a2	0.000270143	36.30378774	M6
ENSMUSG00000063780	Olfr282	0.035515391	-19.62963313	M6
ENSMUSG00000022993	4930415O20Rik	0.011035906	-14.88816739	M6
ENSMUSG00000033306	Lpp	0.012317496	20.27836282	M6
ENSMUSG00000081605	NA	0.008851493	16.26624431	M6
ENSMUSG00000049436	Upk1b	0.054019606	-7.471264368	M6
ENSMUSG00000022664	Slc35a5	0.026142027	20.44439672	M6
ENSMUSG00000022601	Zbtb11	0.04328328	27.33249693	M6
ENSMUSG00000039956	Mrap	0.000894748	24.75677686	M6
ENSMUSG00000022971	Ifnar2	0.058411871	13.04045398	M6
ENSMUSG00000039763	Dnajc28	0.016545794	19.5795076	M6
ENSMUSG00000085637	1700048M11Rik	0.059905172	-21.09552397	M6
ENSMUSG00000055602	Tcp10b	0.016815625	-29.57954899	M6
ENSMUSG00000096696	Zfp960	0.013124371	-5.88146965	M6
ENSMUSG00000094892	Vmn2r101	0.074426009	19.25809069	M6
ENSMUSG00000061544	Zfp229	0.000361203	-29.51265772	M6
ENSMUSG00000043782	Bicdl2	0.006119461	29.96547963	M6
ENSMUSG00000024124	Prss30	0.000775863	28.53503357	M6
ENSMUSG00000024124	Prss30	1.01E-10	-32.62065948	M6
ENSMUSG00000050762	Prss27	0.023567243	-30.70558526	M6
ENSMUSG00000036820	Amdhd2	0.066037281	23.00586689	M6
ENSMUSG00000024118	Tedc2	0.00827143	-17.09401709	M6
ENSMUSG00000035435	Abca17	0.000355365	-40.27304794	M6
ENSMUSG00000024155	Meiob	0.076018333	-24.66537515	M6
ENSMUSG00000046070	Igfals	4.72E-06	-41.48182972	M6
ENSMUSG00000046070	Igfals	2.67E-05	-32.24893127	M6
ENSMUSG00000046070	Igfals	0.00203377	30.58006808	M6
ENSMUSG00000039183	Nubp2	0.000214839	27.39086956	M6
ENSMUSG00000039183	Nubp2	0.004784876	-35.97976098	M6
ENSMUSG00000039183	Nubp2	1.50E-09	-43.8491455	M6
ENSMUSG00000039183	Nubp2	0.00243667	36.87950112	M6
ENSMUSG00000024169	Ift140	0.000266267	-41.84173992	M6
ENSMUSG00000024170	Telo2	0.085735773	-21.22600732	M6
ENSMUSG00000059562	Ccdc154	6.75E-06	-16.92857143	M6
ENSMUSG00000015126	Tsr3	0.04188001	24.6506423	M6
ENSMUSG00000047507	Baiap3	0.000773053	-27.19454045	M6
ENSMUSG00000033200	Tpsg1	0.000229898	-34.22457172	M6

ENSMUSG00000036775	Decr2	0.000594929	26.54570151	M6
ENSMUSG00000024182	Axin1	0.002187439	19.20066548	M6
ENSMUSG00000024186	Rgs11	0.045107384	22.42334635	M6
ENSMUSG00000062753	AI413582	3.53E-06	32.19251641	M6
ENSMUSG00000117161	NA	0.005961127	33.57072714	M6
ENSMUSG00000041119	Pde9a	2.36E-21	-37.04027184	M6
ENSMUSG00000061613	U2af1	0.026138537	20.72893268	M6
ENSMUSG00000079563	Pglyrp2	3.15E-08	-27.51172368	M6
ENSMUSG00000062464	Cyp4f37	2.43E-06	-34.71850862	M6
ENSMUSG00000073424	Cyp4f15	0.044089168	-23.45329776	M6
ENSMUSG00000023350	4921501E09Rik	0.040979225	23.53055503	M6
ENSMUSG00000048602	Morc2b	0.001435981	-34.3696427	M6
ENSMUSG00000048602	Morc2b	1.03E-05	-39.14133198	M6
ENSMUSG00000092602	NA	9.95E-05	-27.68009768	M6
ENSMUSG00000117603	NA	0.003147278	-23.04113991	M6
ENSMUSG00000008668	Rps18	0.023321398	27.63248579	M6
ENSMUSG00000008668	Rps18	0.020934721	30.30269608	M6
ENSMUSG00000067203	NA	7.65E-06	-10.49382716	M6
ENSMUSG00000092512	NA	0.001177659	-7.5	M6
ENSMUSG00000098197	BC051537	0.000399539	6.172839506	M6
ENSMUSG00000024335	Brd2	0.016679622	29.70442432	M6
ENSMUSG00000036322	H2-Ea-ps	1.11E-09	38.9438649	M6
ENSMUSG00000073420	NA	1.55E-07	29.09295977	M6
ENSMUSG00000015468	Notch4	1.37E-06	-46.32815386	M6
ENSMUSG00000015468	Notch4	0.0519772	-18.16570684	M6
ENSMUSG00000015468	Notch4	2.26E-06	-34.93028536	M6
ENSMUSG00000015468	Notch4	0.001941695	25.6902814	M6
ENSMUSG00000034254	Agpat1	8.84E-05	32.62409449	M6
ENSMUSG00000033327	Tnxb	0.087851481	6.400627473	M6
ENSMUSG00000073418	C4b	0.00054791	-13.08684885	M6
ENSMUSG00000040356	Skiv2l	9.63E-05	36.11238825	M6
ENSMUSG00000090231	Cfb	0.003811464	-18.41986425	M6
ENSMUSG00000090231	Cfb	2.13E-11	-33.93489763	M6
ENSMUSG00000090231	Cfb	1.36E-07	-34.02632009	M6
ENSMUSG00000024371	C2	0.042178465	-32.89306327	M6
ENSMUSG00000036185	Sapcd1	0.000238149	28.60190531	M6
ENSMUSG00000007039	Ddah2	0.028203075	18.47416762	M6
ENSMUSG00000007039	Ddah2	2.56E-06	38.90285495	M6
ENSMUSG00000007039	Ddah2	4.17E-06	34.53790191	M6
ENSMUSG00000092586	Ly6g6c	0.091728561	-23.68780543	M6
ENSMUSG00000034482	Ly6g5c	0.049016065	-25.49603175	M6
ENSMUSG00000034482	Ly6g5c	0.010205139	-27.90352373	M6
ENSMUSG00000024387	Csnk2b	0.013849953	-22.95340401	M6

ENSMUSG00000073412	Lst1	3.71E-07	39.02477819	M6
ENSMUSG00000073412	Lst1	0.032351477	27.88610655	M6
ENSMUSG00000024401	Tnf	0.000210622	38.9154169	M6
ENSMUSG00000024401	Tnf	0.003591777	27.77980627	M6
ENSMUSG00000098269	Mir8094	0.008085283	24.59025817	M6
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ENSMUSG00000073411	H2-D1	0.02483945	10.06864007	M6
ENSMUSG00000073411	H2-D1	0.093236458	-25.42864007	M6
ENSMUSG00000073411	H2-D1	0.024310662	23.30957447	M6
ENSMUSG00000073411	H2-D1	0.007592435	24.59235815	M6
ENSMUSG00000073411	H2-D1	1.13E-08	42.60631101	M6
ENSMUSG00000073411	H2-D1	1.76E-11	36.79726038	M6
ENSMUSG00000079507	H2-Q1	7.09E-07	34.98253615	M6
ENSMUSG00000024406	Pou5f1	0.002042471	21.5007215	M6
ENSMUSG00000039518	Cdsn	0.000888717	-7.894736842	M6
ENSMUSG00000090509	Sfta2	0.099993309	-24.08035102	M6
ENSMUSG00000090509	Sfta2	0.007777338	19.43241133	M6
ENSMUSG00000077931	Mir877	0.001595089	26.74041501	M6
ENSMUSG00000054128	H2-T18	6.40E-05	-27.63201265	M6
ENSMUSG00000054128	H2-T18	0.000575695	-25.47931857	M6
ENSMUSG00000045409	Trim39	0.008710275	26.31595137	M6
ENSMUSG00000037246	H2-M10.5	0.01119037	-9.770114943	M6
ENSMUSG00000073399	Trim40	0.00088142	-31.98889302	M6
ENSMUSG00000073399	Trim40	0.062172469	-28.50889017	M6
ENSMUSG00000058063	Trim31	2.86E-05	-34.28709433	M6
ENSMUSG00000092239	1700031A10Rik	0.000287175	-23.20702489	M6
ENSMUSG00000036036	Zfp57	4.42E-06	-35.2740544	M6
ENSMUSG00000036036	Zfp57	0.002273133	-24.17234758	M6
ENSMUSG00000054951	9130008F23Rik	0.000366559	-31.81058338	M6
ENSMUSG00000091043	Glyatl3	0.083843464	-18.18026896	M6
ENSMUSG00000117272	NA	0.035143064	-12.62078955	M6
ENSMUSG00000041293	Adgrf1	0.000169606	-30.71420888	M6
ENSMUSG00000040140	Tdrd6	0.015671831	18.15454139	M6
ENSMUSG00000023960	Enpp5	0.01205963	18.90563526	M6
ENSMUSG00000023961	Enpp4	0.00400576	15.92535393	M6
ENSMUSG00000070209	NA	0.0091139	22.41372359	M6
ENSMUSG00000037089	Slc35b2	0.000502941	-39.22008547	M6
ENSMUSG00000023942	Slc29a1	0.069381441	-29.31586405	M6
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ENSMUSG00000058626	Capn11	0.055311976	-23.7025012	M6
ENSMUSG00000076141	Mir693	0.054866914	-19.07950048	M6
ENSMUSG00000036858	Ptcra	0.00041861	22.18277301	M6
ENSMUSG00000063888	Rpl7l1	0.00666074	28.35893031	M6

ENSMUSG00000036568	Bicral	0.000827895	20.83441918	M6
ENSMUSG00000036568	Bicral	7.31E-06	27.14946383	M6
ENSMUSG00000023982	Guca1a	0.017840239	17.6984127	M6
ENSMUSG00000047150	1700001C19Rik	3.06E-06	25.33114297	M6
ENSMUSG00000047150	1700001C19Rik	0.007857456	27.41955267	M6
ENSMUSG00000023980	Taf8	0.012162426	18.97306397	M6
ENSMUSG00000034165	Ccnd3	0.01381902	18.17653343	M6
ENSMUSG00000090115	Usp49	0.010389931	20.05973639	M6
ENSMUSG00000084880	Tomm6os	0.001465945	26.72142477	M6
ENSMUSG00000023266	Frs3	0.003456988	23.82128171	M6
ENSMUSG00000023990	Tfeb	0.087525011	18.83009887	M6
ENSMUSG00000073386	9830107B12Rik	0.006639975	-10.97980522	M6
ENSMUSG00000023992	Trem2	0.038420211	-29.8545855	M6
ENSMUSG00000023992	Trem2	5.24E-06	36.12316471	M6
ENSMUSG00000023993	Treml1	0.000795596	27.52090943	M6
ENSMUSG00000043592	Unc5cl	0.039122449	-26.55502392	M6
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ENSMUSG00000043592	Unc5cl	1.10E-09	37.38303365	M6
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ENSMUSG00000097095	NA	8.03E-09	25.55555556	M6
ENSMUSG00000091504	Vmn2r118	9.42E-14	23.55072464	M6
ENSMUSG00000041831	Sytl3	0.064297669	19.6548135	M6
ENSMUSG00000003279	Dlgap1	0.001299593	-18.41931217	M6
ENSMUSG00000024066	Xdh	2.37E-05	28.76027187	M6
ENSMUSG00000024066	Xdh	1.36E-08	37.65346032	M6
ENSMUSG00000038541	Srd5a2	5.14E-06	41.45768834	M6
ENSMUSG00000038541	Srd5a2	0.003255122	29.53720978	M6
ENSMUSG00000117358	NA	7.43E-08	39.60910596	M6
ENSMUSG00000024073	Birc6	0.004542509	38.507602	M6
ENSMUSG00000001870	Ltbp1	0.000105612	21.99429306	M6
ENSMUSG00000117399	NA	4.26E-11	31.54295051	M6
ENSMUSG00000037689	Tmem247	0.080418878	17.42276914	M6
ENSMUSG00000117409	NA	0.000855452	-26.21687136	M6
ENSMUSG00000117409	NA	0.000303912	-28.57876403	M6
ENSMUSG00000117633	NA	0.067569054	-7.18189391	M6
ENSMUSG00000034774	Dsg1c	0.046466419	13.69213006	M6
ENSMUSG00000024395	Lims2	1.87E-10	39.35980524	M6
ENSMUSG00000024388	Myo7b	0.000178388	-40.00640588	M6
ENSMUSG00000024354	Slc23a1	0.090330094	-6.833835247	M6
ENSMUSG00000099300	Mir6356	0.07029594	-19.03935576	M6
ENSMUSG00000038903	Ccdc68	0.002833862	12.05774097	M6
ENSMUSG00000035394	Cfap53	0.016642228	-6.060606061	M6
ENSMUSG00000057440	Mpp7	0.000321403	-18.06492728	M6

ENSMUSG00000025885	Myo5b	0.023194179	23.41393965	M6
ENSMUSG00000088689	NA	0.013954293	23.73492752	M6
ENSMUSG00000035765	Dym	1.12E-09	32.22737008	M6
ENSMUSG00000102047	2010010A06Rik	7.38E-06	26.68281692	M6
ENSMUSG00000117385	NA	0.044365875	-13.55384993	M6
ENSMUSG00000036372	Tmem258	0.00578469	-28.85641106	M6
ENSMUSG00000024738	Pga5	0.001505238	-30.99363599	M6
ENSMUSG00000048832	Vps37c	0.042170259	18.59546543	M6
ENSMUSG00000024670	Cd6	0.000690253	19.13029959	M6
ENSMUSG00000024737	Slc15a3	0.006123414	20.13395632	M6
ENSMUSG00000024731	Ms4a10	2.13E-11	-48.60402955	M6
ENSMUSG00000024731	Ms4a10	2.33E-05	-45.23352751	M6
ENSMUSG00000067571	Ms4a15	0.003607482	23.52774986	M6
ENSMUSG00000067571	Ms4a15	2.44E-05	26.00352858	M6
ENSMUSG00000067571	Ms4a15	0.001028586	-44.78714268	M6
ENSMUSG00000067571	Ms4a15	2.05E-09	-38.73838882	M6
ENSMUSG00000075010	AW112010	0.037173444	20.05368205	M6
ENSMUSG00000024679	Ms4a6d	0.035748226	-19.57349896	M6
ENSMUSG00000063683	Glyat	7.19E-06	42.86383187	M6
ENSMUSG00000063683	Glyat	0.001665451	30.58865027	M6
ENSMUSG00000024694	Keg1	0.000655037	35.2266849	M6
ENSMUSG00000095484	Olfr1480	0.000387813	37.74891775	M6
ENSMUSG00000059105	Olfr1504	0.082940193	-22.98718831	M6
ENSMUSG00000024697	Gna14	0.001807481	-28.67569522	M6
ENSMUSG00000037847	Nmrk1	6.23E-08	-34.80817299	M6
ENSMUSG00000035171	1110059E24Rik	0.009017811	-25.34559123	M6
ENSMUSG00000024771	Lipk	0.002632913	25.22676462	M6
ENSMUSG00000024907	Gal	1.80E-09	-44.40777204	M6
ENSMUSG00000024774	Ankrd22	0.009685448	19.06917532	M6
ENSMUSG00000035783	Acta2	9.36E-08	-20.19607843	M6
ENSMUSG00000035783	Acta2	6.17E-11	-23.67424242	M6
ENSMUSG00000079339	Ifit1bl1	0.000815014	26.25747133	M6
ENSMUSG00000065594	Mir107	0.000209474	22.0012785	M6
ENSMUSG00000001750	Tcirg1	0.000541871	-22.84279964	M6
ENSMUSG00000059734	Ndufs8	0.000207742	-24.68107256	M6
ENSMUSG00000025190	Got1	0.00073273	-11.05263158	M6
ENSMUSG00000025202	Scd3	0.029897681	-19.97076371	M6
ENSMUSG00000036961	Wnt8b	0.000807553	27.09866694	M6
ENSMUSG00000025221	Kcnip2	0.017120394	-9.150725817	M6
ENSMUSG00000055491	Pprc1	0.021194717	-8.780234945	M6
ENSMUSG00000024979	Tectb	0.033921378	-25.37318179	M6
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ENSMUSG00000079478	Sssca1	0.027505685	-26.98122621	M6

ENSMUSG00000097785	B230217O12Rik	0.033170719	27.65031735	M6
ENSMUSG00000117655	NA	0.008166109	-29.71588955	M6
ENSMUSG00000027164	Traf6	0.067379742	-9.523809524	M6
ENSMUSG00000005089	Slc1a2	0.008382675	12.35609439	M6
ENSMUSG00000074997	Pin1rt1	0.000173838	24.96430579	M6
ENSMUSG00000063751	Platr8	3.42E-05	-15.78525641	M6
ENSMUSG00000063751	Platr8	0.000862721	-18.14102564	M6
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ENSMUSG00000096566	Olfr1306	0.030587261	-8.641975309	M6
ENSMUSG00000074946	Olfr1313	0.004672388	-7.75	M6
ENSMUSG00000027355	Tmco5	0.001023917	26.2101746	M6
ENSMUSG00000086221	4930412B13Rik	8.27E-07	-33.66287332	M6
ENSMUSG00000040061	Plcb2	0.040979225	-19.7495198	M6
ENSMUSG00000074884	Serf2	0.013790819	9.320987654	M6
ENSMUSG00000048327	Ckap2l	0.071413851	-18.38754197	M6
ENSMUSG00000027403	Tgm6	0.030848775	-26.17549602	M6
ENSMUSG00000089662	NA	6.40E-05	-26.98540136	M6
ENSMUSG00000082990	NA	0.078985903	-16.51061569	M6
ENSMUSG00000037376	Trmt6	1.66E-14	-49.82934638	M6
ENSMUSG00000082399	NA	0.0603527	-12.99896037	M6
ENSMUSG00000027420	Bfsp1	1.41E-06	29.5052896	M6
ENSMUSG00000074754	Smim26	0.057025184	30.33419711	M6
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ENSMUSG00000063873	Slc24a3	3.41E-10	-44.65079365	M6
ENSMUSG00000063873	Slc24a3	0.002422605	-34.33789336	M6
ENSMUSG00000085958	A930019D19Rik	2.49E-12	43.47622041	M6
ENSMUSG00000055177	Cstl1	0.009629209	-17.63814443	M6
ENSMUSG00000027447	Cst3	5.21E-10	38.54643277	M6
ENSMUSG00000027447	Cst3	0.000144026	28.62840648	M6
ENSMUSG00000079009	Gm14139	1.43E-08	-24.26884434	M6
ENSMUSG00000074731	Zfp345	0.009160071	-20.48524003	M6
ENSMUSG00000074731	Zfp345	0.062172469	-18.25244534	M6
ENSMUSG00000068129	Cst7	0.09075003	-17.8397327	M6
ENSMUSG00000027452	Acss1	0.027505685	-20.38786256	M6
ENSMUSG00000033068	Entpd6	0.00156271	-25.9335431	M6
ENSMUSG00000087890	NA	0.000100592	-25.07447745	M6
ENSMUSG00000087433	Gm14167	0.041340543	15.86310559	M6
ENSMUSG00000044364	Tmem74b	1.89E-06	13.24521814	M6
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ENSMUSG00000027460	Angpt4	2.44E-12	-54.19004986	M6
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ENSMUSG00000027459	Fam110a	0.00017101	14.29043179	M6
ENSMUSG00000027463	Slc52a3	7.38E-06	-23.03082449	M6

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ENSMUSG00000027465	Tbc1d20	0.00141604	-26.8035658	M6
ENSMUSG00000081434	NA	0.000602393	-25.9344167	M6
ENSMUSG00000088139	NA	1.03E-05	22.38095238	M6
ENSMUSG00000042631	Xkr7	0.070408492	-7.843321553	M6
ENSMUSG00000027480	Sun5	0.032887536	-26.83878577	M6
ENSMUSG00000068009	Bpifb6	0.002368776	25.08274349	M6
ENSMUSG00000000876	Pxmp4	0.075074474	24.5754848	M6
ENSMUSG00000000876	Pxmp4	0.015050779	22.10943164	M6
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ENSMUSG00000074656	Eif2s2	0.039048237	-23.77938015	M6
ENSMUSG00000038324	Trpc4ap	0.096074563	-18.20462103	M6
ENSMUSG00000027611	Procr	0.006694578	-28.23173767	M6
ENSMUSG00000027613	Eif6	0.092332626	-22.12121212	M6
ENSMUSG00000027613	Eif6	0.066740968	-21.60161878	M6
ENSMUSG00000027613	Eif6	0.003811464	-22.95089576	M6
ENSMUSG00000074646	6430550D23Rik	0.006343677	-22.84259259	M6
ENSMUSG00000013338	Fer1l4	7.12E-18	-53.52081068	M6
ENSMUSG00000046229	Scand1	0.00238984	-21.5442918	M6
ENSMUSG00000067818	Myl9	0.001556129	24.05311367	M6
ENSMUSG00000084113	NA	0.020924571	18.19209249	M6
ENSMUSG00000027642	Rpn2	0.044185023	23.90047267	M6
ENSMUSG00000027650	Tti1	3.69E-06	27.84263473	M6
ENSMUSG00000027650	Tti1	0.000610768	27.41427246	M6
ENSMUSG00000027650	Tti1	0.097236471	25.64430775	M6
ENSMUSG00000016024	Lbp	3.12E-06	-32.27315964	M6
ENSMUSG00000016024	Lbp	0.079264023	-21.34168751	M6
ENSMUSG00000085385	NA	0.000772229	36.1935988	M6
ENSMUSG00000085385	NA	1.82E-11	53.87008127	M6
ENSMUSG00000044349	Snhg11	0.099082669	8.094979049	M6
ENSMUSG00000044405	Adig	2.44E-07	-36.91537812	M6
ENSMUSG00000093120	Mir3474	4.26E-06	38.93803419	M6
ENSMUSG00000027654	Fam83d	2.93E-16	45.3231038	M6
ENSMUSG00000070544	Top1	0.043665303	5.779509917	M6
ENSMUSG00000039621	Prex1	0.004145624	-8.666666667	M6
ENSMUSG00000074582	Arfgef2	6.65E-06	-26.76587302	M6
ENSMUSG00000017969	Ptgis	0.013775188	-26.3680243	M6
ENSMUSG00000027551	Zfp64	0.019531757	-15.31644968	M6
ENSMUSG00000087382	Ctcflos	1.15E-05	35.8433207	M6
ENSMUSG00000087382	Ctcflos	4.22E-10	39.60264105	M6
ENSMUSG00000039001	Rps21	0.082145118	11.78059879	M6
ENSMUSG00000038848	Ythdf1	0.000339646	8.951065891	M6
ENSMUSG00000016356	Col20a1	1.28E-08	17.54385965	M6

ENSMUSG00000098505	Gm14496	0.003951741	-16.90067002	M6
ENSMUSG00000037683	Armc3	1.93E-15	-52.17574973	M6
ENSMUSG00000085206	NA	0.09075003	-25.91783217	M6
ENSMUSG00000085057	NA	0.070679233	-8.828100005	M6
ENSMUSG00000026959	Grin1	0.097084889	-5.838385484	M6
ENSMUSG00000026956	Uap1l1	0.073382331	14.32891137	M6
ENSMUSG00000026837	Col5a1	0.007644054	-37.77740291	M6
ENSMUSG00000085491	NA	0.026358971	-6.37254902	M6
ENSMUSG00000075415	Fnbp1	0.079055187	-7.971014493	M6
ENSMUSG00000009566	Fpgs	0.000213435	-21.53197672	M6
ENSMUSG00000009566	Fpgs	0.015398013	-32.15367965	M6
ENSMUSG00000009566	Fpgs	2.52E-07	-27.57592569	M6
ENSMUSG00000053746	Ptrh1	0.002140193	-26.03444811	M6
ENSMUSG00000026864	Hspa5	0.062917326	26.82925762	M6
ENSMUSG00000070953	Rabepk	0.000384454	34.6307088	M6
ENSMUSG00000035949	Fbxw2	0.082145118	21.5096855	M6
ENSMUSG00000084768	NA	1.57E-05	24.62121212	M6
ENSMUSG00000106961	NA	0.00106985	17.26459815	M6
ENSMUSG00000049744	Arhgap15	0.001588921	18.95005241	M6
ENSMUSG00000039145	Camk1d	0.001413038	-26.30225056	M6
ENSMUSG00000025815	Dhtkd1	0.010654905	-27.06819704	M6
ENSMUSG00000087455	5330411J11Rik	5.44E-07	-31.53883556	M6
ENSMUSG00000026989	Dapl1	3.58E-08	-39.05492304	M6
ENSMUSG00000026989	Dapl1	0.002919231	-25.03576974	M6
ENSMUSG00000060703	Cd302	3.56E-16	45.67113397	M6
ENSMUSG00000075325	Gm13582	1.00E-05	38.44766818	M6
ENSMUSG00000075325	Gm13582	6.28E-05	41.19423161	M6
ENSMUSG00000102887	Gm10857	0.002948199	-27.25553909	M6
ENSMUSG00000035000	Dpp4	0.003657224	21.58625796	M6
ENSMUSG00000035000	Dpp4	0.036332793	24.57967836	M6
ENSMUSG00000041966	Dcaf17	0.009629209	8.333333333	M6
ENSMUSG00000006494	Pdk1	0.065007487	19.38927209	M6
ENSMUSG00000006494	Pdk1	0.005664837	22.01705106	M6
ENSMUSG00000006494	Pdk1	7.83E-20	59.69751351	M6
ENSMUSG00000075256	Cerkl	0.000154501	-26.45040119	M6
ENSMUSG00000059173	Pde1a	0.029043757	-30.72104529	M6
ENSMUSG00000027082	Tfpi	0.016568353	-25.57688767	M6
ENSMUSG00000027082	Tfpi	2.81E-05	-29.03030715	M6
ENSMUSG00000027082	Tfpi	0.017405827	-18.30601119	M6
ENSMUSG00000075222	Olfr988	0.006473669	21.38995131	M6
ENSMUSG00000102091	Olfr1034	0.046454256	-17.45536437	M6
ENSMUSG00000075174	Olfr1087	0.015905942	-22.17320085	M6
ENSMUSG00000075163	Olfr1107	0.035748226	-27.51447148	M6

ENSMUSG00000081041	NA	0.059145954	14.39627366	M6
ENSMUSG00000027243	Harbi1	0.021298112	-18.6986308	M6
ENSMUSG00000027860	Vangl1	0.057087395	-9.164143919	M6
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ENSMUSG00000105891	A230001M10Rik	0.036867905	-20.85173339	M6
ENSMUSG00000086745	Tspan2os	0.003255122	27.79650915	M6
ENSMUSG00000086745	Tspan2os	0.000278619	31.1388658	M6
ENSMUSG00000086745	Tspan2os	1.43E-05	-32.09535379	M6
ENSMUSG00000086745	Tspan2os	0.027119229	31.66056166	M6
ENSMUSG00000027848	Olfml3	0.007178586	-18.71035218	M6
ENSMUSG00000078620	NA	7.99E-10	-50.14064507	M6
ENSMUSG00000085754	NA	4.56E-09	50.79784373	M6
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ENSMUSG00000032952	Ap4b1	2.43E-06	30.1193981	M6
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ENSMUSG00000044165	Bcl2l15	2.65E-05	34.98595182	M6
ENSMUSG00000044165	Bcl2l15	0.000732624	32.75352734	M6
ENSMUSG00000027843	Ptpn22	0.066226611	26.58227299	M6
ENSMUSG00000032913	Lrig2	6.09E-05	38.21350763	M6
ENSMUSG00000027905	Ddx20	0.001568656	-31.47342995	M6
ENSMUSG00000048458	Fam212b	0.02702447	-20.97748969	M6
ENSMUSG00000028121	Bcar3	0.034802683	-28.77048061	M6
ENSMUSG00000054091	1810037I17Rik	0.074590056	14.1177349	M6
ENSMUSG00000037922	Bank1	0.00662307	25.5878555	M6
ENSMUSG00000098008	A930001A20Rik	1.62E-08	36.22626757	M6
ENSMUSG00000102699	4930433B08Rik	7.89E-08	31.74007976	M6
ENSMUSG00000099105	Mir7007	0.039063446	26.31020214	M6
ENSMUSG00000063887	Nlgn1	0.086696745	5.943324373	M6
ENSMUSG00000037737	Actrt3	0.00302921	-23.63033808	M6
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ENSMUSG00000027663	Zmat3	2.52E-06	-28.28713841	M6
ENSMUSG00000027708	Dcun1d1	0.011330506	7.070707071	M6
ENSMUSG00000053706	NA	0.019243412	10.21367521	M6
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ENSMUSG00000049404	Rarres1	0.032722389	-28.37599187	M6
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ENSMUSG00000033981	Gria2	0.069152269	8.75	M6
ENSMUSG00000028059	Arhgef2	0.077065065	-20.80179032	M6
ENSMUSG00000028059	Arhgef2	4.91E-09	27.0307001	M6
ENSMUSG00000028059	Arhgef2	1.54E-11	30.07988722	M6

ENSMUSG00000028059	Arhgef2	1.80E-11	27.25719779	M6
ENSMUSG00000028059	Arhgef2	3.07E-10	30.37563131	M6
ENSMUSG00000093390	NA	0.000355365	16.6968599	M6
ENSMUSG00000093390	NA	6.04E-09	27.09447415	M6
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ENSMUSG00000049741	Rxfp4	0.035072564	-29.70369908	M6
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ENSMUSG00000041237	Pklr	0.026306494	-21.72469519	M6
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ENSMUSG00000027506	Tpd52	0.005714925	23.40693023	M6
ENSMUSG00000094018	S100a2	0.007832045	16.46998209	M6
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ENSMUSG00000042250	Pglyrp4	0.054198649	18.09592855	M6
ENSMUSG00000086377	4930529C04Rik	0.049016065	-19.84634238	M6
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ENSMUSG00000042212	Sprr2d	9.36E-05	-23.4539072	M6
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ENSMUSG00000045539	Sprr3	0.015694696	-16.83232889	M6
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ENSMUSG00000106324	NA	0.00052719	-19.65277778	M6
ENSMUSG00000027869	Hsd3b6	0.013881491	-25.46048723	M6
ENSMUSG00000028528	Dnajc6	5.73E-05	28.24883859	M6
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ENSMUSG00000085041	BB031773	0.039503659	17.60786327	M6
ENSMUSG00000086080	1700123O12Rik	0.044365875	23.52182266	M6
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ENSMUSG00000033295	Ptprf	0.022230096	16.79467085	M6
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ENSMUSG00000028536	2610528J11Rik	0.015905942	13.62370196	M6
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ENSMUSG00000023247	Guca2a	0.041912838	21.72039125	M6
ENSMUSG00000042616	Oscp1	0.011645594	-5.837014033	M6
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ENSMUSG00000042616	Oscp1	0.067718552	-6.391680092	M6

ENSMUSG00000042616	Oscp1	3.32E-05	-9.089996191	M6
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ENSMUSG00000042616	Oscp1	3.28E-08	-13.39380048	M6
ENSMUSG00000042616	Oscp1	7.62E-06	-13.91682209	M6
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ENSMUSG00000028845	Tekt2	0.010890034	12.12121212	M6
ENSMUSG00000028906	Epb41	0.00166184	-20.93870734	M6
ENSMUSG00000007880	Arid1a	0.000173579	10.85737179	M6
ENSMUSG00000048003	Catsper4	2.91E-07	19.81632384	M6
ENSMUSG00000050989	Selenon	0.021194717	14.70465379	M6
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ENSMUSG00000028749	Pla2g2f	0.050782262	17.51590987	M6
ENSMUSG00000028751	Pla2g2e	0.000905826	23.86530428	M6
ENSMUSG00000040964	Arhgef10l	5.45E-07	40.82658493	M6
ENSMUSG00000040964	Arhgef10l	1.09E-05	41.84372887	M6
ENSMUSG00000040964	Arhgef10l	0.000224328	35.06882898	M6
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ENSMUSG00000086159	NA	0.000324529	37.42445055	M6
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ENSMUSG00000028923	Necap2	7.79E-05	14.4593254	M6
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ENSMUSG00000006445	Epha2	0.051724848	8.888888889	M6
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ENSMUSG00000006216	Clcnkb	9.60E-09	17.38095238	M6
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ENSMUSG00000029068	Ccnl2	0.061605164	-28.03799917	M6
ENSMUSG00000029070	Mxra8	9.67E-05	-33.48020087	M6
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ENSMUSG00000028573	Fggy	0.00446184	20.43293649	M6
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ENSMUSG00000053873	Aym1	0.019126248	28.50397831	M6
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ENSMUSG00000107144	4930413E15Rik	0.004465842	10.82043791	M6
ENSMUSG00000032690	Oas2	0.057087395	14.45142191	M6
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ENSMUSG00000025538	Sumf2	0.000692706	-22.16074689	M6
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ENSMUSG00000099197	Mir7034	0.090106034	-23.68591128	M6
ENSMUSG00000079165	Sap25	0.078380961	18.84094603	M6
ENSMUSG00000029547	Ints1	0.004211017	-24.17568543	M6
ENSMUSG00000036555	Iqce	0.002882053	31.21267042	M6
ENSMUSG00000055991	Zkscan5	0.073736504	-7.662032154	M6
ENSMUSG00000106820	D5Ertd605e	0.095119062	20.90609962	M6
ENSMUSG00000107313	NA	5.80E-09	41.21007787	M6
ENSMUSG00000029660	Tex26	0.006034812	-31.81843498	M6
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ENSMUSG00000104667	Gm4961	0.059281521	-15.30462802	M6
ENSMUSG00000011034	Slc5a1	0.035209862	-25.62440646	M6
ENSMUSG00000098830	Mir7024	0.003595377	18.85576923	M6
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ENSMUSG00000007415	Gatad1	0.002431118	28.97546402	M6
ENSMUSG00000040351	Ankib1	0.021655796	21.0110406	M6
ENSMUSG00000040351	Ankib1	0.061256875	25.28649591	M6
ENSMUSG00000029082	Bst1	1.39E-07	45.28213333	M6
ENSMUSG00000029082	Bst1	8.00E-08	-37.58189036	M6
ENSMUSG00000029082	Bst1	1.09E-05	-44.3926673	M6
ENSMUSG00000029086	Prom1	0.003095219	-22.10193293	M6
ENSMUSG00000029086	Prom1	1.73E-05	32.63633221	M6
ENSMUSG00000015879	Fam184b	0.037960875	-19.08331916	M6

ENSMUSG00000029186	Pi4k2b	0.009853909	-10.80917874	M6
ENSMUSG00000029179	Zcchc4	0.000915652	-26.2345679	M6
ENSMUSG00000029188	Slc34a2	0.024033111	13.48460681	M6
ENSMUSG00000079666	1700015F17Rik	0.088290032	20.04601882	M6
ENSMUSG00000079666	1700015F17Rik	0.002368702	22.22511259	M6
ENSMUSG00000073234	Gm8773	0.004124522	26.41678009	M6
ENSMUSG00000090326	Dthd1	0.002005114	-22.12086253	M6
ENSMUSG00000090326	Dthd1	0.002777206	-9.25245098	M6
ENSMUSG00000051498	Tlr6	0.067388765	15.55665025	M6
ENSMUSG00000051498	Tlr6	0.032977748	16.64908942	M6
ENSMUSG00000051498	Tlr6	0.017724808	19.25722745	M6
ENSMUSG00000051498	Tlr6	8.60E-05	21.02067649	M6
ENSMUSG00000051498	Tlr6	0.001639383	19.33620003	M6
ENSMUSG00000051498	Tlr6	0.000200856	22.19542913	M6
ENSMUSG00000051498	Tlr6	0.001028827	18.58381079	M6
ENSMUSG00000005220	Corin	0.082145118	15.95436865	M6
ENSMUSG00000036256	Igfbp7	0.082145118	14.14992925	M6
ENSMUSG00000003161	Sri	0.003799417	29.36399711	M6
ENSMUSG00000003161	Sri	0.000920292	26.73065404	M6
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ENSMUSG00000003161	Sri	0.000685606	25.89440871	M6
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ENSMUSG00000054099	Slc25a40	0.044125245	25.9120227	M6
ENSMUSG00000061184	Tmprss11c	1.30E-07	44.82778876	M6
ENSMUSG00000048764	Tmprss11f	0.01755219	24.1045991	M6
ENSMUSG00000048764	Tmprss11f	0.001462613	35.50673401	M6
ENSMUSG00000067156	Gm7337	0.080899744	-16.35611298	M6
ENSMUSG00000067156	Gm7337	2.75E-06	36.23248516	M6
ENSMUSG00000042476	Abcb4	0.001112299	27.15855829	M6
ENSMUSG00000029410	Ppef2	0.002724359	27.727335	M6
ENSMUSG00000030271	Ogg1	0.001538101	20.34009737	M6
ENSMUSG00000030322	Mbd4	0.009478545	20.08840818	M6
ENSMUSG00000007827	Ankrd26	0.036518034	-13.22874121	M6
ENSMUSG00000007458	M6pr	0.009718153	21.10122431	M6
ENSMUSG00000061769	Klra6	0.003706559	-12.43386243	M6
ENSMUSG00000079852	Klra4	0.000253971	-15.86448199	M6
ENSMUSG00000033024	Klra9	8.32E-07	-15.0249616	M6
ENSMUSG00000067599	Klra7	0.059905172	13.64097258	M6
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ENSMUSG00000101894	1700016P04Rik	8.64E-05	-33.45190937	M6
ENSMUSG00000101894	1700016P04Rik	0.004947279	-28.28067335	M6
ENSMUSG00000101894	1700016P04Rik	0.00085746	-34.10866301	M6
ENSMUSG00000046733	Gprc5a	0.059350601	-14.04520918	M6

ENSMUSG00000030205	Gprc5d	0.030726858	-10.30701754	M6
ENSMUSG00000042770	Hebp1	1.05E-06	-18.31140351	M6
ENSMUSG00000042770	Hebp1	0.010508244	-13.81886088	M6
ENSMUSG00000042770	Hebp1	5.59E-05	-15.29072083	M6
ENSMUSG00000042770	Hebp1	6.78E-06	-16.26984127	M6
ENSMUSG00000042770	Hebp1	2.14E-06	-18.20289855	M6
ENSMUSG00000108239	Gm19434	0.000500246	-15.81415175	M6
ENSMUSG00000108239	Gm19434	0.016517436	-13.1108324	M6
ENSMUSG00000030232	Aebp2	0.080446419	29.24707602	M6
ENSMUSG00000107456	Gm10400	0.001457676	26.98725395	M6
ENSMUSG00000030235	Slco1c1	0.000807553	-34.78008046	M6
ENSMUSG00000030245	Golt1b	1.97E-05	-26.31569665	M6
ENSMUSG00000071112	Spx	4.46E-17	-44.75339666	M6
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ENSMUSG00000071112	Spx	1.76E-11	-48.55959017	M6
ENSMUSG00000071112	Spx	1.29E-11	-65.7269734	M6
ENSMUSG00000030244	Gys2	1.29E-06	-42.24240614	M6
ENSMUSG00000030244	Gys2	2.36E-21	-51.37469459	M6
ENSMUSG00000030246	Ldhb	4.12E-24	-56.51771155	M6
ENSMUSG00000030246	Ldhb	4.30E-24	-58.00287816	M6
ENSMUSG00000104234	5330439B14Rik	4.49E-13	-61.55548988	M6
ENSMUSG00000030249	Abcc9	3.14E-05	-22.57057979	M6
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ENSMUSG00000048473	Sult6b2	6.26E-19	-62.10544319	M6
ENSMUSG00000072683	Gm7457	5.24E-26	-59.48285426	M6
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ENSMUSG00000072683	Gm7457	3.15E-17	-54.86213269	M6
ENSMUSG00000030279	C2cd5	1.94E-29	-71.77771077	M6
ENSMUSG00000030279	C2cd5	4.34E-29	-71.52839485	M6
ENSMUSG00000030275	Etnk1	0.021342117	30.61192744	M6
ENSMUSG00000072679	NA	9.28E-17	-66.07107083	M6
ENSMUSG00000072679	NA	4.99E-12	-55.00076778	M6
ENSMUSG00000086887	1700060C16Rik	1.04E-18	-72.35575742	M6
ENSMUSG00000086887	1700060C16Rik	6.04E-25	-71.01283721	M6
ENSMUSG00000030268	Bcat1	0.002017152	33.78092668	M6
ENSMUSG00000030268	Bcat1	3.67E-05	32.8767999	M6
ENSMUSG00000087204	NA	0.000397779	22.58081546	M6
ENSMUSG00000054966	Lmntd1	0.097084889	-32.32585361	M6
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ENSMUSG00000030259	Rassf8	0.001318011	-32.74696214	M6
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ENSMUSG00000030292	Smco2	0.022531853	-9.523809524	M6
ENSMUSG00000030292	Smco2	0.037870546	-7.352941176	M6
ENSMUSG00000072660	NA	0.090274022	-24.27025541	M6
ENSMUSG00000030303	Far2	0.067539699	-12.14146477	M6
ENSMUSG00000029534	St7	3.10E-10	-39.3726806	M6
ENSMUSG00000029848	Stra8	0.029158592	-22.27712801	M6
ENSMUSG00000029847	Slc23a4	0.035985029	-10.0194117	M6
ENSMUSG00000029830	Svopl	0.013293805	-22.90956575	M6
ENSMUSG00000100121	1700025N23Rik	0.055111421	-21.61558382	M6
ENSMUSG00000068536	Doxl2	0.040150072	13.15353598	M6
ENSMUSG00000053604	Rpia	0.030448835	27.13024703	M6
ENSMUSG00000054422	Fabp1	0.034490142	16.63878347	M6
ENSMUSG00000037621	Atoh8	0.006111385	26.48636991	M6
ENSMUSG00000055850	Rnf181	0.028175505	21.92994491	M6
ENSMUSG00000072999	NA	0.019039982	17.69036384	M6
ENSMUSG00000107408	1700065L07Rik	0.075113364	17.81899561	M6
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ENSMUSG00000108072	Gm20362	0.004775894	-19.00529101	M6
ENSMUSG00000068299	Nat8f4	0.010000575	25.03236568	M6
ENSMUSG00000098531	Mir7041	1.32E-10	39.42144863	M6
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ENSMUSG00000035158	Mitf	2.44E-07	-27.670392	M6
ENSMUSG00000032875	Arhgef17	0.050591282	-25.60846561	M6
ENSMUSG00000044814	Olfr543	0.000284466	-25.78869896	M6
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ENSMUSG00000044814	Olfr543	0.001111225	27.60102139	M6
ENSMUSG00000043925	Olfr544	4.48E-11	34.53748504	M6
ENSMUSG00000044824	Olfr545	0.000723904	25.66383524	M6
ENSMUSG00000073979	Olfr547	1.47E-05	-13.30536807	M6
ENSMUSG00000073977	Olfr549	0.003371298	30.12388671	M6
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ENSMUSG00000030966	Trim21	1.73E-08	33.43225061	M6
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ENSMUSG00000073975	Olfr550	0.004099665	31.44982554	M6
ENSMUSG00000073974	Olfr551	1.56E-05	34.33889221	M6
ENSMUSG00000073974	Olfr551	1.36E-08	38.64454298	M6
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ENSMUSG00000073971	Olfr554	5.97E-05	30.74969654	M6
ENSMUSG00000073970	Olfr555	0.000975278	28.71653105	M6
ENSMUSG00000073969	Olfr556	6.71E-07	35.39959626	M6
ENSMUSG00000066273	Olfr33	5.95E-06	31.96417982	M6
ENSMUSG00000110122	NA	0.00166184	37.89994605	M6
ENSMUSG00000060888	Olfr566	0.00020693	18.104377	M6
ENSMUSG00000109878	NA	0.00327833	31.46441644	M6
ENSMUSG00000062142	Olfr569	0.003608891	31.17046352	M6
ENSMUSG00000073964	Olfr570	0.001569158	31.79670991	M6
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ENSMUSG00000073960	Olfr583	2.81E-14	52.50438728	M6
ENSMUSG00000051362	Olfr589	0.000698087	31.6395694	M6
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ENSMUSG00000073950	Olfr599	0.031010299	29.96918609	M6
ENSMUSG00000082739	NA	0.00080881	27.2924743	M6
ENSMUSG00000109659	Olfr605	3.31E-07	38.52451842	M6
ENSMUSG00000073948	Olfr608	0.000601354	40.09166466	M6
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ENSMUSG00000046396	Olfr609	1.03E-07	-44.00239234	M6
ENSMUSG00000045584	Olfr610	2.58E-05	-39.94199346	M6
ENSMUSG00000047544	Olfr616	1.42E-07	-32.60087884	M6
ENSMUSG00000045780	Olfr624	8.69E-08	-40.139335	M6
ENSMUSG00000050281	Olfr630	4.41E-06	-40.29462844	M6
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ENSMUSG00000058662	Olfr69	1.89E-11	37.78078466	M6
ENSMUSG00000061626	Olfr68	0.000614872	-31.54061625	M6
ENSMUSG00000052187	Hbb-y	0.000389838	-39.72235532	M6
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ENSMUSG00000052187	Hbb-y	1.93E-07	-38.17839775	M6
ENSMUSG00000073937	Olfr633	1.83E-06	31.27318288	M6
ENSMUSG00000094063	Olfr638	0.001299593	24.65935468	M6
ENSMUSG00000066262	Olfr640	0.000355447	24.8883902	M6
ENSMUSG00000073932	Olfr641	0.072006924	24.39432321	M6
ENSMUSG00000110012	Olfr644	0.000421993	28.20532812	M6
ENSMUSG00000110012	Olfr644	5.14E-05	33.80814721	M6
ENSMUSG00000051618	Ubqln3	0.000916456	24.75698138	M6

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ENSMUSG00000051437	Ubqlnl	0.003706559	20.76889883	M6
ENSMUSG00000044899	Olfr649	7.55E-06	35.00350879	M6
ENSMUSG00000072244	Trim6	1.70E-07	34.12608367	M6
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ENSMUSG00000078616	NA	1.39E-06	-33.11284437	M6
ENSMUSG00000057596	Trim30d	1.93E-08	-46.6721463	M6
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ENSMUSG00000057596	Trim30d	1.48E-08	-39.38857858	M6
ENSMUSG00000073928	Olfr651	3.74E-09	-55.05920283	M6
ENSMUSG00000073928	Olfr651	1.49E-12	-47.30583921	M6
ENSMUSG00000073927	Olfr652	0.000576776	33.82459393	M6
ENSMUSG00000073925	Olfr654	1.17E-06	32.93415339	M6
ENSMUSG00000073923	Olfr657	1.81E-10	36.64266879	M6
ENSMUSG00000073920	Olfr661	6.65E-06	35.71557047	M6
ENSMUSG00000096773	Olfr675	0.042145272	25.73613524	M6
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ENSMUSG00000073914	Olfr677	0.001069731	33.43567251	M6
ENSMUSG00000095248	Olfr681	9.13E-07	33.72657182	M6
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ENSMUSG00000048425	Olfr686	3.30E-10	35.30727177	M6
ENSMUSG00000073906	Olfr692	3.51E-14	37.87570212	M6
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ENSMUSG00000044465	Fam160a2	5.55E-08	38.24389747	M6
ENSMUSG00000110366	NA	0.040188695	24.56700943	M6
ENSMUSG00000030897	Cnga4	0.006331846	27.29451061	M6
ENSMUSG00000037060	Cavin3	5.15E-06	36.01224585	M6
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ENSMUSG00000037032	Apbb1	0.000100196	26.1221883	M6
ENSMUSG00000030895	Hpx	0.002529967	25.12738331	M6
ENSMUSG00000030888	Rrp8	1.91E-10	38.42012728	M6
ENSMUSG00000059087	Olfr698	2.79E-08	34.89398866	M6
ENSMUSG00000109354	Olfr706	0.059312794	24.39622442	M6
ENSMUSG00000045581	Olfr710	1.47E-08	-30.63680281	M6
ENSMUSG00000073897	Olfr17	4.17E-06	-20.93253968	M6
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ENSMUSG00000095910	Olfr469	0.001424095	14.58700044	M6

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ENSMUSG00000110253	Olfr495	0.035143064	21.94378406	M6
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ENSMUSG00000060759	Olfr503	0.00587148	22.73216979	M6
ENSMUSG00000066240	Olfr517	1.32E-07	26.68111629	M6
ENSMUSG00000090714	Zscan4d	0.002945663	7.171281111	M6
ENSMUSG00000030982	9030624J02Rik	0.08274395	-22.25809664	M6
ENSMUSG00000062017	Abca14	0.088290032	11.30163818	M6
ENSMUSG00000030779	Rbbp6	3.20E-06	34.52650884	M6
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ENSMUSG00000052707	Tnrc6a	0.000806396	28.23255757	M6
ENSMUSG00000030766	Arhgap17	0.00520618	11.22101772	M6
ENSMUSG00000030766	Arhgap17	0.013261695	10.97995879	M6
ENSMUSG00000030766	Arhgap17	3.73E-06	22.68960864	M6
ENSMUSG00000054715	Zscan22	3.18E-08	-28.36839596	M6
ENSMUSG00000033961	Zfp446	0.000308624	-23.82509316	M6
ENSMUSG00000073804	Nps	0.027217265	20.05211893	M6
ENSMUSG00000099092	Mir7062	0.002055612	24.73110543	M6
ENSMUSG00000045733	Sprn	0.029672029	-21.57818533	M6
ENSMUSG00000045733	Sprn	0.027106551	-23.93318537	M6
ENSMUSG00000045733	Sprn	0.01086966	-15.19503602	M6
ENSMUSG00000062031	Pgghg	0.035933201	-11.14774279	M6
ENSMUSG00000048677	Tpcn2	0.019418705	-6.590022297	M6
ENSMUSG00000074364	Ehd2	0.000525116	-12.82051282	M6
ENSMUSG00000044903	Psg22	2.43E-08	-44.54227682	M6
ENSMUSG00000109490	NA	1.50E-05	-42.98067027	M6
ENSMUSG00000040866	Rsph6a	0.035931324	-25.88086221	M6
ENSMUSG00000040866	Rsph6a	0.005335144	-29.28483561	M6
ENSMUSG00000044317	Gpr4	0.016793476	28.03522733	M6
ENSMUSG00000030402	Ppm1n	0.013954293	-19.96795192	M6
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ENSMUSG00000030399	Ckm	0.060052086	-23.32644819	M6
ENSMUSG00000062300	Nectin2	0.04633243	-18.66011067	M6
ENSMUSG00000092496	NA	0.031164481	-20.75926616	M6
ENSMUSG00000090715	Vmn1r167	0.053417312	-21.53109913	M6
ENSMUSG00000090715	Vmn1r167	1.88E-06	-22.37141838	M6
ENSMUSG00000090715	Vmn1r167	0.011147225	-18.8000383	M6

ENSMUSG00000035523	Vmn1r172	0.00463157	-24.82447575	M6
ENSMUSG00000068962	Zfp114	0.020111227	-22.1592702	M6
ENSMUSG00000068962	Zfp114	1.36E-06	-28.49202601	M6
ENSMUSG00000003379	Cd79a	0.075995651	-15.76241115	M6
ENSMUSG00000030483	Cyp2b10	0.004412671	-15.38789087	M6
ENSMUSG00000109142	NA	0.008778695	-16.96573258	M6
ENSMUSG00000062132	Arhgap33os	0.029752381	-17.97467007	M6
ENSMUSG00000107470	NA	0.015905942	-14.22962462	M6
ENSMUSG00000056216	Cebpg	0.010465648	21.69444444	M6
ENSMUSG00000058818	Pirb	0.000168411	-24.51885861	M6
ENSMUSG00000058818	Pirb	0.00011811	-29.26636422	M6
ENSMUSG00000108438	NA	0.095518413	16.91349257	M6
ENSMUSG00000091177	NA	0.059350601	22.86874221	M6
ENSMUSG00000046456	Tmem150b	0.003699402	-15.7378741	M6
ENSMUSG00000044876	Zfp444	0.092385772	-9.632841574	M6
ENSMUSG00000048067	Olfr1349	6.63E-09	37.3590942	M6
ENSMUSG00000098353	Mir7057	0.032085673	-16.23167322	M6
ENSMUSG00000097697	4833412C05Rik	0.033270801	17.45576141	M6
ENSMUSG00000097697	4833412C05Rik	0.031625877	19.96899286	M6
ENSMUSG00000097697	4833412C05Rik	0.027198027	14.20454545	M6
ENSMUSG00000097697	4833412C05Rik	0.010482648	20.41321252	M6
ENSMUSG00000108530	4930429H19Rik	0.040479331	-28.67945301	M6
ENSMUSG00000025790	Slco3a1	0.011587609	-32.0664431	M6
ENSMUSG00000030606	Hapln3	0.0296507	-11.21169835	M6
ENSMUSG00000108757	NA	4.13E-09	24.82835046	M6
ENSMUSG00000082954	NA	3.87E-08	30.32768905	M6
ENSMUSG00000038930	Rccd1	0.000351717	-17.96157059	M6
ENSMUSG00000038930	Rccd1	3.55E-07	-25.50553427	M6
ENSMUSG00000030533	Unc45a	0.001826417	22.56652426	M6
ENSMUSG00000031727	Pmfbp1	0.071336092	16.09909568	M6
ENSMUSG00000040263	Klhdc4	0.00096648	-24.31657848	M6
ENSMUSG00000040010	Slc7a5	0.074426009	-8.083471188	M6
ENSMUSG00000025317	Car5a	2.73E-05	34.31059605	M6
ENSMUSG00000050930	Map10	0.001116699	30.98714966	M6
ENSMUSG00000085795	Zfp703	0.01269084	12.63073549	M6
ENSMUSG00000039720	Got1l1	0.088600118	-22.19699425	M6
ENSMUSG00000062991	Nrg1	0.00689496	10.91730605	M6
ENSMUSG00000062991	Nrg1	0.021167535	10.29915846	M6
ENSMUSG00000079070	Gm3985	4.50E-10	-23.33333333	M6
ENSMUSG00000031583	Wrn	1.59E-13	-27.83956888	M6
ENSMUSG00000031583	Wrn	1.32E-05	-19.33170996	M6
ENSMUSG00000049184	Purg	1.60E-16	-37.8527158	M6
ENSMUSG00000031584	Gsr	7.46E-13	-39.62429467	M6

ENSMUSG00000049476	NA	1.76E-08	-20.14208909	M6
ENSMUSG00000049476	NA	4.81E-12	-25.09930385	M6
ENSMUSG00000071113	Mboat4	0.066165675	-25.42501007	M6
ENSMUSG00000071113	Mboat4	0.06930514	-27.43932507	M6
ENSMUSG00000071113	Mboat4	0.000153627	-36.6734429	M6
ENSMUSG00000031521	Aga	1.03E-06	28.78174603	M6
ENSMUSG00000090003	NA	0.023251328	-21.01190476	M6
ENSMUSG00000025519	Tktl2	0.027198027	-30.65094713	M6
ENSMUSG00000036306	Lzts1	9.10E-10	29.32341873	M6
ENSMUSG00000060427	Zfp868	1.44E-13	29.46836789	M6
ENSMUSG00000043090	Zfp866	6.24E-06	24.44852941	M6
ENSMUSG00000036246	Gmip	4.63E-05	22.09494324	M6
ENSMUSG00000036246	Gmip	7.09E-08	26.59454586	M6
ENSMUSG00000031861	Lpar2	2.09E-13	-36.67203955	M6
ENSMUSG00000031861	Lpar2	2.91E-06	-33.47902963	M6
ENSMUSG00000047654	Tssk6	1.32E-07	23.80952381	M6
ENSMUSG00000047654	Tssk6	5.64E-11	21.31313131	M6
ENSMUSG00000110545	NA	0.000421005	17.767507	M6
ENSMUSG00000036151	Tm6sf2	0.00327833	10.96104154	M6
ENSMUSG00000036151	Tm6sf2	0.010000575	-22.32786415	M6
ENSMUSG00000007594	Hapln4	7.91E-26	57.66151723	M6
ENSMUSG00000002341	Ncan	8.34E-11	27.35520528	M6
ENSMUSG00000071078	Nr2c2ap	4.41E-05	14.47356631	M6
ENSMUSG00000071078	Nr2c2ap	9.41E-06	15.94932845	M6
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ENSMUSG00000036120	Rfxank	0.002833862	14.74580975	M6
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ENSMUSG00000079033	Mef2b	1.31E-06	14.52533784	M6
ENSMUSG00000036054	Sugp2	2.35E-06	30.2744709	M6
ENSMUSG00000036054	Sugp2	5.57E-09	21.95067791	M6
ENSMUSG00000003573	Homer3	0.000975152	17.64323248	M6
ENSMUSG00000003573	Homer3	6.00E-12	45.29408908	M6
ENSMUSG00000057788	Ddx49	7.72E-17	45.36231884	M6
ENSMUSG00000007888	Crlf1	0.000627361	18.2455045	M6
ENSMUSG00000090137	Uba52	2.20E-07	32.2975173	M6
ENSMUSG00000090137	Uba52	5.49E-11	29.43374527	M6
ENSMUSG00000055553	Kxd1	0.044089168	-24.60432335	M6
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ENSMUSG00000038508	Gdf15	2.15E-19	49.02104906	M6
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ENSMUSG00000031848	Lsm4	4.55E-11	41.54766651	M6
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ENSMUSG00000031848	Lsm4	3.92E-21	54.46457664	M6
ENSMUSG00000110575	NA	0.056787742	11.65329768	M6
ENSMUSG00000031834	Pik3r2	9.75E-13	49.30476655	M6
ENSMUSG00000000791	Il12rb1	4.03E-15	39.64646465	M6
ENSMUSG00000002910	Arrdc2	3.82E-05	27.86796537	M6
ENSMUSG00000002910	Arrdc2	7.98E-14	31.27739346	M6
ENSMUSG00000002908	Kcnn1	1.88E-12	42.31573586	M6
ENSMUSG00000002908	Kcnn1	1.78E-25	42.42117267	M6
ENSMUSG00000007721	Ccdc124	0.02071246	11.12144629	M6
ENSMUSG00000007721	Ccdc124	8.36E-13	41.7183919	M6
ENSMUSG00000000792	Slc5a5	0.07029594	9.211898101	M6
ENSMUSG00000088248	Mir1969	7.12E-18	42.75054554	M6
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ENSMUSG00000002395	Use1	0.006492953	13.17488984	M6
ENSMUSG00000002396	Ocel1	9.21E-08	43.97251141	M6
ENSMUSG00000031820	Babam1	2.63E-15	48.76655017	M6
ENSMUSG00000046295	Ankle1	2.65E-22	50.44054185	M6
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ENSMUSG00000046295	Ankle1	7.38E-19	37.25818296	M6
ENSMUSG00000034863	Ano8	1.52E-13	50.17717906	M6
ENSMUSG00000034845	Plvap	3.85E-11	46.9657907	M6
ENSMUSG00000031813	Mvb12a	0.005636076	29.53994547	M6
ENSMUSG00000031807	Pgls	0.020391439	9.581738193	M6
ENSMUSG00000043243	Fam129c	1.35E-17	44.43800579	M6
ENSMUSG00000043243	Fam129c	2.31E-14	38.3685287	M6
ENSMUSG00000043243	Fam129c	0.000120456	16.4399646	M6
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ENSMUSG00000034807	Colgalt1	1.78E-19	53.71074746	M6
ENSMUSG00000098976	Mir6769b	2.65E-22	54.26495159	M6
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ENSMUSG00000031805	Jak3	0.001789329	15.59591579	M6
ENSMUSG00000031805	Jak3	0.002425659	8.303010803	M6
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ENSMUSG00000066880	Zfp617	1.22E-09	38.44298403	M6
ENSMUSG00000069998	Olfr372	1.37E-13	35.83365211	M6
ENSMUSG00000061561	Olfr373	3.87E-12	43.91697654	M6
ENSMUSG00000061561	Olfr373	1.92E-13	39.27330428	M6
ENSMUSG00000046881	Olfr374	3.85E-16	47.21727437	M6
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ENSMUSG00000003039	Fam32a	0.029474011	6.303257674	M6
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ENSMUSG00000003033	Ap1m1	1.43E-13	37.29010735	M6
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ENSMUSG00000019732	Calr3	9.75E-13	47.11695576	M6
ENSMUSG00000019732	Calr3	8.99E-12	46.77567788	M6
ENSMUSG00000099079	Mir7068	0.034544856	11.06907743	M6
ENSMUSG00000099079	Mir7068	4.50E-23	46.4147854	M6
ENSMUSG00000052488	Cherp	2.17E-24	57.61535223	M6
ENSMUSG00000044600	Smim7	0.007306689	30.52948159	M6
ENSMUSG00000048148	Nwd1	2.00E-09	40.21133959	M6
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ENSMUSG00000031622	Sin3b	4.60E-13	-31.21078435	M6
ENSMUSG00000005413	Hmox1	2.54E-11	50.16461677	M6
ENSMUSG00000005413	Hmox1	3.52E-05	38.0719159	M6
ENSMUSG00000031618	Nr3c2	0.044323701	27.05780367	M6
ENSMUSG00000097882	0610038B21Rik	0.01756211	24.13925454	M6
ENSMUSG00000097882	0610038B21Rik	0.002490787	30.69702645	M6
ENSMUSG00000031709	Tbc1d9	0.022629544	15.26268116	M6
ENSMUSG00000031709	Tbc1d9	0.006842823	-14.63335588	M6
ENSMUSG00000005481	Ddx39	0.084729416	-7.347417411	M6
ENSMUSG00000004994	Ccdc130	0.088290032	-17.60692588	M6
ENSMUSG00000031659	Adcy7	0.007411811	-19.3612787	M6
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ENSMUSG00000031660	Brd7	6.22E-05	11.46839147	M6
ENSMUSG00000031660	Brd7	0.005471481	10.37037037	M6
ENSMUSG00000031661	Nkd1	0.006494252	14.32065756	M6
ENSMUSG00000031661	Nkd1	3.52E-07	17.2142094	M6
ENSMUSG00000031661	Nkd1	0.000773053	19.87826988	M6
ENSMUSG00000071047	Ces1a	1.61E-16	51.94336089	M6
ENSMUSG00000110499	NA	2.28E-30	73.89450056	M6
ENSMUSG00000031757	Mt4	1.88E-16	67.97591448	M6
ENSMUSG00000110524	NA	3.27E-12	61.86269749	M6
ENSMUSG00000032527	Pccb	8.03E-12	26.05870838	M6
ENSMUSG00000032527	Pccb	1.07E-05	23.51956815	M6
ENSMUSG00000077393	NA	0.005794863	23.51063476	M6
ENSMUSG00000032534	Cep63	0.082145118	16.08796296	M6
ENSMUSG00000032557	Uba5	0.085854209	16.60355216	M6
ENSMUSG00000074061	Fbxw19	7.03E-06	-16.24011105	M6
ENSMUSG00000074061	Fbxw19	0.002012857	-15.16010503	M6
ENSMUSG00000066319	Rtp3	0.050841042	-11.41999018	M6

ENSMUSG00000087038	2900079G21Rik	0.000594845	-33.43339912	M6
ENSMUSG00000036138	Acaa1a	0.016093678	6.319444444	M6
ENSMUSG00000036138	Acaa1a	0.033340376	6.500224921	M6
ENSMUSG00000032508	Myd88	0.087158077	6.018518519	M6
ENSMUSG00000032508	Myd88	0.087851481	6.509539843	M6
ENSMUSG00000034533	Scn10a	0.005736668	22.07517988	M6
ENSMUSG00000110863	Gm34655	0.099433561	23.38440427	M6
ENSMUSG00000025787	Tgm4	0.005335144	8.974358974	M6
ENSMUSG00000049307	Fut4	0.032256701	11.09943978	M6
ENSMUSG00000070319	Eif3g	0.039220553	-9.233716475	M6
ENSMUSG00000099147	Mir7081	0.00311304	-10.78976641	M6
ENSMUSG00000032194	Kank2	0.068949782	-17.52381362	M6
ENSMUSG00000066829	Zfp810	0.097350903	5.536666542	M6
ENSMUSG00000041248	Kcnj1	0.088290032	-19.87485441	M6
ENSMUSG00000110526	Olfr151	0.025903295	15.49474921	M6
ENSMUSG00000096167	Olfr887	0.067073478	15.27396787	M6
ENSMUSG00000093901	Olfr893	0.089488628	17.23938987	M6
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ENSMUSG00000094588	Olfr898	1.94E-20	28.20678746	M6
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ENSMUSG00000096757	Olfr900	0.00335168	20.52993705	M6
ENSMUSG00000096794	Olfr905	0.009792596	22.90005014	M6
ENSMUSG00000060114	Olfr910	0.033845209	21.73941799	M6
ENSMUSG00000092770	Mirlet7a-2	0.009160409	18.54413702	M6
ENSMUSG00000070304	Scn2b	0.043095784	17.64842048	M6
ENSMUSG00000032091	Tmprss4	0.056522216	-7.742544812	M6
ENSMUSG00000037129	Tmprss13	0.019299752	-12.23389356	M6
ENSMUSG00000085831	1700003G13Rik	6.44E-06	-23.91067538	M6
ENSMUSG00000085831	1700003G13Rik	0.000201125	-17.65873016	M6
ENSMUSG00000085831	1700003G13Rik	1.96E-08	-17.65765766	M6
ENSMUSG00000063543	NA	0.016792059	32.8481241	M6
ENSMUSG00000042293	Gm5617	0.006494252	-24.40814361	M6
ENSMUSG00000111662	NA	1.63E-07	15.42161856	M6
ENSMUSG00000111662	NA	0.003831598	-15.15421747	M6
ENSMUSG00000098886	Mir6385	0.002357748	10	M6
ENSMUSG00000047766	Lrrc49	0.004699771	23.283857	M6
ENSMUSG00000018623	Mmp7	0.057900619	-30.93851997	M6
ENSMUSG00000018623	Mmp7	0.001505238	-36.16774168	M6
ENSMUSG00000032342	Mto1	0.06457478	27.79575363	M6
ENSMUSG00000031998	1700128F08Rik	0.011148714	-37.20030894	M6
ENSMUSG00000084747	Mir1899	0.012926001	-24.93783069	M6

ENSMUSG00000084747	Mir1899	0.003639219	-32.82993627	M6
ENSMUSG00000103165	NA	0.052267083	-24.05942186	M6
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ENSMUSG00000052549	Arl13a	6.19E-07	-31.40891367	M6
ENSMUSG00000072844	G530011O06Rik	0.093504727	-13.22027343	M6
ENSMUSG00000035299	Mid1	0.000116319	-17.94154345	M6
ENSMUSG00000035299	Mid1	0.055060338	-12.78263279	M6
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ENSMUSG00000056815	Gm6812	0.009217736	27.92371028	M6
ENSMUSG00000025151	Maged1	4.12E-24	-64.63076028	M6
ENSMUSG00000026442	Nfasc	1.40E-05	32.58573268	1Yr
ENSMUSG00000026443	Lrrn2	1.80E-10	47.4609534	1Yr
ENSMUSG00000103421	Golt1a	1.14E-14	43.69131489	1Yr
ENSMUSG00000070644	Etnk2	5.35E-13	46.6976709	1Yr
ENSMUSG00000070644	Etnk2	0.008079945	20.32173382	1Yr
ENSMUSG00000090553	Snrpe	3.61E-08	33.05720899	1Yr
ENSMUSG00000010311	Optc	0.001302698	34.1263924	1Yr
ENSMUSG00000041577	Prelp	6.83E-08	48.50786476	1Yr

ENSMUSG00000097711	Gm5523	0.001024023	19.79949875	1Yr
ENSMUSG00000026565	Pou2f1	0.030071408	28.93292698	1Yr
ENSMUSG00000000544	Gpa33	0.000171944	34.69397133	1Yr
ENSMUSG00000098356	NA	0.002694675	-11.19896908	1Yr
ENSMUSG00000038026	Kcnj9	0.068653289	26.32714307	1Yr
ENSMUSG00000026546	Cfap45	0.006028516	-8.764534884	1Yr
ENSMUSG00000085184	4933439K11Rik	0.066011205	-12.5	1Yr
ENSMUSG00000059503	Olfr248	0.02957584	6.995651352	1Yr
ENSMUSG00000078184	NA	0.000738586	20.74534381	1Yr
ENSMUSG00000060743	H3f3a	0.077757033	24.51298701	1Yr
ENSMUSG00000037499	Nenf	3.40E-05	38.95741577	1Yr
ENSMUSG00000026131	Dst	0.042297188	12.4057971	1Yr
ENSMUSG00000026131	Dst	0.055663497	19.82461874	1Yr
ENSMUSG00000037447	Arid5a	0.004207055	-31.73226556	1Yr
ENSMUSG00000026112	Coa5	0.001478103	-32.13246658	1Yr
ENSMUSG00000026074	Map4k4	0.005301918	23.06944444	1Yr
ENSMUSG00000041945	Mfsd9	0.000279346	33.51154513	1Yr
ENSMUSG00000026094	Stk17b	0.013244178	22.46280904	1Yr
ENSMUSG00000045336	Hsfy2	5.22E-08	37.74358065	1Yr
ENSMUSG00000026207	Speg	0.010098831	-15.30555556	1Yr
ENSMUSG00000098634	Mir8096	0.001691739	26.82301123	1Yr
ENSMUSG00000098634	Mir8096	0.005722598	26.7268236	1Yr
ENSMUSG00000100217	9930111H07Rik	0.002444301	-32.35562865	1Yr
ENSMUSG00000100217	9930111H07Rik	0.006667912	-34.05624411	1Yr
ENSMUSG00000026253	Chrng	0.004804625	-23.70341816	1Yr
ENSMUSG00000026305	Lrrfip1	0.031601633	12.15277778	1Yr
ENSMUSG00000026305	Lrrfip1	0.0087755	11.45833333	1Yr
ENSMUSG00000097001	NA	1.94E-06	-35.10085643	1Yr
ENSMUSG00000108131	NA	0.000264106	-29.81839587	1Yr
ENSMUSG00000095826	NA	0.06880924	-28.86363636	1Yr
ENSMUSG00000019820	Utrn	0.012205676	34.72853535	1Yr
ENSMUSG00000037370	Enpp1	3.30E-07	42.43626744	1Yr
ENSMUSG00000037370	Enpp1	1.04E-06	45.02978503	1Yr
ENSMUSG00000099181	Mir6905	2.93E-05	57.34126984	1Yr
ENSMUSG00000101537	Gm29571	0.014798469	41.28306878	1Yr
ENSMUSG00000005355	Casp14	0.006432658	-36.71236171	1Yr
ENSMUSG00000005355	Casp14	3.58E-05	-38.7895006	1Yr
ENSMUSG00000020310	Madcam1	0.000141642	-38.86165577	1Yr
ENSMUSG00000020167	Tcf3	0.003646631	-38.50166174	1Yr
ENSMUSG00000035370	NA	9.45E-05	-44.46022727	1Yr
ENSMUSG00000004933	Matk	0.004003588	-29.70562968	1Yr
ENSMUSG00000020250	Txnrd1	5.75E-05	28.57903262	1Yr
ENSMUSG00000020250	Txnrd1	8.61E-09	31.4877451	1Yr

ENSMUSG00000048981	Krt31	6.35E-06	40.2226314	1Yr
ENSMUSG00000078627	10-Mar	0.005221792	-11.60714286	1Yr
ENSMUSG00000098704	Mir6934	0.070102844	25.28427409	1Yr
ENSMUSG00000084822	NA	0.01434769	29.13665311	1Yr
ENSMUSG00000025145	Lrrc45	0.039704596	29.36924343	1Yr
ENSMUSG00000020401	Fam71b	0.049270199	-26.03391232	1Yr
ENSMUSG00000078924	Gm12169	0.018882556	-10.49382716	1Yr
ENSMUSG00000060030	Olfr317	0.00147924	5.833333333	1Yr
ENSMUSG00000094805	Olfr311	1.15E-09	22.40601504	1Yr
ENSMUSG00000036964	Trim17	0.012612707	17.65873016	1Yr
ENSMUSG00000085882	NA	0.00329097	-13.46153846	1Yr
ENSMUSG00000005417	Mprip	0.014183856	38.43754199	1Yr
ENSMUSG00000005417	Mprip	9.68E-07	26.93110252	1Yr
ENSMUSG00000005417	Mprip	7.19E-07	27.36400296	1Yr
ENSMUSG00000005417	Mprip	3.94E-10	31.30186006	1Yr
ENSMUSG00000088950	NA	1.50E-07	27.73199023	1Yr
ENSMUSG00000000318	Clec10a	0.039856783	27.3038043	1Yr
ENSMUSG00000020808	Pimreg	0.00025402	-35.21004924	1Yr
ENSMUSG00000020807	4933427D14Rik	0.000249695	-35.42229067	1Yr
ENSMUSG00000005950	P2rx5	0.009682937	31.18015565	1Yr
ENSMUSG00000040158	Tax1bp3	3.13E-09	52.76175214	1Yr
ENSMUSG00000005949	Ctns	4.76E-09	52.33736171	1Yr
ENSMUSG00000005952	Trpv1	0.000143234	49.59363553	1Yr
ENSMUSG00000078771	Evi2a	0.069307935	28.19698959	1Yr
ENSMUSG00000010342	Tex14	0.068394555	-9.782608696	1Yr
ENSMUSG00000020872	Tac4	0.038282986	32.77328665	1Yr
ENSMUSG00000078700	D030028A08Rik	0.017214796	31.14745444	1Yr
ENSMUSG00000001445	Mrpl10	0.000384704	35.55105896	1Yr
ENSMUSG00000038013	Wipf2	6.65E-05	-38.2936659	1Yr
ENSMUSG00000021081	Serpina1f	0.020343584	26.12983889	1Yr
ENSMUSG00000098338	Mir6941	0.040641911	-25.27732474	1Yr
ENSMUSG00000098879	Mir7675	1.95E-18	-54.84261975	1Yr
ENSMUSG00000006356	Crip2	0.001076115	-26.70797274	1Yr
ENSMUSG00000006356	Crip2	0.02315327	-23.06519139	1Yr
ENSMUSG00000043945	Adam6a	0.000938603	-33.33574054	1Yr
ENSMUSG00000101930	Gm5441	0.018607521	19.09722222	1Yr
ENSMUSG00000113550	Gm29687	0.007324606	-21.36160941	1Yr
ENSMUSG00000061477	Rps7	3.32E-05	-12.78735632	1Yr
ENSMUSG00000112876	NA	0.005301918	-23.40926617	1Yr
ENSMUSG00000035860	Cdhr3	0.014715494	28.07017837	1Yr
ENSMUSG00000061603	Akap6	0.031238057	-13.29051383	1Yr
ENSMUSG00000052374	Actn2	2.76E-07	57.58907759	1Yr
ENSMUSG00000039233	Tbce	4.67E-07	48.3426704	1Yr

ENSMUSG00000113819	NA	0.02345757	24.64944557	1Yr
ENSMUSG00000113819	NA	0.011627161	-32.81249476	1Yr
ENSMUSG00000113338	A530046M15Rik	2.75E-07	53.70567885	1Yr
ENSMUSG00000021360	Gcnt2	0.005823035	-38.99304671	1Yr
ENSMUSG00000021510	Zfp729a	0.030700457	-20.88715423	1Yr
ENSMUSG00000113121	NA	0.001812223	16.46420995	1Yr
ENSMUSG00000021675	F2rl2	0.014183856	15.60457516	1Yr
ENSMUSG00000041534	Rbp3	0.007166646	27.42368538	1Yr
ENSMUSG00000047441	Antxrl	0.00329097	35.7287099	1Yr
ENSMUSG00000095493	A630023A22Rik	0.016152143	38.13117438	1Yr
ENSMUSG00000095493	A630023A22Rik	0.000263762	44.66185983	1Yr
ENSMUSG00000048337	Npy4r	0.000603987	46.66813307	1Yr
ENSMUSG00000043681	Fam25c	0.003022512	37.76019911	1Yr
ENSMUSG00000043681	Fam25c	0.010798584	46.31063381	1Yr
ENSMUSG00000021797	9230112D13Rik	0.012634079	25.10117148	1Yr
ENSMUSG00000014453	Blk	0.045449465	28.52541983	1Yr
ENSMUSG00000021966	Prss52	3.07E-06	22.79495411	1Yr
ENSMUSG00000033712	Ccar2	0.00621013	33.97590216	1Yr
ENSMUSG00000044551	9930012K11Rik	0.053956418	26.47384409	1Yr
ENSMUSG00000022090	Pdlim2	0.000571422	26.92307692	1Yr
ENSMUSG00000100172	NA	0.077851599	-28.18612914	1Yr
ENSMUSG00000115381	NA	0.065722609	-21.6171024	1Yr
ENSMUSG00000061731	Ext1	5.27E-06	42.28066868	1Yr
ENSMUSG00000037085	Trmt12	7.50E-05	52.42704826	1Yr
ENSMUSG00000101026	D730001G18Rik	0.007657744	-32.6532207	1Yr
ENSMUSG00000063522	2010109I03Rik	0.004131048	-26.04726071	1Yr
ENSMUSG00000022586	Ly6i	0.001834252	-29.25392509	1Yr
ENSMUSG00000022582	Ly6g	0.003191276	-39.15965978	1Yr
ENSMUSG00000022558	Mroh1	0.047783068	-35.22918483	1Yr
ENSMUSG00000022558	Mroh1	0.002206193	-33.37315462	1Yr
ENSMUSG00000033565	Rbfox2	0.029109428	32.24049505	1Yr
ENSMUSG00000050014	Apol10b	0.019740754	-21.99129452	1Yr
ENSMUSG00000050014	Apol10b	0.013486218	11.80609514	1Yr
ENSMUSG00000071716	Apol7e	0.004118455	21.03817799	1Yr
ENSMUSG00000062154	Tex33	8.98E-09	42.79238197	1Yr
ENSMUSG00000052496	Pkdrej	0.00763388	18.72766247	1Yr
ENSMUSG00000022387	Brd1	0.006753814	-36.60844465	1Yr
ENSMUSG00000023272	Creld2	0.008230073	-31.94086637	1Yr
ENSMUSG00000098442	Mir6959	0.000879265	-39.63959856	1Yr
ENSMUSG00000091680	Klhdc7b	0.055028594	-30.16849696	1Yr
ENSMUSG00000055022	Cntn1	2.46E-09	-40	1Yr
ENSMUSG00000036218	Pdzrn4	0.000212854	-34.13461538	1Yr
ENSMUSG00000049436	Upk1b	0.035183049	32.5	1Yr

ENSMUSG00000117239	NA	0.042113112	13.53204136	1Yr
ENSMUSG00000052270	Fpr2	0.066725095	-26.9202714	1Yr
ENSMUSG00000061544	Zfp229	4.59E-07	-31.60564925	1Yr
ENSMUSG00000091945	Vmn2r114	0.002696056	-28.89245939	1Yr
ENSMUSG00000091945	Vmn2r114	0.088969354	-28.63253606	1Yr
ENSMUSG00000091076	Vmn2r115	0.003559158	-27.68834454	1Yr
ENSMUSG00000099123	Mir6965	0.02957584	-19.19465779	1Yr
ENSMUSG00000039183	Nubp2	0.075733966	31.2394676	1Yr
ENSMUSG00000015126	Tsr3	0.039179916	40.00992063	1Yr
ENSMUSG00000047507	Baiap3	0.042468533	-25.19453456	1Yr
ENSMUSG00000097217	NA	0.00090441	25.06944444	1Yr
ENSMUSG00000008668	Rps18	1.57E-05	29.70358712	1Yr
ENSMUSG00000067203	NA	2.24E-06	19.10731244	1Yr
ENSMUSG00000092512	NA	2.93E-05	25.79069201	1Yr
ENSMUSG00000092512	NA	0.00126144	19.33333333	1Yr
ENSMUSG00000092512	NA	0.050150896	13.55875576	1Yr
ENSMUSG00000024325	Ring1	0.008747511	20.78564809	1Yr
ENSMUSG00000098197	BC051537	0.000263762	15.52853919	1Yr
ENSMUSG00000092618	Btnl6	5.32E-07	14.5264964	1Yr
ENSMUSG00000092618	Btnl6	1.00E-06	11.06500775	1Yr
ENSMUSG00000007029	Vars	0.016173596	16.54135338	1Yr
ENSMUSG00000035929	H2-Q4	5.26E-07	11.23685838	1Yr
ENSMUSG00000039518	Cdsn	0.031990013	13.37285903	1Yr
ENSMUSG00000039269	2300002M23Rik	0.000832783	17.42424242	1Yr
ENSMUSG00000037246	H2-M10.5	2.60E-05	27.80092593	1Yr
ENSMUSG00000054951	9130008F23Rik	0.007452312	21.79891983	1Yr
ENSMUSG00000057899	Adgrf2	0.012732135	-19.00326797	1Yr
ENSMUSG00000090307	1700071M16Rik	1.28E-06	25.56584989	1Yr
ENSMUSG00000040140	Tdrd6	4.50E-05	-13.78800676	1Yr
ENSMUSG00000023266	Frs3	9.68E-07	39.18198397	1Yr
ENSMUSG00000023987	Pgc	0.000101365	33.21664925	1Yr
ENSMUSG00000023806	Rsph3b	0.098132234	18.83921319	1Yr
ENSMUSG00000079722	Ttll2	0.035389814	10.85142539	1Yr
ENSMUSG00000024066	Xdh	4.87E-05	36.21841946	1Yr
ENSMUSG00000071042	Rasgrp3	0.06725257	28.18199108	1Yr
ENSMUSG00000032624	Eml4	0.000467977	-31.08974359	1Yr
ENSMUSG00000097047	1110020A21Rik	0.079531236	11.92911255	1Yr
ENSMUSG00000097047	1110020A21Rik	0.005434986	20.58109496	1Yr
ENSMUSG00000097047	1110020A21Rik	0.00013483	20.84404387	1Yr
ENSMUSG00000097047	1110020A21Rik	7.92E-05	22.60551454	1Yr
ENSMUSG00000097047	1110020A21Rik	0.01195156	19.32410719	1Yr
ENSMUSG00000097047	1110020A21Rik	0.00121312	20.22205272	1Yr
ENSMUSG00000097047	1110020A21Rik	0.038792981	12.9265873	1Yr

ENSMUSG00000093922	NA	0.035015424	16.24892225	1Yr
ENSMUSG00000117572	NA	0.005222169	-29.36476097	1Yr
ENSMUSG00000024421	Lama3	0.000223919	32.24067599	1Yr
ENSMUSG00000117536	NA	0.003360948	17.16699155	1Yr
ENSMUSG00000024502	Jakmip2	0.025583321	-30.69489591	1Yr
ENSMUSG00000043079	Synpo	0.021969426	-21.60680102	1Yr
ENSMUSG00000098247	Mir7220	0.000843158	25.76588251	1Yr
ENSMUSG00000098475	Mir6982	1.08E-06	30.60703272	1Yr
ENSMUSG00000098475	Mir6982	0.000863908	-26.94331876	1Yr
ENSMUSG00000024617	Camk2a	2.24E-05	31.576139	1Yr
ENSMUSG00000046610	Oacyl	5.67E-05	-34.37753036	1Yr
ENSMUSG00000035394	Cfap53	0.003191276	9.803921569	1Yr
ENSMUSG00000048832	Vps37c	1.69E-05	36.05361033	1Yr
ENSMUSG00000024670	Cd6	0.000824593	31.75711407	1Yr
ENSMUSG00000024737	Slc15a3	0.001076115	32.78379028	1Yr
ENSMUSG00000024737	Slc15a3	0.099716437	29.44938103	1Yr
ENSMUSG00000067571	Ms4a15	9.13E-05	34.30067953	1Yr
ENSMUSG00000067571	Ms4a15	4.87E-05	32.67850332	1Yr
ENSMUSG00000067571	Ms4a15	7.50E-05	-28.01341416	1Yr
ENSMUSG00000075010	AW112010	0.017540572	26.01035973	1Yr
ENSMUSG00000024673	Ms4a1	0.078234217	29.13288982	1Yr
ENSMUSG00000079419	Ms4a6c	0.005052531	30.57832862	1Yr
ENSMUSG00000063777	Olfr1469	0.045728706	-32.37502693	1Yr
ENSMUSG00000093373	NA	0.000921787	32.43339768	1Yr
ENSMUSG00000024798	Htr7	0.095843979	28.98855897	1Yr
ENSMUSG00000042041	2010003K11Rik	6.58E-11	39.13733609	1Yr
ENSMUSG00000071691	Gm960	3.07E-06	26.97679434	1Yr
ENSMUSG00000025064	Col17a1	0.006664774	-25.76439634	1Yr
ENSMUSG00000006463	Zdhhc24	0.027369368	-35.65282361	1Yr
ENSMUSG00000101088	1810018F18Rik	0.020464754	-27.52734108	1Yr
ENSMUSG00000027165	B230118H07Rik	0.020982503	32.36240511	1Yr
ENSMUSG00000005089	Slc1a2	0.006141431	-33.97375453	1Yr
ENSMUSG00000026730	Pter	0.047882554	-24.93119133	1Yr
ENSMUSG00000027403	Tgm6	0.004333301	-22.27880815	1Yr
ENSMUSG00000027403	Tgm6	0.000121695	-32.66087576	1Yr
ENSMUSG00000089662	NA	0.012698167	-29.09018065	1Yr
ENSMUSG00000089662	NA	0.006753814	-30.62909313	1Yr
ENSMUSG00000027420	Bfsp1	0.000476587	16.05090312	1Yr
ENSMUSG00000074649	BC029722	0.025803539	8.333333333	1Yr
ENSMUSG00000017002	Slpi	0.06428442	10	1Yr
ENSMUSG00000027670	Ocstamp	0.002240869	31.10411369	1Yr
ENSMUSG00000017897	Eya2	0.027423948	19.88636364	1Yr
ENSMUSG00000087382	Ctcflos	0.000333043	-42.95460259	1Yr

ENSMUSG00000087382	Ctcflos	0.014657012	-33.59162397	1Yr
ENSMUSG00000087382	Ctcflos	0.047783068	-29.25323221	1Yr
ENSMUSG00000026736	4930426L09Rik	0.05611074	-28.55265344	1Yr
ENSMUSG00000037683	Armc3	0.0008099	38.89705882	1Yr
ENSMUSG00000026985	Il1f8	0.055984767	27.06180166	1Yr
ENSMUSG00000026979	Psd4	5.81E-05	29.03629935	1Yr
ENSMUSG00000048186	Bend7	0.039856783	27.94922913	1Yr
ENSMUSG00000057182	Scn3a	0.096452353	-18.04641813	1Yr
ENSMUSG00000059173	Pde1a	0.001975162	29.93326118	1Yr
ENSMUSG00000040213	Kyat3	0.098132234	-39.02116402	1Yr
ENSMUSG00000078161	Erich3	3.31E-07	-53.81313131	1Yr
ENSMUSG00000078161	Erich3	6.58E-11	-58.22003487	1Yr
ENSMUSG00000037174	Elf2	0.093679246	36.72619048	1Yr
ENSMUSG00000036615	Rfxap	0.055956643	-13.25491588	1Yr
ENSMUSG00000036353	P2ry12	0.03550057	13.96367521	1Yr
ENSMUSG00000082280	NA	0.036548256	25.64028972	1Yr
ENSMUSG00000041734	Kirrel	2.83E-05	-13.57142857	1Yr
ENSMUSG00000068922	Msto1	0.035994467	-32.16269841	1Yr
ENSMUSG00000028099	Polr3c	0.080139572	-35.04041249	1Yr
ENSMUSG00000028528	Dnajc6	0.028670143	28.46182018	1Yr
ENSMUSG00000085041	BB031773	0.090217576	33.21047009	1Yr
ENSMUSG00000078599	Skint8	0.023233311	-30.98769651	1Yr
ENSMUSG00000028637	Ccdc30	0.018720934	31.71401261	1Yr
ENSMUSG00000028636	Ppcs	8.81E-05	41.89484127	1Yr
ENSMUSG00000086788	1700029M20Rik	0.090217576	-11.93810427	1Yr
ENSMUSG00000028741	Mrto4	6.58E-05	-31.47689786	1Yr
ENSMUSG00000041025	Iffo2	0.02036479	-24.02086724	1Yr
ENSMUSG00000028738	Tas1r2	0.060197824	-29.42472262	1Yr
ENSMUSG00000047719	Ubiad1	0.000619511	20.93740274	1Yr
ENSMUSG00000028936	Rpl22	0.014657012	-28.88178464	1Yr
ENSMUSG00000029064	Gnb1	0.001743934	14.98316498	1Yr
ENSMUSG00000028294	Cfap206	0.005274516	-33.75339834	1Yr
ENSMUSG00000028232	Tmem68	0.00300999	33.06272574	1Yr
ENSMUSG00000028232	Tmem68	0.000151811	-24.40164719	1Yr
ENSMUSG00000028232	Tmem68	7.20E-05	-24.22817874	1Yr
ENSMUSG00000028467	Gba2	7.90E-06	-41.27833895	1Yr
ENSMUSG00000028467	Gba2	8.34E-05	-39.42727802	1Yr
ENSMUSG00000028467	Gba2	6.24E-06	43.50872395	1Yr
ENSMUSG00000078719	Msmp	0.000965238	36.13959985	1Yr
ENSMUSG00000066324	Impad1	8.14E-09	45.59634997	1Yr
ENSMUSG00000053863	Mepe	0.002332102	-30.10776663	1Yr
ENSMUSG00000043036	Ccdc63	0.046162774	-21.40694714	1Yr
ENSMUSG00000106082	NA	0.049506413	-18.61009361	1Yr

ENSMUSG00000029430	Ran	0.054058096	-23.40510367	1Yr
ENSMUSG00000008843	Cldn13	0.000617699	32.07354737	1Yr
ENSMUSG00000042985	Upk3b	0.000233605	41.11410586	1Yr
ENSMUSG00000001739	Cldn15	2.19E-05	35.87166858	1Yr
ENSMUSG00000037364	Srrt	0.06978812	23.89180672	1Yr
ENSMUSG00000029526	1700123K08Rik	1.00E-06	21.05228462	1Yr
ENSMUSG00000045482	Trrap	0.017732051	-30.44871795	1Yr
ENSMUSG00000007812	Zfp655	0.045257666	30.91397624	1Yr
ENSMUSG00000007812	Zfp655	0.006509888	35.74882272	1Yr
ENSMUSG00000029017	Pmpcb	0.002796837	33.53835979	1Yr
ENSMUSG00000105987	AI506816	0.002161645	40.98024782	1Yr
ENSMUSG00000105987	AI506816	2.54E-08	59.23904303	1Yr
ENSMUSG00000097180	2700038G22Rik	5.32E-07	50.08597884	1Yr
ENSMUSG00000097180	2700038G22Rik	2.22E-09	41.97892858	1Yr
ENSMUSG00000038276	Asic3	0.004861438	-38.13334083	1Yr
ENSMUSG00000038276	Asic3	1.68E-08	-47.19068962	1Yr
ENSMUSG00000038276	Asic3	0.000324273	-42.13416894	1Yr
ENSMUSG00000038204	Asb10	9.33E-08	-41.40103107	1Yr
ENSMUSG00000038181	Chpf2	5.48E-10	-50.52281052	1Yr
ENSMUSG00000098830	Mir7024	0.000685554	23.54172727	1Yr
ENSMUSG00000054520	Sh3bp2	0.000113493	-22.56944444	1Yr
ENSMUSG00000054520	Sh3bp2	0.039028329	-19.91399818	1Yr
ENSMUSG00000054520	Sh3bp2	0.000477332	-29.78883861	1Yr
ENSMUSG00000104950	NA	0.007411298	-29.73349092	1Yr
ENSMUSG00000040351	Ankib1	7.14E-06	-43.36630877	1Yr
ENSMUSG00000053178	Mterf1b	2.47E-06	-37.36599512	1Yr
ENSMUSG00000104974	NA	0.004861438	-19.14473684	1Yr
ENSMUSG00000104974	NA	0.002273071	-20.46052632	1Yr
ENSMUSG00000106807	NA	0.001743934	43.61639858	1Yr
ENSMUSG00000079666	1700015F17Rik	0.007570669	-29.55800483	1Yr
ENSMUSG00000079666	1700015F17Rik	0.00068292	-31.54720816	1Yr
ENSMUSG00000073234	Gm8773	0.061124675	-24.1563582	1Yr
ENSMUSG00000029174	Tbc1d1	2.12E-07	-40.55771489	1Yr
ENSMUSG00000051498	Tlr6	0.033782431	22.74574303	1Yr
ENSMUSG00000051498	Tlr6	0.03901835	21.85545936	1Yr
ENSMUSG00000051498	Tlr6	0.005742205	17.67210145	1Yr
ENSMUSG00000051498	Tlr6	0.002696056	17.98276887	1Yr
ENSMUSG00000029153	Ociad2	0.096953108	20.44322692	1Yr
ENSMUSG00000042476	Abcb4	0.001310348	38.74449624	1Yr
ENSMUSG00000042476	Abcb4	0.024467175	34.21969974	1Yr
ENSMUSG00000057604	Lmcd1	0.070128433	25.51279765	1Yr
ENSMUSG00000079304	Tex52	0.000189149	39.25253355	1Yr
ENSMUSG00000030325	Klrb1c	0.09000742	20.40305011	1Yr

ENSMUSG00000030199	Etv6	0.00022471	-14.12337662	1Yr
ENSMUSG00000030199	Etv6	0.000166589	-12.16216216	1Yr
ENSMUSG00000072683	Gm7457	0.012365585	17.92580982	1Yr
ENSMUSG00000072683	Gm7457	0.020878765	17.18181818	1Yr
ENSMUSG00000072683	Gm7457	0.034639567	16.56455863	1Yr
ENSMUSG00000072683	Gm7457	0.004244069	16.59722222	1Yr
ENSMUSG00000030279	C2cd5	0.004118455	15.45679012	1Yr
ENSMUSG00000030279	C2cd5	0.098616913	14.15842491	1Yr
ENSMUSG00000086887	1700060C16Rik	0.001024023	25.43902176	1Yr
ENSMUSG00000030268	Bcat1	0.020929289	-27.80885781	1Yr
ENSMUSG00000108161	NA	0.001706847	29.80682092	1Yr
ENSMUSG00000040121	Rep15	0.06428442	20.46155106	1Yr
ENSMUSG00000076361	Mir182	0.000970508	21.0520434	1Yr
ENSMUSG00000090019	Gimap1	0.077107302	20.83180708	1Yr
ENSMUSG00000068536	Doxl2	2.05E-05	-24.78816314	1Yr
ENSMUSG00000107935	Gm4872	0.007341665	-19.4649699	1Yr
ENSMUSG00000004633	Chn2	0.054692884	7.073170732	1Yr
ENSMUSG00000076526	NA	3.86E-07	46.59210955	1Yr
ENSMUSG00000054422	Fabp1	0.001927675	25.48340639	1Yr
ENSMUSG00000055027	Smyd1	0.008718217	27.91199813	1Yr
ENSMUSG00000055027	Smyd1	3.83E-06	30.19363241	1Yr
ENSMUSG00000055027	Smyd1	0.044289212	22.26342118	1Yr
ENSMUSG00000052656	Rnf103	5.44E-05	34.96043066	1Yr
ENSMUSG00000063884	Ptcd3	0.085930427	25.72726981	1Yr
ENSMUSG00000056370	Sftpb	0.001425197	33.30744161	1Yr
ENSMUSG00000056737	Capg	0.002337872	24.72994394	1Yr
ENSMUSG00000056737	Capg	0.075733966	22.08606879	1Yr
ENSMUSG00000056737	Capg	0.033782431	24.80375502	1Yr
ENSMUSG00000072999	NA	0.024590531	20.93479667	1Yr
ENSMUSG00000107408	1700065L07Rik	0.048253997	24.64161371	1Yr
ENSMUSG00000107408	1700065L07Rik	0.004131048	27.14571465	1Yr
ENSMUSG00000107408	1700065L07Rik	0.021410522	30.50505051	1Yr
ENSMUSG00000002870	Mcm2	0.00035912	38.47457367	1Yr
ENSMUSG00000098531	Mir7041	0.006664774	38.26684185	1Yr
ENSMUSG00000030888	Rrp8	0.000840488	36.22415575	1Yr
ENSMUSG00000030888	Rrp8	0.004625866	39.03732039	1Yr
ENSMUSG00000030894	Tpp1	0.006209518	35.31389749	1Yr
ENSMUSG00000059087	Olfr698	0.077473434	35.63640226	1Yr
ENSMUSG00000045581	Olfr710	0.079572824	-35.22727273	1Yr
ENSMUSG00000110253	Olfr495	2.93E-05	29.14451559	1Yr
ENSMUSG00000062434	Olfr516	0.011447474	21.33825914	1Yr
ENSMUSG00000031026	Trim66	0.017257181	24.77572468	1Yr
ENSMUSG00000031023	Akip1	0.07822042	10.95795043	1Yr

ENSMUSG00000031022	BC051019	0.00012537	38.2975358	1Yr
ENSMUSG00000035951	Ascl3	0.032775827	32.80512309	1Yr
ENSMUSG00000005686	Ampd3	0.025803539	-21.52194211	1Yr
ENSMUSG00000005611	Mrvi1	0.051169058	26.39856938	1Yr
ENSMUSG00000030770	Parva	1.50E-11	-36.22081065	1Yr
ENSMUSG00000090457	4930571K23Rik	7.34E-05	34.48962149	1Yr
ENSMUSG00000044701	Il27	0.0122398	28.05404374	1Yr
ENSMUSG00000106552	NA	0.037423927	22.71560583	1Yr
ENSMUSG00000074364	Ehd2	0.002170595	-33.2906341	1Yr
ENSMUSG00000007209	Ceacam9	2.82E-05	-34.53017631	1Yr
ENSMUSG00000070797	Psg27	0.096919972	31.68336565	1Yr
ENSMUSG00000070797	Psg27	0.017178629	26.48979302	1Yr
ENSMUSG00000085601	Gm4969	0.057498808	30.3640261	1Yr
ENSMUSG00000030402	Ppm1n	1.78E-05	-37.24674817	1Yr
ENSMUSG00000003549	Ercc1	0.008221277	27.76679842	1Yr
ENSMUSG00000040714	Klc3	0.000204628	-33.21972521	1Yr
ENSMUSG00000062300	Nectin2	0.006110556	-28.21923335	1Yr
ENSMUSG00000002980	Bcam	0.05699929	-28.08121981	1Yr
ENSMUSG00000015721	Nlrp5	0.006300465	31.34147488	1Yr
ENSMUSG00000092496	NA	0.017540572	-24.26848348	1Yr
ENSMUSG00000090715	Vmn1r167	0.020582316	-21.15226976	1Yr
ENSMUSG00000092456	V1rd19	2.32E-06	-36.72243077	1Yr
ENSMUSG00000068962	Zfp114	0.004861438	-24.76117544	1Yr
ENSMUSG00000004056	Akt2	0.026836093	32.76582241	1Yr
ENSMUSG00000053964	Lgals4	0.099716437	-20.20890094	1Yr
ENSMUSG00000046056	Sbsn	2.13E-05	-20.26041667	1Yr
ENSMUSG00000046056	Sbsn	0.001358847	-25.22319317	1Yr
ENSMUSG00000057092	Fxyd3	0.000433725	-14.98316498	1Yr
ENSMUSG00000001249	Hpn	0.037211162	-25.78462224	1Yr
ENSMUSG00000101554	Scgb2b1	3.86E-07	-29.9793956	1Yr
ENSMUSG00000101658	NA	3.23E-06	-19.16666667	1Yr
ENSMUSG00000099729	Scgb2b11	7.19E-06	-29.74805237	1Yr
ENSMUSG00000068566	Myadm	7.19E-06	50.40060785	1Yr
ENSMUSG00000107620	NA	0.000877502	31.2721874	1Yr
ENSMUSG00000058818	Pirb	0.000824593	29.54508585	1Yr
ENSMUSG00000038695	Josd2	0.069452285	-14.65451269	1Yr
ENSMUSG00000109236	NA	0.001065344	-26.5952381	1Yr
ENSMUSG00000038539	Atf5	0.015690318	-21.46435345	1Yr
ENSMUSG00000003190	Bcl2l12	0.000970508	34.04319893	1Yr
ENSMUSG00000098839	Mir7054	0.046944525	31.5728022	1Yr
ENSMUSG00000035458	Tnni3	3.39E-10	-46.27787671	1Yr
ENSMUSG00000058743	Kcnj14	0.000232197	-33.94248522	1Yr
ENSMUSG00000030838	Ush1c	0.00532042	-29.62961467	1Yr

ENSMUSG00000095349	NA	0.077107302	10.72681704	1Yr
ENSMUSG00000094274	NA	0.014422349	-24.27992382	1Yr
ENSMUSG00000048067	Olfr1349	0.000596412	31.151489	1Yr
ENSMUSG00000030606	Hapln3	0.032699725	-11	1Yr
ENSMUSG00000108757	NA	2.54E-05	-28.50365896	1Yr
ENSMUSG00000030534	Vps33b	0.020227056	26.64021164	1Yr
ENSMUSG00000038930	Rccd1	0.019047552	19.33455433	1Yr
ENSMUSG00000038930	Rccd1	0.011447474	22.6090372	1Yr
ENSMUSG00000038930	Rccd1	5.67E-05	29.25339367	1Yr
ENSMUSG00000018909	Arrb1	0.036033045	-13.63846801	1Yr
ENSMUSG00000041949	Tango6	1.91E-13	-51.34338187	1Yr
ENSMUSG00000031727	Pmfbp1	0.041327126	29.08023263	1Yr
ENSMUSG00000069895	Atxn1l	0.017485383	28.46039732	1Yr
ENSMUSG00000044676	Zfp612	0.001834252	-23.20512821	1Yr
ENSMUSG00000039720	Got1l1	0.099112376	-21.42804138	1Yr
ENSMUSG00000098785	Mir6395	0.079984003	-21.91738542	1Yr
ENSMUSG00000036120	Rfxank	0.054692884	-18.83333333	1Yr
ENSMUSG00000005413	Hmox1	0.079572824	-32.97167946	1Yr
ENSMUSG00000031709	Tbc1d9	0.007373843	-22.85922443	1Yr
ENSMUSG00000031659	Adcy7	0.026368748	24.24736149	1Yr
ENSMUSG00000031659	Adcy7	0.016295736	25.83017012	1Yr
ENSMUSG00000031661	Nkd1	1.00E-06	-25.36363636	1Yr
ENSMUSG00000031789	Cngb1	0.0028577	-32.18594811	1Yr
ENSMUSG00000031789	Cngb1	0.001255788	-30.6426833	1Yr
ENSMUSG00000031789	Cngb1	0.008158196	-37.04281523	1Yr
ENSMUSG00000031789	Cngb1	0.014091231	-33.21099497	1Yr
ENSMUSG00000110447	Gm31518	1.62E-05	40.87079587	1Yr
ENSMUSG00000089935	NA	0.02123119	-13.75	1Yr
ENSMUSG00000074061	Fbxw19	0.05462508	14.38578687	1Yr
ENSMUSG00000053820	Bcl2a1c	0.000508008	37.52050935	1Yr
ENSMUSG00000053820	Bcl2a1c	0.019529854	24.91488258	1Yr
ENSMUSG00000025787	Tgm4	0.000111393	-22.4137931	1Yr
ENSMUSG00000049307	Fut4	0.038465281	20.00330688	1Yr
ENSMUSG00000036777	Anln	0.005781074	27.52825878	1Yr
ENSMUSG00000042293	Gm5617	0.036129985	-21.44230769	1Yr
ENSMUSG00000037410	Tbc1d2b	0.026053922	31.74242424	1Yr
ENSMUSG00000037410	Tbc1d2b	0.012634079	39.84848485	1Yr
ENSMUSG00000048573	Cypt3	0.017178629	12.24650621	1Yr
ENSMUSG00000048573	Cypt3	0.007341665	17.65873016	1Yr
ENSMUSG00000035299	Mid1	0.085930427	-19.03765527	1Yr

Appendix 4

Manuscript I: All enriched gene ontologies identified

Category	GO	Description	Timepoint	LogP	#GeneInGO AndHitList	Hits
GO Biological Processes	GO:0072698	protein localization to microtubule cytoskeleton	D1	-4.5	6	Diaph1|Dvl1|Cep250|Mid1|Cep63|Fam83d
GO Biological Processes	GO:0044380	protein localization to cytoskeleton	D1	-4.2	6	Diaph1|Dvl1|Cep250|Mid1|Cep63|Fam83d
GO Biological Processes	GO:0048668	collateral sprouting	D1	-3.3	4	Cobl|Dvl1|Ulk2|Rtn4
GO Biological Processes	GO:0035372	microtubule	D1	-3	3	Diaph1|Dvl1|Mid1
GO Biological Processes	GO:0021885	forebrain cell migration	D1	-2.7	5	Cxcr4|Tyro3|Rtn4|P2ry12|Cul5
Reactome Gene Sets	R-MMU-392170	purinoceptor 12	D1	-2.7	3	Gnb1|Gnb5|P2ry12
GO Cellular Components	GO:1990234	transferase complex	D1	-2.7	19	Acvrl1|Itch|Rb1|Rpn2|Zfp64|Dcaf11|Cdc23|Tmem258|Ankib1|Riok1|Fbxl20|Brap|Prps1l1|Cul5|Cul9|Naa35|Hdac9|Dcun1d1|Brd1
GO Biological Processes	GO:0032102	negative regulation of response to external stimulus	D1	-2.6	11	Adcy7|Dvl1|Acod1|Itch|Rb1|Ryk|Tyro3|Mapkbp1|Nenf|Rtn4|Dusp3
Reactome Gene Sets	R-MMU-1236977	Endosomal/Vacuolar pathway	D1	-2.4	3	H2-K1|H2-Q4|H2-M1
GO Cellular Components	GO:0070971	site	D1	-2.4	3	H2-K1|H2-Q4|Sec23b
GO Biological Processes	GO:0002507	tolerance induction	D1	-2.4	3	Acod1|Itch|Icos
Reactome Gene Sets	R-MMU-2514856	The phototransduction cascade	D1	-2.3	3	Calm1|Gnb1|Gnb5
Reactome Gene Sets	R-MMU-418597	G alpha (z) signalling events	D1	-2.3	3	Adcy7|Gnb1|Gnb5
GO Biological Processes	GO:0051924	regulation of calcium ion transport	D1	-2.2	9	Ahr|Capn3|Cxcr4|Diaph1|Gnb5|Rgs4|Gpr35|P2ry12|Jph4
Reactome Gene Sets	R-MMU-451326	upon glutamate binding	D1	-2.2	3	Calm1|Gnb1|Gnb5
Reactome Gene Sets	R-MMU-112314	and postsynaptic signal transmission	D1	-2.2	6	Adcy7|Calm1|Gabrr1|Gnb1|Gnb5|Chrnb4

GO Biological Processes	GO:0002486	presentation of endogenous peptide antigen via MHC class	D1	-2.2	3	H2-K1|H2-Q4|H2-M1
Reactome Gene Sets	R-MMU-392518	Signal amplification	D1	-2.2	3	Gnb1|Gnb5|P2ry12
GO Biological Processes	GO:0002476	presentation of endogenous peptide antigen via MHC class	D1	-2.2	3	H2-K1|H2-Q4|H2-M1
GO Biological Processes	GO:0002484	presentation of endogenous peptide antigen via MHC class	D1	-2.2	3	H2-K1|H2-Q4|H2-M1
GO Cellular Components	GO:0000151	ubiquitin ligase complex	D1	-2.1	9	Itch|Dcaf11|Cdc23|Ankib1|Fbxl20|Brap|Cul5|Cul9|Dcun1d1
KEGG Pathway	mmu05166	HTLV-I infection	D1	-2.1	9	Adcy7|Dvl1|H2-K1|H2-Q4|Rb1|Wnt8a|Cdc23|Tnfrsf13c|H2-M1
GO Biological Processes	GO:0009611	response to wounding	D1	-2.1	13	Macf1|Acta2|Acvrl1|Adam17|Capn3|Cxcr4|Clec10a|Tyro3|Rtn4|P2ry12|Treml1|3300005D01Rik|Enpp4
GO Biological Processes	GO:0006487	protein N-linked glycosylation	D1	-2.1	4	Rpn2|Alg2|Tmem258|Mgat4b
GO Biological Processes	GO:0002428	presentation of peptide	D1	-2.1	3	H2-K1|H2-Q4|H2-M1
GO Biological Processes	GO:0002224	toll-like receptor signaling pathway	D1	-2.1	5	Cd14|Acod1|Tyro3|Rtn4|Mapkapk3
Reactome Gene Sets	R-MMU-1236974	ER-Phagosome pathway	D1	-2.1	3	H2-K1|H2-Q4|H2-M1
GO Molecular Functions	GO:0060589	nucleoside-triphosphatase regulator activity	D1	-2	9	Gnb5|Rangap1|Rgs4|Sec23b|Tbc1d2b|Smap2|Tor1aip1|Tor1aip2|Sipa1l2
Reactome Gene Sets	R-MMU-111885	Opioid Signalling	D1	-2	4	Adcy7|Calm1|Gnb1|Gnb5
GO Biological Processes	GO:0045446	endothelial cell differentiation	D1	-2	5	Acvrl1|Cxcr4|Ren1|Xdh|Rtn4
GO Biological Processes	GO:0021799	oriented cell migration	D1	-2	3	Rtn4|P2ry12|Cul5
GO Biological Processes	GO:0060071	cell polarity pathway	D1	-2	3	Dvl1|Ryk|Nkd1

GO Biological Processes	GO:0001782	B cell homeostasis	D1	-2	3	Ahr|Tnfrsf13c|Dock10
GO Biological Processes	GO:0022029	telencephalon cell migration	D1	-2	4	Cxcr4|Rtn4|P2ry12|Cul5
GO Molecular Functions	GO:0005198	structural molecule activity	D1	-2	15	Macf1|Bglap3|Capn3|Col7a1|Krt31|Lamc2|Rpl22|Rps7|Sprr2b|Sprr2d|Igfbp7|Cldn15|Mrps14|Prelp|Krt26
Reactome Gene Sets	R-MMU-112315	Transmission across Chemical Synapses	D1	-2	7	Adcy7|Calm1|Gabrr1|Gnb1|Gnb5|Naaa|Chrnb4
GO Biological Processes	GO:0002475	presentation via MHC class Ib	D1	-2	3	H2-K1|H2-Q4|H2-M1
GO Biological Processes	GO:0002483	presentation of endogenous	D1	-1.9	3	H2-K1|H2-Q4|H2-M1
GO Biological Processes	GO:0019885	presentation of endogenous peptide antigen via MHC class	D1	-1.9	3	H2-K1|H2-Q4|H2-M1
GO Biological Processes	GO:0090175	planar polarity	D1	-1.9	3	Dvl1|Ryk|Nkd1
GO Biological Processes	GO:1990845	adaptive thermogenesis	D1	-1.9	6	Adam17|Aldh1a1|Cxcr4|Rb1|Ucp3|Ybx2
GO Biological Processes	GO:1903036	to wounding	D1	-1.9	4	Capn3|Cxcr4|Rtn4|Enpp4
KEGG Pathway	mmu04725	Cholinergic synapse	D1	-1.9	5	Adcy7|Gnb1|Gnb5|Chrnb4|Kcnj14
GO Biological Processes	GO:0032101	regulation of response to external stimulus	D1	-1.9	17	Adam17|Adcy7|Cd5l|Capn3|Cxcr4|Dvl1|Acod1|Itch|Rb1|Ryk|Tyro3|Mapkbp1|Nenf|Rtn4|P2ry12|Dusp3|Enpp4
GO Biological Processes	GO:0000266	mitochondrial fission	D1	-1.9	3	Ggnbp1|Opa1|Ddhd1
GO Biological Processes	GO:0042060	wound healing	D1	-1.9	10	Macf1|Acta2|Acvrl1|Capn3|Cxcr4|Clec10a|Tyro3|P2ry12|Treml1|Enpp4
GO Biological Processes	GO:0051303	establishment of chromosome localization	D1	-1.9	4	Cep63|Cdc23|Fam83d|Trappc12
GO Biological Processes	GO:0002832	response to biotic stimulus	D1	-1.9	3	Acod1|Itch|Mapkbp1

GO Biological Processes	GO:1903170	ion transmembrane transport	D1	-1.9	3	Ahr|Gnb5|Gpr35
GO Biological Processes	GO:0050000	chromosome localization	D1	-1.9	4	Cep63|Cdc23|Fam83d|Trappc12
GO Biological Processes	GO:0048041	focal adhesion assembly	D1	-1.9	4	Macf1|Acvrl1|Dusp3|Tesk2
GO Biological Processes	GO:0007045	cell-substrate adherens junction assembly	D1	-1.9	4	Macf1|Acvrl1|Dusp3|Tesk2
Reactome Gene Sets	R-MMU-3858494	WNT signaling	D1	-1.9	4	Calm1|Dvl1|Gnb1|Gnb5
Reactome Gene Sets	R-MMU-983170	assembly and peptide loading of class I MHC	D1	-1.9	3	H2-K1|H2-Q4|H2-M1
GO Molecular Functions	GO:0005109	frizzled binding	D1	-1.9	3	Dvl1|Ryk|Wnt8a
GO Biological Processes	GO:0019883	presentation of endogenous	D1	-1.9	3	H2-K1|H2-Q4|H2-M1
Reactome Gene Sets	R-MMU-4086398	Ca2+ pathway	D1	-1.8	3	Calm1|Gnb1|Gnb5
GO Cellular Components	GO:0009925	basal plasma membrane	D1	-1.8	3	Myo1c|P2ry12|Slco2b1
KEGG Pathway	mmu04672	IgA production	D1	-1.8	3	Cxcr4|Icos|Tnfrsf13c
GO Molecular Functions	GO:1901618	transmembrane transporter	D1	-1.8	3	Stra6|Slc16a3|Slco2b1
GO Molecular Functions	GO:0019199	protein kinase activity	D1	-1.8	4	Acvrl1|Ryk|Tyro3|Epha10
GO Biological Processes	GO:0003158	endothelium development	D1	-1.8	5	Acvrl1|Cxcr4|Ren1|Xdh|Rtn4
Reactome Gene Sets	R-MMU-1227986	Signaling by ERBB2	D1	-1.8	3	Diaph1|Grb7|Cul5
Reactome Gene Sets	R-MMU-112316	Neuronal System	D1	-1.8	9	Adcy7|Calm1|Gabrr1|Gnb1|Gnb5|Naaa|Chrnb4|Kcnj14|Kcnk18
GO Cellular Components	GO:0001750	photoreceptor outer segment	D1	-1.8	4	Gnb1|Gnb5|Cep250|Prom1
KEGG Pathway	mmu04514	Cell adhesion molecules (CAMs)	D1	-1.8	6	Cntn1|H2-K1|H2-Q4|Icos|Cldn15|H2-M1
GO Biological Processes	GO:0060560	developmental growth involved in morphogenesis	D1	-1.8	8	Ahr|Cxcr4|Cobl|Dvl1|Ryk|Ulk2|Rtn4|Nkd1
GO Biological Processes	GO:0001961	mediated signaling pathway	D1	-1.8	3	Adam17|Cxcr4|Txk
GO Molecular Functions	GO:0005044	scavenger receptor activity	D1	-1.8	3	Cd5l|Lgals3bp|Tmprss13

GO Molecular Functions	GO:0044389	ubiquitin-like protein ligase binding	D1	-1.8	9	Cxcr4|Itch|Mid1|Rangap1|Rb1|Traf5|Rtn4|Cul5|Cul9
GO Biological Processes	GO:1901888	regulation of cell junction assembly	D1	-1.8	4	Macf1|Acvrl1|Myo1c|Dusp3
GO Biological Processes	GO:0048536	spleen development	D1	-1.8	3	Adam17|Ahr|Flvcr1
GO Biological Processes	GO:0007212	pathway	D1	-1.8	3	Gnb5|Nsg2|Rgs4
GO Molecular Functions	GO:0042605	peptide antigen binding	D1	-1.8	3	H2-K1|H2-Q4|H2-M1
GO Biological Processes	GO:0048640	developmental growth	D1	-1.7	5	Rgs4|Ryk|Ulk2|Rtn4|Nkd1
GO Biological Processes	GO:0031644	regulation of neurological system process	D1	-1.7	6	Dvl1|Rgs4|Gpr35|Rtn4|Chrnb4|Zfhx2
GO Biological Processes	GO:0120163	induced thermogenesis	D1	-1.7	3	Adam17|Aldh1a1|Rb1
GO Biological Processes	GO:0034333	adherens junction assembly	D1	-1.7	4	Macf1|Acvrl1|Dusp3|Tesk2
Reactome Gene Sets	R-MMU-1236975	presentation	D1	-1.7	3	H2-K1|H2-Q4|H2-M1
GO Biological Processes	GO:0007131	recombination	D1	-1.7	3	Cep63|Tex11|Fancm
GO Cellular Components	GO:0005795	Golgi stack	D1	-1.7	4	H2-K1|H2-Q4|Nsg2|Mgat4b
GO Biological Processes	GO:0032606	type I interferon production	D1	-1.7	4	Cd14|Acod1|Irf9|Zfp64
GO Biological Processes	GO:0007044	cell-substrate junction assembly	D1	-1.7	4	Macf1|Acvrl1|Dusp3|Tesk2
GO Biological Processes	GO:0035825	homologous recombination	D1	-1.7	3	Cep63|Tex11|Fancm
KEGG Pathway	mmu00510	N-Glycan biosynthesis	D1	-1.7	3	Rpn2|Alg2|Mgat4b
GO Biological Processes	GO:0001916	mediated cytotoxicity	D1	-1.7	3	H2-K1|H2-Q4|H2-M1
GO Biological Processes	GO:0002474	presentation of peptide	D1	-1.7	3	H2-K1|H2-Q4|H2-M1
GO Biological Processes	GO:1903034	regulation of response to wounding	D1	-1.7	6	Acta2|Adam17|Capn3|Cxcr4|Rtn4|Enpp4
KEGG Pathway	mmu04727	GABAergic synapse	D1	-1.7	4	Adcy7|Gabrr1|Gnb1|Gnb5
KEGG Pathway	mmu05203	Viral carcinogenesis	D1	-1.7	7	H2-K1|H2-Q4|Irf9|Rb1|Traf5|Hdac9|H2-M1

GO Molecular Functions	GO:0004713	protein tyrosine kinase activity	D1	-1.7	5	Ryk|Txk|Tyro3|Tesk2|Epha10
GO Biological Processes	GO:0030098	lymphocyte differentiation	D1	-1.7	10	Adam17|Ahr|Rpl22|Txk|Tyro3|Nfam1|Rhoh|Hdac9|Dock10|Btnl6
GO Biological Processes	GO:1904063	transmembrane transport	D1	-1.7	4	Ahr|Gnb5|Rgs4|Gpr35
KEGG Pathway	mmu04144	Endocytosis	D1	-1.7	8	Cxcr4|H2-K1|H2-Q4|Itch|Wipf2|Smap2|Dnajc6|H2-M1
GO Biological Processes	GO:1900076	to insulin stimulus	D1	-1.6	4	Bglap3|Grb7|Myo1c|Opa1
GO Cellular Components	GO:0060170	ciliary membrane	D1	-1.6	3	Gnb1|Prom1|Ift46
GO Biological Processes	GO:0060760	to cytokine stimulus	D1	-1.6	3	Adam17|Cxcr4|Txk
GO Biological Processes	GO:0007032	endosome organization	D1	-1.6	3	Stx6|Ggnbp1|Pheta2
Reactome Gene Sets	R-MMU-2424491	DAP12 signaling	D1	-1.6	3	H2-K1|H2-Q4|H2-M1
GO Biological Processes	GO:0046683	response to organophosphorus	D1	-1.6	4	Ahr|Ren1|Dntt|P2ry12
GO Biological Processes	GO:0002221	pattern recognition receptor signaling pathway	D1	-1.6	5	Cd14|Acod1|Tyro3|Rtn4|Mapkapk3
KEGG Pathway	mmu05032	Morphine addiction	D1	-1.6	4	Adcy7|Gabrr1|Gnb1|Gnb5
Reactome Gene Sets	R-MMU-2187338	Visual phototransduction	D1	-1.6	4	Calm1|Gnb1|Gnb5|Stra6
GO Molecular Functions	GO:0005096	GTPase activator activity	D1	-1.6	7	Gnb5|Rangap1|Rgs4|Sec23b|Tbc1d2b|Smap2|Sipa1l2
Reactome Gene Sets	R-MMU-977443	GABA receptor activation	D1	-1.6	3	Adcy7|Gabrr1|Gnb1
GO Biological Processes	GO:0002758	innate immune response-activating signal transduction	D1	-1.6	5	Cd14|Acod1|Tyro3|Rtn4|Mapkapk3
GO Cellular Components	GO:0030425	dendrite	D1	-1.6	15	Acvrl1|Bglap3|Cobl|Dvl1|Gnb1|Nsg2|Rangap1|Rtn4|Ggnbp1|Opa1|Dock10|Kcnj14|Farp1|Brd1|Jph4
KEGG Pathway	mmu04120	Ubiquitin mediated proteolysis	D1	-1.6	5	Itch|Mid1|Cdc23|Cul5|Nhlrc1

KEGG Pathway	mmu04371	Apelin signaling pathway	D1	-1.6	5	Acta2|Adcy7|Calm1|Gnb1|Gnb5
GO Biological Processes	GO:0001914	cytotoxicity	D1	-1.6	3	H2-K1|H2-Q4|H2-M1
Reactome Gene Sets	R-MMU-72187	mRNA 3'-end processing	D1	-1.6	3	Cpsf3|Ddx39|Cstf2t
GO Biological Processes	GO:0070838	divalent metal ion transport	D1	-1.6	11	Ahr|Capn3|Cxcr4|Diaph1|Gnb5|Rgs4|Gpr35|P2ry12|Slc39a4|Opa1|Jph4
GO Biological Processes	GO:0051304	chromosome separation	D1	-1.6	4	Rb1|Cdc23|Tex11|Fancm
GO Cellular Components	GO:0097447	dendritic tree	D1	-1.6	15	Acvrl1|Bglap3|Cobl|Dvl1|Gnb1|Nsg2|Rangap1|Rtn4|Ggnbp1|Opa1|Dock10|Kcnj14|Farp1|Brd1|Jph4
GO Biological Processes	GO:0021795	cerebral cortex cell migration	D1	-1.6	3	Rtn4|P2ry12|Cul5
GO Biological Processes	GO:0106106	cold-induced thermogenesis	D1	-1.6	5	Adam17|Aldh1a1|Cxcr4|Rb1|Ybx2
GO Biological Processes	GO:0120161	regulation of cold-induced thermogenesis	D1	-1.6	5	Adam17|Aldh1a1|Cxcr4|Rb1|Ybx2
GO Biological Processes	GO:0072511	divalent inorganic cation transport	D1	-1.5	11	Ahr|Capn3|Cxcr4|Diaph1|Gnb5|Rgs4|Gpr35|P2ry12|Slc39a4|Opa1|Jph4
GO Biological Processes	GO:0090303	healing	D1	-1.5	3	Capn3|Cxcr4|Enpp4
GO Biological Processes	GO:1905517	macrophage migration	D1	-1.5	3	Gpr35|Rtn4|P2ry12
GO Biological Processes	GO:0035567	pathway	D1	-1.5	3	Dvl1|Ryk|Nkd1
KEGG Pathway	mmu04713	Circadian entrainment	D1	-1.5	4	Adcy7|Calm1|Gnb1|Gnb5
Reactome Gene Sets	R-MMU-6805567	Keratinization	D1	-1.5	6	Krt31|Krtap9-1|Sprr2d|Krt26|Gm11568|Gm11563
Reactome Gene Sets	R-MMU-418594	G alpha (i) signalling events	D1	-1.5	9	Adcy7|Calm1|Cxcr4|Gnb1|Gnb5|Rgs4|Stra6|P2ry12|Npb
GO Biological Processes	GO:0051310	metaphase plate congression	D1	-1.5	3	Cdc23|Fam83d|Trappc12

GO Biological Processes	GO:0001736	polarity	D1	-1.5	3	Dvl1|Ryk|Nkd1
GO Biological Processes	GO:0051893	assembly	D1	-1.5	3	Macf1|Acvrl1|Dusp3
GO Biological Processes	GO:0090109	junction assembly	D1	-1.5	3	Macf1|Acvrl1|Dusp3
GO Cellular Components	GO:0001917	photoreceptor inner segment	D1	-1.5	3	Gnb1|Gnb5|Cep250
GO Biological Processes	GO:0010959	regulation of metal ion transport	D1	-1.5	10	Ahr|Capn3|Cxcr4|Cntn1|Diaph1|Gnb5|Rgs4|Gpr35|P2ry12|Jph4
GO Molecular Functions	GO:0031625	ubiquitin protein ligase binding	D1	-1.5	8	Cxcr4|Mid1|Rangap1|Rb1|Traf5|Rtn4|Cul5|Cul9
GO Biological Processes	GO:0006816	calcium ion transport	D1	-1.5	10	Ahr|Capn3|Cxcr4|Diaph1|Gnb5|Rgs4|Gpr35|P2ry12|Opa1|Jph4
GO Biological Processes	GO:0031343	killing	D1	-1.5	4	Cd5l|H2-K1|H2-Q4|H2-M1
KEGG Pathway	mmu04916	Melanogenesis	D1	-1.5	4	Adcy7|Calm1|Dvl1|Wnt8a
GO Cellular Components	GO:0016328	lateral plasma membrane	D1	-1.5	3	Dvl1|Myo1c|Cldn15
GO Biological Processes	GO:0007164	polarity	D1	-1.5	3	Dvl1|Ryk|Nkd1
GO Biological Processes	GO:0007264	small GTPase mediated signal transduction	D1	-1.5	11	Mapkapk5|Arpp19|Gpr35|Ift22|Rtn4|Ggnbp1|Brap|Rhoh|Dock10|Farp1|Sipa1l2
GO Biological Processes	GO:0048469	cell maturation	D1	-1.5	6	Rb1|Ren1|Opa1|Flvcr1|Svs3b|Angptl8
Reactome Gene Sets	R-MMU-2172127	DAP12 interactions	D1	-1.5	3	H2-K1|H2-Q4|H2-M1
KEGG Pathway	mmu04723	signaling	D1	-1.5	4	Adcy7|Gabrr1|Gnb1|Gnb5
GO Biological Processes	GO:0048729	tissue morphogenesis	D1	-1.5	14	Macf1|Acvrl1|Ahr|Aldh1a1|Cxcr4|Cobl|Col7a1|Dvl1|Rps7|Ryk|Txnrd1|Ccdc103|Opa1|Nkd1
GO Biological Processes	GO:0030183	B cell differentiation	D1	-1.5	5	Adam17|Ahr|Nfam1|Hdac9|Dock10

GO Molecular Functions	GO:0030695	GTPase regulator activity	D1	-1.5	7	Gnb5|Rangap1|Rgs4|Sec23b|Tbc1d2b|Smap2|Sipa1l2
GO Biological Processes	GO:0098813	nuclear chromosome segregation	D1	-1.4	7	Rb1|Cep63|Cdc23|Fam83d|Tex11|Fancm|Trappc12
GO Biological Processes	GO:0048588	developmental cell growth	D1	-1.4	7	Cxcr4|Cobl|Dvl1|Rgs4|Ryk|Ulk2|Rtn4
GO Biological Processes	GO:0034766	transmembrane transport	D1	-1.4	4	Ahr|Gnb5|Rgs4|Gpr35
GO Biological Processes	GO:0007059	chromosome segregation	D1	-1.4	8	Rb1|Cep63|Cdc23|Fam83d|Tex11|Fancm|Trappc12|Banf2
GO Cellular Components	GO:0031985	Golgi cisterna	D1	-1.4	3	H2-K1|H2-Q4|Nsg2
GO Molecular Functions	GO:0004714	protein tyrosine kinase activity	D1	-1.4	3	Ryk|Tyro3|Epha10
Reactome Gene Sets	R-MMU-198933	between a Lymphoid and a non-Lymphoid cell	D1	-1.4	4	H2-K1|H2-Q4|Treml1|H2-M1
GO Biological Processes	GO:0060840	artery development	D1	-1.4	4	Acvrl1|Cxcr4|Stra6|Rtn4
GO Cellular Components	GO:0072686	mitotic spindle	D1	-1.4	4	Diaph1|Rangap1|Mapkbp1|Fam83d
GO Biological Processes	GO:0014074	compound	D1	-1.4	4	Ahr|Ren1|Dntt|P2ry12
GO Biological Processes	GO:0046579	protein signal transduction	D1	-1.4	3	Arpp19|Gpr35|Rtn4
GO Biological Processes	GO:0034121	signaling pathway	D1	-1.4	3	Acod1|Tyro3|Rtn4
Reactome Gene Sets	R-MMU-73856	Transcription Termination	D1	-1.4	3	Cpsf3|Ddx39|Cstf2t
KEGG Pathway	mmu05330	Allograft rejection	D1	-1.4	3	H2-K1|H2-Q4|H2-M1
GO Biological Processes	GO:0051926	ion transport	D1	-1.4	3	Ahr|Gnb5|Gpr35
GO Biological Processes	GO:1903391	junction organization	D1	-1.4	3	Macf1|Acvrl1|Dusp3
GO Cellular Components	GO:0031461	cullin-RING ubiquitin ligase complex	D1	-1.4	5	Dcaf11|Cdc23|Fbxl20|Cul5|Cul9
KEGG Pathway	mmu05332	Graft-versus-host disease	D1	-1.4	3	H2-K1|H2-Q4|H2-M1
GO Biological Processes	GO:0001843	neural tube closure	D1	-1.4	4	Cobl|Dvl1|Rps7|Opa1
GO Biological Processes	GO:0001776	leukocyte homeostasis	D1	-1.4	4	Adam17|Ahr|Tnfrsf13c|Dock10

GO Biological Processes	GO:1903169	regulation of calcium ion transmembrane transport	D1	-1.4	5	Ahr|Capn3|Diaph1|Gnb5|Gpr35
GO Biological Processes	GO:0060606	tube closure	D1	-1.4	4	Cobl|Dvl1|Rps7|Opa1
GO Cellular Components	GO:0045178	basal part of cell	D1	-1.4	3	Myo1c|P2ry12|Slco2b1
GO Biological Processes	GO:1901184	pathway	D1	-1.4	3	Adam17|Rtn4|Dusp3
GO Biological Processes	GO:0016049	cell growth	D1	-1.3	11	Acvrl1|Adam17|Cxcr4|Cobl|Dvl1|Rb1|Rgs4|Ryk|Igfbp7|Ulk2|Rtn4
Reactome Gene Sets	R-MMU-9006934	Signaling by Receptor Tyrosine Kinases	D1	-1.3	9	Calm1|Diaph1|Grb7|Itch|Dusp3|Cul5|Rbfox2|Mapkapk3|Atp6v0b
GO Biological Processes	GO:0033365	protein localization to organelle	D1	-1.3	15	Macf1|Diaph1|Dvl1|Cep250|Mid1|Rangap1|Rb1|Cep63|Rtn4|Fam83d|Tor1aip1|Trappc12|Tor1aip2|1700015F17Rik|Mir208b
GO Biological Processes	GO:0050771	axonogenesis	D1	-1.3	3	Ryk|Ulk2|Rtn4
GO Cellular Components	GO:0005819	spindle	D1	-1.3	7	Diaph1|Cep250|Rangap1|Rb1|Mapkbp1|Fam83d|Bora
GO Cellular Components	GO:0097733	photoreceptor cell cilium	D1	-1.3	4	Gnb1|Gnb5|Cep250|Prom1
GO Biological Processes	GO:0002218	activation of innate immune response	D1	-1.3	5	Cd14|Acod1|Tyro3|Rtn4|Mapkapk3
KEGG Pathway	mmu05200	Pathways in cancer	D1	-1.3	9	Adcy7|Cxcr4|Dvl1|Gnb1|Gnb5|Lamc2|Rb1|Wnt8a|Traf5
GO Biological Processes	GO:0048002	presentation of peptide	D1	-1.3	3	H2-K1|H2-Q4|H2-M1
GO Cellular Components	GO:0043235	receptor complex	D1	-1.3	9	Acvrl1|Ahr|Cd14|Gabrr1|Ryk|Traf5|Tyro3|Chrnb4|Epha10

GO Biological Processes	GO:0048285	organelle fission	D1	-1.3	10	Rb1|Cep63|Cdc23|Ggnbp1|Opa1|Bora|Cul9|Tex11|Fancm|Ddhd1
GO Biological Processes	GO:0031348	negative regulation of defense response	D1	-1.3	6	Adcy7|Acod1|Itch|Rb1|Tyro3|Mapkbp1
GO Cellular Components	GO:0097731	9+0 non-motile cilium	D1	-1.3	4	Gnb1|Gnb5|Cep250|Prom1
GO Biological Processes	GO:0043122	regulation of I-kappaB kinase/NF-kappaB signaling	D1	-1.3	5	Capn3|Traf5|Mapkbp1|Rhoh|Unc5cl
GO Cellular Components	GO:0032587	ruffle membrane	D1	-1.3	3	Adam17|Diaph1|Myo1c
GO Biological Processes	GO:0048678	response to axon injury	D1	-1.3	3	Adam17|Rtn4|P2ry12
GO Cellular Components	GO:0005793	intermediate compartment	D1	-1.3	3	Prom1|Mgat4b|Trappc12
GO Biological Processes	GO:0060997	dendritic spine morphogenesis	D1	-1.3	3	Dvl1|Opa1|Dock10
GO Molecular Functions	GO:0043236	laminin binding	W2	-4.8	5	Itga2|Rpsa|2300002M23Rik|Tinagl1|Itga9
GO Biological Processes	GO:0018149	peptide cross-linking	W2	-4.3	6	Sprr2d|Sprr2e|Sprr3|Tgm2|Lelp1|Lce3e
GO Molecular Functions	GO:0005184	neuropeptide hormone activity	W2	-3.9	4	Gal|Ppy|Qrfp|Nppa
GO Biological Processes	GO:0086016	AV node cell action potential	W2	-3.7	3	Cacna1g|Ryr2|Scn10a
GO Biological Processes	GO:0086027	cell signaling	W2	-3.7	3	Cacna1g|Ryr2|Scn10a
Reactome Gene Sets	R-MMU-6809371	Formation of the cornified envelope	W2	-3.6	7	Krt31|Krt6a|Sprr2d|Sprr2e|Sprr3|Lelp1|Lipk
GO Cellular Components	GO:0001533	cornified envelope	W2	-3.5	5	Sprr2d|Sprr2e|Sprr3|Lelp1|Lce3e
GO Biological Processes	GO:0086067	cell communication	W2	-3.5	3	Cacna1g|Ryr2|Scn10a
GO Biological Processes	GO:0030029	actin filament-based process	W2	-3.4	19	Bst1|Cacna1g|Capn3|Capza3|Epb41l1|Myh2|Ran|Ryr2|Tesk1|Shroom3|Wipf2|Rhoh|Elmo1|Mical3|Pdlim2|Rasa1|Fhdc1|Gba2|Ablim3

GO Molecular Functions	GO:0050840	extracellular matrix binding	W2	-3.4	5	Itga2|Rpsa|2300002M23Rik|Tinagl1|Itga9
GO Molecular Functions	GO:0005198	structural molecule activity	W2	-3.3	17	Capn3|Col4a1|Epb41l1|Krt31|Rpsa|Sprr2d|Sprr2e|Sprr3|Igfbp7|Col6a4|Lelp1|Lce3e|Tinagl1|Mrps2|Nup214|Otol1|Sntg2
GO Biological Processes	GO:0031424	keratinization	W2	-3.3	4	Krt6a|Sprr2d|Sprr2e|Sprr3
GO Molecular Functions	GO:0003779	actin binding	W2	-3.2	13	Capza3|Cxcr4|Epb41l1|Tns1|Mprip|Shroom3|Wipf2|Mical3|Pdlim2|Tns4|Fhdc1|Sntg2|Ablim3
GO Biological Processes	GO:0030216	keratinocyte differentiation	W2	-3.2	7	Krt6a|Foxc1|Sprr2d|Sprr2e|Sprr3|Lelp1|Lce3e
GO Molecular Functions	GO:0140097	catalytic activity, acting on DNA	W2	-3	8	Dnmt1|Ercc1|Rad54l|Tert|Top2a|Ercc5|Mutyh|Eri2
GO Biological Processes	GO:0043588	skin development	W2	-2.9	10	Gal|Itga2|Krt6a|Foxc1|Spr2d|Sprr2e|Sprr3|Elovl1|Lelp1|Lce3e
GO Molecular Functions	GO:0008327	methyl-CpG binding	W2	-2.9	3	Dnmt1|Mbd3l2|Zbtb38
GO Biological Processes	GO:0006941	striated muscle contraction	W2	-2.8	7	Chrng|Cacna1g|Cxcr4|Gaa|Ryr2|Scn10a|Nppa
GO Biological Processes	GO:0030036	actin cytoskeleton organization	W2	-2.7	16	Bst1|Capn3|Capza3|Epb41l1|Ran|Tesk1|Shroom3|Wipf2|Rhoh|Elmo1|Mical3|Pdlim2|Rasa1|Fhdc1|Gba2|Ablim3
GO Biological Processes	GO:0060048	cardiac muscle contraction	W2	-2.7	6	Cacna1g|Cxcr4|Gaa|Ryr2|Scn10a|Nppa
GO Biological Processes	GO:0086019	cardiac conduction	W2	-2.6	3	Cacna1g|Ryr2|Scn10a

GO Biological Processes	GO:0090316	positive regulation of intracellular protein transport	W2	-2.6	6	Ran|Ccl2|Sorl1|Pdzk1|Fis1|Edem2
GO Biological Processes	GO:0090303	healing	W2	-2.5	4	Capn3|Cxcr4|Ccl2|Enpp4
GO Biological Processes	GO:0090314	targeting to membrane	W2	-2.5	3	Ccl2|Pdzk1|Fis1
GO Biological Processes	GO:0034764	positive regulation of transmembrane transport	W2	-2.5	8	Capn3|Gal|Ryr2|Ccl2|Tert|Pdzk1|Rasa1|Nppa
GO Biological Processes	GO:0070098	pathway	W2	-2.4	4	Cxcr4|Foxc1|Ccl2|Ccl7
GO Biological Processes	GO:0006936	muscle contraction	W2	-2.4	9	Chrng|Cacna1g|Cxcr4|Gaa|Itga2|Myh2|Ryr2|Scn10a|Nppa
GO Cellular Components	GO:0044215	other organism	W2	-2.4	3	C4b|Top2a|Iigp1
GO Molecular Functions	GO:0071855	neuropeptide receptor binding	W2	-2.4	3	Gal|Qrfp|Nppa
GO Cellular Components	GO:0044217	other organism part	W2	-2.4	3	C4b|Top2a|Iigp1
GO Cellular Components	GO:0044216	other organism cell	W2	-2.4	3	C4b|Top2a|Iigp1
GO Cellular Components	GO:0030864	cortical actin cytoskeleton	W2	-2.4	5	Capza3|Myh2|Shroom3|Wipf2|Pdlim2
Reactome Gene Sets	R-MMU-6805567	Keratinization	W2	-2.3	7	Krt31|Krt6a|Sprr2d|Sprr2e|Sprr3|Lelp1|Lipk
GO Cellular Components	GO:0031012	extracellular matrix	W2	-2.3	12	Col4a1|Rpsa|Lgals4|Tgm2|Gpc6|Igfbp7|Hapln3|Col6a4|2300002M23Rik|Rarres2|Tinagl1|Otol1
GO Cellular Components	GO:0062023	collagen-containing extracellular matrix	W2	-2.3	10	Col4a1|Rpsa|Lgals4|Tgm2|Gpc6|Igfbp7|Col6a4|2300002M23Rik|Rarres2|Tinagl1
GO Cellular Components	GO:0045178	basal part of cell	W2	-2.3	4	Itga2|Slco2b1|Itga9|Oscp1
GO Biological Processes	GO:0090313	to membrane	W2	-2.3	3	Ccl2|Pdzk1|Fis1
GO Biological Processes	GO:0032388	positive regulation of intracellular transport	W2	-2.3	7	Ran|Ccl2|Sorl1|Pdzk1|Fis1|Edem2|Nppa

GO Biological Processes	GO:0014823	response to activity	W2	-2.2	3	Capn3|Myh2|Ryr2
GO Biological Processes	GO:1990868	response to chemokine	W2	-2.2	4	Cxcr4|Foxc1|Ccl2|Ccl7
GO Biological Processes	GO:1990869	cellular response to chemokine	W2	-2.2	4	Cxcr4|Foxc1|Ccl2|Ccl7
GO Cellular Components	GO:0044448	cell cortex part	W2	-2.2	7	Capza3|Fabp1|Myh2|Shroom3|Exoc7|Wipf2|Pdlim2
GO Biological Processes	GO:0086065	cardiac conduction	W2	-2.2	3	Cacna1g|Ryr2|Scn10a
GO Biological Processes	GO:0033157	regulation of intracellular protein transport	W2	-2.1	7	Bard1|Ran|Ccl2|Sorl1|Pdzk1|Fis1|Edem2
GO Biological Processes	GO:0032414	transmembrane transporter activity	W2	-2.1	5	Gal|Ryr2|Ccl2|Pdzk1|Nppa
GO Biological Processes	GO:1903036	to wounding	W2	-2.1	4	Capn3|Cxcr4|Ccl2|Enpp4
GO Biological Processes	GO:0009913	epidermal cell differentiation	W2	-2.1	7	Krt6a|Foxc1|Sprr2d|Sprr2e|Sprr3|Lelp1|Lce3e
GO Biological Processes	GO:1904064	positive regulation of cation transmembrane transport	W2	-2.1	6	Capn3|Gal|Ryr2|Ccl2|Pdzk1|Nppa
GO Biological Processes	GO:0003012	muscle system process	W2	-2	10	Chrng|Cacna1g|Cxcr4|Gaa|Itga2|Myh2|Ryr2|Scn10a|Lmcd1|Nppa
GO Biological Processes	GO:0032411	positive regulation of transporter activity	W2	-2	5	Gal|Ryr2|Ccl2|Pdzk1|Nppa
GO Biological Processes	GO:0071621	granulocyte chemotaxis	W2	-2	5	Bst1|Ccl2|Ccl7|Rarres2|Itga9
GO Cellular Components	GO:0009925	basal plasma membrane	W2	-2	3	Slco2b1|Itga9|Oscp1
GO Molecular Functions	GO:0016798	hydrolase activity, acting on glycosyl bonds	W2	-2	5	Bst1|Gaa|Mutyh|Edem2|Gba2
GO Biological Processes	GO:0007218	pathway	W2	-2	4	Gal|Ppy|Qrfp|Nppa
GO Cellular Components	GO:0001750	photoreceptor outer segment	W2	-2	4	Cep250|Prom1|Ahi1|Shoc2
GO Biological Processes	GO:0001569	vessel morphogenesis	W2	-1.9	3	Cxcr4|Col4a1|Notch4
KEGG Pathway	mmu04512	ECM-receptor interaction	W2	-1.9	4	Col4a1|Itga2|Col6a4|Itga9

GO Molecular Functions	GO:0005179	hormone activity	W2	-1.9	5	Gal|Ppy|Qrfp|Nppa|Angptl8
GO Biological Processes	GO:0010951	negative regulation of endopeptidase activity	W2	-1.9	6	Serpina6|Cdkn2d|Fabp1|Sorl1|Serpina1f|Nle1
GO Biological Processes	GO:0034767	positive regulation of ion transmembrane transport	W2	-1.9	6	Capn3|Gal|Ryr2|Ccl2|Pdzk1|Nppa
GO Biological Processes	GO:0010259	multicellular organism aging	W2	-1.9	3	Ercc1|Rad54l|Ercc5
GO Cellular Components	GO:0030863	cortical cytoskeleton	W2	-1.9	5	Capza3|Myh2|Shroom3|Wipf2|Pdlim2
GO Cellular Components	GO:0005912	adherens junction	W2	-1.8	8	Itga2|Nectin2|Tns1|Shroom3|Ahi1|Pdlim2|Tns4|Nup214
GO Biological Processes	GO:1903829	positive regulation of cellular protein localization	W2	-1.8	8	Cep250|Ran|Ccl2|Sorl1|Tert|Pdzk1|Fis1|Edem2
GO Molecular Functions	GO:0016829	lyase activity	W2	-1.8	6	Bst1|Car8|Me1|Rnase2b|Gadl1|Gldc
KEGG Pathway	mmu05414	Dilated cardiomyopathy	W2	-1.8	4	Itga2|Prkacb|Ryr2|Itga9
GO Biological Processes	GO:0071622	chemotaxis	W2	-1.8	3	Bst1|Ccl2|Rarres2
Reactome Gene Sets	R-MMU-1266738	Developmental Biology	W2	-1.8	11	Cxcr4|Col4a1|Krt31|Krt6a|Sprr2d|Sprr2e|Sprr3|Lelp1|Itga9|Rasa1|Lipk
GO Molecular Functions	GO:0005201	extracellular matrix structural constituent	W2	-1.8	5	Col4a1|Igfbp7|Col6a4|Tinagl1|Otol1
GO Biological Processes	GO:0002027	regulation of heart rate	W2	-1.8	4	Cacna1g|Ryr2|Scn10a|Nppa
GO Biological Processes	GO:0097035	distribution	W2	-1.8	3	Gba2|Plscr4|Plscr5
GO Cellular Components	GO:0005938	cell cortex	W2	-1.7	8	Capza3|Fabp1|Myh2|Shroom3|Exoc7|Wipf2|Rhoh|Pdlim2

GO Cellular Components	GO:0070161	anchoring junction	W2	-1.7	8	Itga2|Nectin2|Tns1|Shroom3|Ahi1|Pdlim2|Tns4|Nup214
GO Biological Processes	GO:1904705	muscle cell proliferation	W2	-1.7	3	Dnmt1|Pdcd4|Tert
GO Biological Processes	GO:1990874	proliferation	W2	-1.7	3	Dnmt1|Pdcd4|Tert
GO Biological Processes	GO:1903533	regulation of protein targeting	W2	-1.7	3	Ccl2|Pdzk1|Fis1
GO Biological Processes	GO:0086001	potential	W2	-1.7	3	Cacna1g|Ryr2|Scn10a
GO Biological Processes	GO:2001251	negative regulation of chromosome organization	W2	-1.7	5	Dnmt1|Ercc1|Rad21|Top2a|Stn1
GO Biological Processes	GO:0097530	granulocyte migration	W2	-1.7	5	Bst1|Ccl2|Ccl7|Rarres2|Itga9
GO Biological Processes	GO:0051196	metabolic process	W2	-1.7	3	Fbp1|Me1|Pdk1
GO Biological Processes	GO:0030593	neutrophil chemotaxis	W2	-1.7	4	Bst1|Ccl2|Ccl7|Itga9
GO Biological Processes	GO:0010256	endomembrane system organization	W2	-1.7	9	Cxcr4|Myh2|Nectin2|Dym|Fhdc1|Plscr4|Dnajc28|Pheta2|Plscr5
GO Biological Processes	GO:0051651	maintenance of location in cell	W2	-1.6	4	Bard1|Gaa|Sorl1|Mprip
GO Biological Processes	GO:0050994	process	W2	-1.6	3	Fabp1|Sorl1|Rarres2
GO Biological Processes	GO:1903827	regulation of cellular protein localization	W2	-1.6	11	Bard1|Cep250|Ran|Ccl2|Sorl1|Tert|Gpc6|Pdzk1|Fis1|Edem2|Dclk3
Reactome Gene Sets	R-MMU-2029482	for phagocytic cup formation	W2	-1.6	3	Myh2|Wipf2|Elmo1
GO Molecular Functions	GO:0004536	deoxyribonuclease activity	W2	-1.6	3	Ercc1|Ercc5|Eri2
GO Biological Processes	GO:0061337	cardiac conduction	W2	-1.6	3	Cacna1g|Ryr2|Scn10a
GO Biological Processes	GO:0008544	epidermis development	W2	-1.6	8	Gal|Krt6a|Foxc1|Sprr2d|Sprr2e|Sprr3|Lelp1|Lce3e
GO Molecular Functions	GO:0005539	glycosaminoglycan binding	W2	-1.6	6	Ptprf|Ccl2|Ccl7|Pglyrp2|Hapln3|2300002M23Rik
GO Biological Processes	GO:0006732	coenzyme metabolic process	W2	-1.6	8	Dnmt1|Fbp1|Fpgs|Me1|Tdo2|Akr1a1|Qdpr|Pdk1
GO Cellular Components	GO:0034704	calcium channel complex	W2	-1.6	3	Cacna1g|Ryr2|Catsper4

GO Biological Processes	GO:0060047	heart contraction	W2	-1.6	6	Cacna1g|Cxcr4|Gaa|Ryr2|Scn10a|Nppa
GO Biological Processes	GO:0048661	muscle cell proliferation	W2	-1.6	4	Dnmt1|Itga2|Tert|Tgm2
GO Biological Processes	GO:0060840	artery development	W2	-1.6	4	Cxcr4|Nprl3|Foxc1|Notch4
GO Biological Processes	GO:0007009	organization	W2	-1.6	4	Cxcr4|Myh2|Plscr4|Plscr5
GO Molecular Functions	GO:0022836	gated channel activity	W2	-1.6	8	Chrng|Cacna1g|Kcnk5|Ryr2|Scn10a|Ttyh2|Tmem150c|Catsper4
GO Biological Processes	GO:0051346	negative regulation of hydrolase activity	W2	-1.6	9	Serpina6|Cdkn2d|Fabp1|Ptprn2|Sorl1|Mprip|Serpina1f|Nle1|Angptl8
GO Biological Processes	GO:0030048	actin filament-based movement	W2	-1.6	4	Cacna1g|Myh2|Ryr2|Wipf2
GO Biological Processes	GO:0030858	epithelial cell differentiation	W2	-1.6	3	Foxc1|Prom1|Ahi1
GO Biological Processes	GO:0035904	aorta development	W2	-1.5	3	Cxcr4|Nprl3|Notch4
GO Biological Processes	GO:1901657	process	W2	-1.5	4	Ran|Akr1a1|Enpp4|Gba2
GO Biological Processes	GO:0048660	regulation of smooth muscle cell proliferation	W2	-1.5	5	Dnmt1|Itga2|Pdcd4|Tert|Tgm2
GO Cellular Components	GO:0044450	microtubule organizing center part	W2	-1.5	5	Cep250|Ran|Top2a|Ahi1|Exoc7
GO Biological Processes	GO:0003015	heart process	W2	-1.5	6	Cacna1g|Cxcr4|Gaa|Ryr2|Scn10a|Nppa
GO Molecular Functions	GO:0016788	hydrolase activity, acting on ester bonds	W2	-1.5	14	Ercc1|Fbp1|Ptprf|Ptprn2|Ercc5|Rnase2b|Shoc2|Nt5dc2|Eri2|Pan3|Them7|Ddhd1|Lipk|Ptrh1
GO Cellular Components	GO:0097733	photoreceptor cell cilium	W2	-1.5	4	Cep250|Prom1|Ahi1|Shoc2
GO Molecular Functions	GO:0140101	catalytic activity, acting on a tRNA	W2	-1.5	4	Farsa|Bcdin3d|Trmt61a|Ptrh1
GO Biological Processes	GO:0046324	regulation of glucose import	W2	-1.5	3	Tert|Ahi1|Rasa1

GO Biological Processes	GO:0048659	smooth muscle cell proliferation	W2	-1.5	5	Dnmt1|Itga2|Pdcd4|Tert|Tgm2
GO Cellular Components	GO:0005814	centriole	W2	-1.5	4	Cep250|Ran|Top2a|Ahi1
GO Cellular Components	GO:0097731	9+0 non-motile cilium	W2	-1.5	4	Cep250|Prom1|Ahi1|Shoc2
GO Biological Processes	GO:0019730	antimicrobial humoral response	W2	-1.5	4	Krt6a|Ccl2|Pglyrp2|Rarres2
GO Molecular Functions	GO:0043177	organic acid binding	W2	-1.5	6	Fabp1|Ryr2|Tdo2|Hapln3|2300002M23Rik|Gldc
GO Biological Processes	GO:0061982	meiosis I cell cycle process	W2	-1.5	4	Ercc1|Rad54l|Top2a|Syce2
GO Biological Processes	GO:0050727	regulation of inflammatory response	W2	-1.5	8	Bst1|Itga2|Pdcd4|Psmb4|Tgm2|Usp18|Pglyrp2|Nppa
GO Biological Processes	GO:0032101	regulation of response to external stimulus	W2	-1.5	14	Bst1|Capn3|Cxcr4|Itga2|Pdcd4|Psmb4|Ptprf|Ccl2|Tgm2|Usp18|Pglyrp2|Rarres2|Enpp4|Nppa
GO Biological Processes	GO:0030855	epithelial cell differentiation	W2	-1.4	12	Cxcr4|Krt6a|Foxc1|Notch4|Prom1|Sprr2d|Sprr2e|Sprr3|Shroom3|Ahi1|Lelp1|Lce3e
GO Biological Processes	GO:0033365	protein localization to organelle	W2	-1.4	14	Bard1|Cep250|Rad21|Ran|Ryr2|Sorl1|Tert|Gpc6|Ahi1|Fis1|Sprn|Nup214|Szt2|Dclk3
GO Molecular Functions	GO:0005518	collagen binding	W2	-1.4	3	Itga2|2300002M23Rik|Itga9
GO Biological Processes	GO:0055117	contraction	W2	-1.4	3	Ryr2|Scn10a|Nppa
GO Biological Processes	GO:0006949	syncytium formation	W2	-1.4	3	Ercc1|Nfe2|Ocstamp
GO Biological Processes	GO:0006855	drug transmembrane transport	W2	-1.4	3	Slc47a1|Slc25a18|Oscp1

KEGG Pathway	mmu01200	Carbon metabolism	W2	-1.4	4	Fbp1|Me1|Tktl2|Gldc
GO Biological Processes	GO:1990266	neutrophil migration	W2	-1.4	4	Bst1|Ccl2|Ccl7|Itga9
GO Biological Processes	GO:0033002	muscle cell proliferation	W2	-1.4	6	Dnmt1|Itga2|Foxc1|Pdcd4|Tert|Tgm2
GO Biological Processes	GO:1901136	carbohydrate derivative catabolic process	W2	-1.4	4	Pglyrp2|Edem2|Enpp4|Gba2
GO Molecular Functions	GO:0140098	catalytic activity, acting on RNA	W2	-1.4	8	Tert|Rnase2b|Farsa|Eri2|Pan3|Bcdin3d|Trmt61a|Ptrh1
GO Biological Processes	GO:0045576	mast cell activation	W2	-1.4	3	Nectin2|Rhoh|Nppa
Reactome Gene Sets	R-MMU-216083	interactions	W2	-1.4	3	Col4a1|Itga2|Itga9
GO Biological Processes	GO:0042255	ribosome assembly	W2	-1.4	3	Rpsa|Mrps2|Nle1
GO Biological Processes	GO:0034762	regulation of transmembrane transport	W2	-1.4	11	Capn3|Gal|Ryr2|Scn10a|Ccl2|Tert|Ahi1|Pdzk1|Rasa1|Nppa|Catsper4
GO Biological Processes	GO:0008286	insulin receptor signaling pathway	W2	-1.4	4	Ptprf|Zfp106|Sorl1|Rarres2
Reactome Gene Sets	R-MMU-5576891	Cardiac conduction	W2	-1.4	4	Kcnk5|Ryr2|Scn10a|Nppa
KEGG Pathway	mmu05412	ventricular cardiomyopathy	W2	-1.4	3	Itga2|Ryr2|Itga9
GO Biological Processes	GO:1903034	regulation of response to wounding	W2	-1.4	5	Capn3|Cxcr4|Ptprf|Ccl2|Enpp4
GO Biological Processes	GO:0008016	regulation of heart contraction	W2	-1.4	5	Cacna1g|Gaa|Ryr2|Scn10a|Nppa
Reactome Gene Sets	R-MMU-6781827	Nucleotide Excision Repair (TC-	W2	-1.4	3	Ercc1|Cops7a|Zfp830
GO Biological Processes	GO:0032386	regulation of intracellular transport	W2	-1.4	9	Bard1|Ran|Ccl2|Sorl1|Pdzk1|Fis1|Edem2|Nup214|Npa
GO Biological Processes	GO:0010466	negative regulation of peptidase activity	W2	-1.4	6	Serpina6|Cdkn2d|Fabp1|Sorl1|Serpina1f|Nle1
GO Biological Processes	GO:0051193	metabolic process	W2	-1.3	3	Fbp1|Me1|Pdk1
GO Biological Processes	GO:0032507	location in cell	W2	-1.3	3	Bard1|Sorl1|Mprip

GO Cellular Components	GO:0000784	telomeric region	W2	-1.3	3	Ercc1|Tert|Stn1
GO Biological Processes	GO:0046323	glucose import	W2	-1.3	3	Tert|Ahi1|Rasa1
GO Biological Processes	GO:0046626	signaling pathway	W2	-1.3	3	Ptprf|Sorl1|Rarres2
GO Biological Processes	GO:1901606	process	W2	-1.3	3	Tdo2|Gldc|Qdpr
GO Biological Processes	GO:0048844	artery morphogenesis	W2	-1.3	3	Nprl3|Foxc1|Notch4
GO Biological Processes	GO:1901343	vasculature development	W2	-1.3	4	Dnmt1|Foxc1|Pdcd4|Ccl2
GO Biological Processes	GO:2001259	channel activity	W2	-1.3	3	Gal|Ccl2|Nppa
GO Biological Processes	GO:0032103	positive regulation of response to external stimulus	W2	-1.3	7	Cxcr4|Itga2|Pdcd4|Ccl2|Tgm2|Rarres2|Nppa
GO Biological Processes	GO:0007568	aging	W2	-1.3	6	Ercc1|Pdcd4|Rad54l|Tert|Ercc5|Mir877
Reactome Gene Sets	R-MMU-2029480	dependent phagocytosis	W2	-1.3	3	Myh2|Wipf2|Elmo1
GO Biological Processes	GO:0033601	mammary gland epithelial cell proliferation	M6	-4.1	4	Rtn4|Rreb1|Kdm5b|Zfp703
GO Molecular Functions	GO:0047961	activity	M6	-3.8	3	Keg1|Glyat|Glyatl3
GO Biological Processes	GO:0031663	lipopolysaccharide-mediated signaling pathway	M6	-3.5	8	Cd6|Acod1|Lbp|Myd88|Ptpn22|Tnf|Traf6|Trem2
GO Biological Processes	GO:0001818	negative regulation of cytokine production	M6	-3.2	20	Adcy7|Epha2|Fn1|Hmox1|Il12b|Acod1|Jak3|Lbp|Ptpn22|Tlr6|Tnf|Homer3|Pglyrp2|Rgcc|Traf3ip1|Trem2|Laptm4b|Nploc4|Bank1|Pglyrp4
GO Molecular Functions	GO:0070891	lipoteichoic acid binding	M6	-3.1	3	Cd6|Lbp|Trem2
GO Biological Processes	GO:2000427	apoptotic cell clearance	M6	-3.1	3	C2|Ccl2|Trem2
GO Molecular Functions	GO:0016775	nitrogenous group as acceptor	M6	-3.1	3	Ckm|Nme2|Map4k4
GO Biological Processes	GO:0098581	detection of external biotic stimulus	M6	-3.1	5	Lbp|Tlr6|Pglyrp2|Trem2|Pglyrp4

GO Biological Processes	GO:0010256	endomembrane system organization	M6	-3	26	Col5a1|Nectin2|Spta1|Pacsin2|Stx6|Use1|Pi4k2b|Tbc1d20|Rtn4|Dym|Fam160a2|Sun5|Sec16b|Rab3gap2|Arfgef2|Laptm4b|Nploc4|Xkr7|Tmem201|Tor1aip2|Dnajc28|Ehd2|Syne2|Myo18a|Tlcd2|Baiap3
GO Molecular Functions	GO:0001727	lipid kinase activity	M6	-2.9	3	Sphk1|Cerk|Cerkl
GO Biological Processes	GO:2000425	clearance	M6	-2.9	3	C2|Ccl2|Trem2
KEGG Pathway	mmu05168	Herpes simplex infection	M6	-2.9	17	Csnk2b|H2-D1|H2-Q1|H2-T3|Ifnar2|Il12b|Irf9|Myd88|Per2|Nectin2|Ccl2|Tnf|Traf6|H2-M10.5|Oas2|Ifit1bl1|H2-Eaps
GO Biological Processes	GO:0001817	regulation of cytokine production	M6	-2.9	39	Adcy7|Cd6|Cebpg|Epha2|Fn1|Hmox1|Ifi204|Il12b|Il12rb1|Acod1|Jak3|Arhgef2|Lbp|Myd88|Ptpn22|Ccl2|Sphk1|Tlr6|Tnf|Traf6|Zfp64|Homer3|Agpat1|Pglyrp2|Rgcc|Rtn4|Traf3ip1|Nfam1|Trem2|Trim6|Arfgef2|Laptm4b|Arid5a|Nploc4|Bank1|Psg22|Ltbp1|Pglyrp4|Isg15
GO Biological Processes	GO:0009595	detection of biotic stimulus	M6	-2.8	5	Lbp|Tlr6|Pglyrp2|Trem2|Pglyrp4
GO Biological Processes	GO:0042059	epidermal growth factor receptor signaling pathway	M6	-2.8	5	Ptprf|Dusp3|Itga1|Chmp6|Gprc5a

GO Biological Processes	GO:0001816	cytokine production	M6	-2.8	42	Adcy7|Cd6|Cebpg|Epha2|Fn1|Hmox1|Ifi204|Il12b|Il12rb1|Acod1|Irf9|Jak3|Arhgef2|Lbp|Myd88|Ptpn22|Ccl2|Sphk1|Tlr6|Tnf|Traf6|Zfp64|Homer3|Tcirg1|Agpat1|Pglyrp2|Rgcc|Rtn4|Traf3ip1|Nfam1|Trem2|Trim6|Arfgef2|Laptm4b|Il25|Arid5a|Nploc4|Bank1|Psg22|Ltbp1|Pglyrp4|Isg15
KEGG Pathway	mmu05332	Graft-versus-host disease	M6	-2.8	8	H2-D1|H2-Q1|H2-T3|Klra7|Klra9|Tnf|H2-M10.5|H2-Ea-ps
Reactome Gene Sets	R-MMU-193704	p75 NTR receptor-mediated signalling	M6	-2.7	9	Arhgef2|Myd88|Traf6|Uba52|Rtn4|Arhgef10l|Arhgef17|Arhgef19|Prex1
GO Biological Processes	GO:1901185	negative regulation of ERBB signaling pathway	M6	-2.7	5	Ptprf|Dusp3|Itga1|Chmp6|Gprc5a
GO Biological Processes	GO:0070886	calcineurin-NFAT signaling	M6	-2.6	4	Tnf|Cherp|Nrg1|Akap6
GO Biological Processes	GO:0032740	positive regulation of interleukin-17 production	M6	-2.6	4	Il12b|Myd88|Sphk1|Arid5a
GO Biological Processes	GO:0106058	calcineurin-mediated signaling	M6	-2.6	4	Tnf|Cherp|Nrg1|Akap6
GO Molecular Functions	GO:1990782	protein tyrosine kinase binding	M6	-2.6	10	Angpt4|Dok2|Pik3r2|Ptpn22|Ptprf|Dusp3|Trem2|Trim6|Nrg1|Bank1
KEGG Pathway	mmu05142	Chagas disease (American trypanosomiasis)	M6	-2.6	10	Gna14|Il12b|Myd88|Pik3cd|Pik3r2|Plcb2|Ccl2|Tlr6|Tnf|Traf6

GO Biological Processes	GO:0050848	regulation of calcium-mediated signaling	M6	-2.6	10	Bst1|Tnf|Zap70|Homer3|Cherp|Selenon|Trem2|Sri|Nrg1|Akap6
KEGG Pathway	mmu04940	Type I diabetes mellitus	M6	-2.6	8	H2-D1|H2-Q1|H2-T3|Il12b|Ptprn2|Tnf|H2-M10.5|H2-Ea-ps
GO Cellular Components	GO:0120103	centriolar subdistal appendage	M6	-2.5	3	Nin|Ccdc68|Cep170
Reactome Gene Sets	R-MMU-110357	glycosylase by APEX1	M6	-2.5	3	Mbd4|Ogg1|Mpg
GO Cellular Components	GO:0005771	multivesicular body	M6	-2.5	6	Cd79a|Cst3|Cst7|Nsg2|Sftpc|Laptm4b
GO Biological Processes	GO:0002711	positive regulation of T cell mediated immunity	M6	-2.5	8	H2-D1|H2-Q1|H2-T3|Il12b|Nectin2|Traf6|Arid5a|H2-M10.5
GO Biological Processes	GO:0009895	negative regulation of catabolic process	M6	-2.5	20	Cst3|Fbp1|Hmox1|Myd88|Ptpn22|Rps7|Tnf|Ube2g2|Pik3cg|Pdcl3|Dapl1|Trim39|Cdk5rap3|Trem2|Laptm4b|Trim40|Lzts1|Nrg1|Thrap3|Lrig2
GO Biological Processes	GO:0018108	peptidyl-tyrosine phosphorylation	M6	-2.4	21	Angpt4|Blk|Bst1|Cntn1|Crlf1|Hpx|Il12b|Il12rb1|Jak3|Arhgef2|Nf2|Ptpn22|Tnf|Zap70|Pdcl3|Traf3ip1|Trem2|Chmp6|Nrg1|Gprc5a|Bank1
GO Biological Processes	GO:0002699	positive regulation of immune effector process	M6	-2.4	18	H2-D1|H2-Q1|H2-T3|Hmox1|Hpx|Il12b|Lbp|Ptpn22|Nectin2|Ccl2|Tnf|Traf6|Rtn4|Trim6|Arid5a|H2-M10.5|Myo18a|H60c

KEGG Pathway	mmu04612	Antigen processing and presentation	M6	-2.4	9	Hspa5|H2-D1|H2-Q1|H2-T3|Hspa4|Rfxank|Tnf|H2-M10.5|H2-Ea-ps
GO Biological Processes	GO:0018212	peptidyl-tyrosine modification	M6	-2.4	21	Angpt4|Blk|Bst1|Cntn1|Crlf1|Hpx|Il12b|Il12rb1|Jak3|Arhgef2|Nf2|Ptpn22|Tnf|Zap70|Pdcl3|Traf3ip1|Trem2|Chmp6|Nrg1|Gprc5a|Bank1
GO Biological Processes	GO:0033599	regulation of mammary gland epithelial cell proliferation	M6	-2.4	4	Rtn4|Rreb1|Kdm5b|Zfp703
KEGG Pathway	mmu00030	Pentose phosphate pathway	M6	-2.3	5	Fbp1|Rpia|Pgls|Tktl2|Prps1l1
GO Biological Processes	GO:0048668	collateral sprouting	M6	-2.3	5	Cobl|Dvl1|Nin|Ulk1|Rtn4
Reactome Gene Sets	R-MMU-8957275	Post-translational protein phosphorylation	M6	-2.3	10	C4b|Cst3|Fn1|Igfbp7|Mxra8|Mepe|Ckap4|Ltbp1|Ano8|Apol7e
GO Biological Processes	GO:0033598	mammary gland epithelial cell proliferation	M6	-2.3	5	Epha2|Rtn4|Rreb1|Kdm5b|Zfp703
GO Biological Processes	GO:0018149	peptide cross-linking	M6	-2.3	7	Fn1|Sprr2d|Sprr2e|Sprr3|Lelp1|Tgm6|Tgm4
GO Biological Processes	GO:0032490	bacterial origin	M6	-2.3	3	Lbp|Tlr6|Trem2
GO Biological Processes	GO:0002709	regulation of T cell mediated immunity	M6	-2.3	9	Dpp4|H2-D1|H2-Q1|H2-T3|Il12b|Nectin2|Traf6|Arid5a|H2-M10.5
GO Biological Processes	GO:0031330	negative regulation of cellular catabolic process	M6	-2.3	17	Cst3|Fbp1|Hmox1|Myd88|Ptpn22|Rps7|Ube2g2|Pik3cg|Pdcl3|Dapl1|Trim39|Cdk5rap3|Trem2|Laptm4b|Lzts1|Thrap3|Lrig2

GO Biological Processes	GO:0050850	positive regulation of calcium-mediated signaling	M6	-2.2	6	Tnf|Zap70|Cherp|Trem2|Nrg1|Akap6
GO Biological Processes	GO:0043408	regulation of MAPK cascade	M6	-2.2	39	Acta2|Axin1|Dok2|Epha2|Fn1|Gcnt2|Mid1|Myd88|Nf2|Pik3r2|Ppef2|Ptpn22|Ccl2|Ccl7|Sphk1|Tlr6|Tnf|Traf6|Xdh|Gdf15|Map3k5|Cops5|Map4k4|Pik3cg|Lpar2|Fam83d|Dusp3|Unc5cl|Cdk5rap3|Tnxb|Trem2|Maged1|Cavin3|Itga1|Spred2|Ankrd26|Bank1|Taok3|Nek10
GO Molecular Functions	GO:0016799	N-glycosyl compounds	M6	-2.2	4	Bst1|Mbd4|Ogg1|Mpg
KEGG Pathway	mmu05330	Allograft rejection	M6	-2.2	7	H2-D1|H2-Q1|H2-T3|Il12b|Tnf|H2-M10.5|H2-Ea-ps
GO Biological Processes	GO:0002697	regulation of immune effector process	M6	-2.2	25	Dpp4|H2-D1|H2-Q1|H2-T3|Hmox1|Hpx|Il12b|Il12rb1|Jak3|Lbp|Ptpn22|Nectin2|Ccl2|Tnf|Traf6|Pglyrp2|Rtn4|Traf3ip1|Trim6|Arid5a|Nploc4|H2-M10.5|Myo18a|Pglyrp4|H60c
GO Biological Processes	GO:0001916	positive regulation of T cell mediated cytotoxicity	M6	-2.2	6	H2-D1|H2-Q1|H2-T3|Il12b|Nectin2|H2-M10.5
GO Biological Processes	GO:0031424	keratinization	M6	-2.2	5	Sprr2d|Sprr2e|Sprr3|Kazn|Gprc5d

GO Molecular Functions	GO:0005539	glycosaminoglycan binding	M6	-2.2	15	Col5a1|Ncan|Fn1|Igfals|Mmp7|Ptprf|Rpl22|Ccl2|Ccl7|Pglyrp2|Hapln3|Tnxb|Trem2|Hapln4|Pglyrp4
Reactome Gene Sets	R-MMU-381426	Growth Factor (IGF) transport and uptake by Insulin-like Growth Factor Bi	M6	-2.2	10	C4b|Cst3|Fn1|Igfbp7|Mxra8|Mepe|Ckap4|Ltbp1|Ano8|Apol7e
GO Molecular Functions	GO:0019901	protein kinase binding	M6	-2.2	38	Acta2|Angpt4|Axin1|Ccnd3|Cd6|Dok2|Dvl1|Gria2|Ifnar2|Pik3r2|Ppef2|Ptpn22|Ptprf|Rbbp6|Rps18|Rps7|Srebf1|Tesk1|Traf6|Ulk1|Wars|Ldb3|Map3k5|Rgcc|Telo2|Fam83d|Dusp3|Bora|Cdk5rap3|Trem2|Tex14|Trim6|Cavin3|Inka2|Spred2|Nrg1|Tpcn2|Bank1
KEGG Pathway	mmu_M00004	(Pentose phosphate cycle)	M6	-2.1	3	Rpia|Pgls|Tktl2
KEGG Pathway	M00004	(Pentose phosphate cycle)	M6	-2.1	3	Rpia|Pgls|Tktl2
GO Molecular Functions	GO:0003951	NAD+ kinase activity	M6	-2.1	3	Sphk1|Nadk|Cerk
Reactome Gene Sets	R-MMU-209543	complexes	M6	-2.1	3	Myd88|Traf6|Uba52
KEGG Pathway	mmu04620	Toll-like receptor signaling pathway	M6	-2.1	9	Ifnar2|Il12b|Lbp|Myd88|Pik3cd|Pik3r2|Tlr6|Tnf|Traf6
KEGG Pathway	mmu05340	Primary immunodeficiency	M6	-2.1	5	Cd79a|Jak3|Rfxank|Zap70|Tnfrsf13b
KEGG Pathway	mmu05162	Measles	M6	-2.1	11	Ccnd3|Csnk2b|Ifnar2|Il12b|Irf9|Jak3|Myd88|Pik3cd|Pik3r2|Traf6|Oas2
GO Biological Processes	GO:1901184	regulation of ERBB signaling pathway	M6	-2.1	7	Ptprf|Rtn4|Dusp3|Mvb12a|Itga1|Chmp6|Gprc5a

GO Biological Processes	GO:0000165	MAPK cascade	M6	-2.1	41	Acta2|Axin1|Dok2|Epha2|Fn1|Gcnt2|Mid1|Myd88|Nf2|Pik3r2|Ppef2|Ptpn22|Ccl2|Ccl7|Sphk1|Tlr6|Tnf|Traf6|Xdh|Gdf15|Map3k5|Cops5|Map4k4|Pik3cg|Lpar2|Fam83d|Dusp3|Unc5cl|Cdk5rap3|Tnxb|Trem2|Plvap|Maged1|Cavin3|Itga1|Spred2|Nrg1|Ankrd26|Bank1|Taok3|Nek10
GO Biological Processes	GO:0031343	positive regulation of cell killing	M6	-2.1	9	H2-D1|H2-Q1|H2-T3|Il12b|Nectin2|Ccl2|H2-M10.5|Pglyrp4|H60c
GO Molecular Functions	GO:0005509	calcium ion binding	M6	-2.1	33	Ncan|Dst|Grin1|Guca1a|Myl7|Nin|Notch4|Plcb2|Ppef2|Spta1|Tnnt2|Tpd52|Pla2g2e|Pla2g2f|Cdhr3|Efcab3|Tbc1d9|Calr3|Col20a1|C2cd5|Selenon|Creld2|Kcnip2|Nkd1|Myl9|Sri|Lpcat1|Dsg1c|Ehd2|Capn11|Ltbp1|Calm5|Baiap3
GO Biological Processes	GO:0032872	regulation of stress-activated MAPK cascade	M6	-2.1	16	Axin1|Mid1|Myd88|Ptpn22|Sphk1|Tlr6|Tnf|Traf6|Xdh|Map3k5|Cops5|Map4k4|Dusp3|Unc5cl|Tnxb|Taok3
Reactome Gene Sets	R-MMU-204998	Cell death signalling via NRAGE, NRIF and NADE	M6	-2.1	7	Arhgef2|Traf6|Uba52|Arhgef10l|Arhgef17|Arhgef19|Prex1

GO Biological Processes	GO:0072643	interferon-gamma secretion	M6	-2.1	4	Ptpn22|Tcirg1|Arid5a|Isg15
GO Biological Processes	GO:0070302	regulation of stress-activated protein kinase signaling cascade	M6	-2.1	16	Axin1|Mid1|Myd88|Ptpn22|Sphk1|Tlr6|Tnf|Traf6|Xdh|Map3k5|Cops5|Map4k4|Dusp3|Unc5cl|Tnxb|Taok3
KEGG Pathway	mmu00230	Purine metabolism	M6	-2	13	Adcy7|Entpd6|Nme2|Pde1a|Pde9a|Pklr|Xdh|Gmpr|Prps1l1|Allc|Atic|Enpp4|Gucy1b2
GO Molecular Functions	GO:0019104	DNA N-glycosylase activity	M6	-2	3	Mbd4|Ogg1|Mpg
GO Biological Processes	GO:0032026	response to magnesium ion	M6	-2	3	Entpd6|Fbp1|Kcnj1
GO Biological Processes	GO:0002824	positive regulation of adaptive immune response based on somatic recombination of immune receptors b	M6	-2	11	H2-D1|H2-Q1|H2-T3|Hpx|Il12b|Il12rb1|Nectin2|Tnf|Traf6|Arid5a|H2-M10.5
GO Cellular Components	GO:0005815	microtubule organizing center	M6	-2	35	Cep131|Birc6|Dync1h1|Mak|Nin|Procr|Rbbp6|Rps7|Tcp10b|Wrn|Tekt2|Nubp2|Cep63|Ddah2|Exoc7|Keg1|Rgcc|Ckap2l|Mvb12a|Kif2c|Atp6v1d|Traf3ip1|Map10|C2cd5|Cdk5rap3|Arfgef2|Ift140|Crocc|Tmem201|Ankrd26|Harbi1|Nphp4|Syne2|Ccdc68|Cep170
GO Biological Processes	GO:0006855	drug transmembrane transport	M6	-2	7	Per2|Abcb4|Slc1a2|Slc7a5|Tnf|Oscp1|Slc47a2

GO Biological Processes	GO:0001912	positive regulation of leukocyte mediated cytotoxicity	M6	-2	8	H2-D1|H2-Q1|H2-T3|Il12b|Nectin2|Ccl2|H2-M10.5|H60c
GO Biological Processes	GO:0050730	regulation of peptidyl-tyrosine phosphorylation	M6	-2	17	Angpt4|Bst1|Cntn1|Crlf1|Hpx|Il12b|Arhgef2|Nf2|Ptpn22|Tnf|Pdcl3|Traf3ip1|Trem2|Chmp6|Nrg1|Gprc5a|Bank1
GO Biological Processes	GO:0032609	interferon-gamma production	M6	-2	10	Cebpg|Il12b|Il12rb1|Ptpn22|Tnf|Tcirg1|Pglyrp2|Arid5a|Pglyrp4|Isg15
Reactome Gene Sets	R-MMU-73887	Death Receptor Signalling	M6	-2	10	Arhgef2|Myd88|Tnf|Traf6|Uba52|Rtn4|Arhgef10l|Arhgef17|Arhgef19|Prex1
GO Biological Processes	GO:0001914	regulation of T cell mediated cytotoxicity	M6	-2	6	H2-D1|H2-Q1|H2-T3|Il12b|Nectin2|H2-M10.5
GO Biological Processes	GO:0043030	regulation of macrophage activation	M6	-2	6	Cst7|Lbp|Sphk1|Tlr6|Trem2|Myo18a
GO Biological Processes	GO:0009267	cellular response to starvation	M6	-2	11	Hspa5|Nprl3|Srebf1|Ulk1|Wrn|Map3k5|Slc39a4|Dapl1|Rrp8|Szt2|Tnrc6a
GO Molecular Functions	GO:0005089	Rho guanyl-nucleotide exchange factor activity	M6	-2	7	Arhgef2|Arhgef10l|Arhgef17|Dock10|Arhgef19|Farp1|Prex1

GO Biological Processes	GO:0051090	regulation of DNA-binding transcription factor activity	M6	-2	23	Cebpg|Hmox1|Acod1|Arhgef2|Myd88|Ptgis|Sphk1|Trim21|Tlr6|Tnf|Traf6|Cops5|Rgcc|Nfam1|Adgrf1|Cdk5rap3|Sri|Card14|Trim40|Trim31|Pprc1|Camk1d|Nwd1
GO Biological Processes	GO:0021932	cell migration	M6	-2	3	Ulk1|Rere|Rbfox2
GO Biological Processes	GO:0098712	plasma membrane	M6	-2	3	Per2|Slc1a2|Tnf
GO Biological Processes	GO:0010457	centriole-centriole cohesion	M6	-2	3	Nin|Crocc|Syne2
GO Molecular Functions	GO:0052742	activity	M6	-2	3	Pik3cd|Pik3cg|Pi4k2b
GO Biological Processes	GO:0002708	positive regulation of lymphocyte mediated immunity	M6	-1.9	11	H2-D1|H2-Q1|H2-T3|Hpx|Il12b|Nectin2|Tnf|Traf6|Arid5a|H2-M10.5|H60c
GO Molecular Functions	GO:0009975	cyclase activity	M6	-1.9	4	Adcy7|Bst1|Dglucy|Gucy1b2
GO Biological Processes	GO:0106056	regulation of calcineurin-mediated signaling	M6	-1.9	5	Tnf|Homer3|Cherp|Nrg1|Akap6
GO Biological Processes	GO:0070884	regulation of calcineurin-NFAT signaling cascade	M6	-1.9	5	Tnf|Homer3|Cherp|Nrg1|Akap6
GO Biological Processes	GO:0045185	maintenance of protein location	M6	-1.9	9	Bard1|Hspa5|Rangap1|Taf8|Sun5|Sri|Tnrc6a|Ltbp1|Syne2
KEGG Pathway	mmu04310	Wnt signaling pathway	M6	-1.9	11	Axin1|Ccnd3|Csnk2b|Dvl1|Mmp7|Plcb2|Tcf7|Wnt8b|Nkd1|Vangl1|Gm5415

GO Biological Processes	GO:0046578	regulation of Ras protein signal transduction	M6	-1.9	15	F2rl2|Fbp1|Arhgef2|Map4k4|Lpar2|Rtn4|Arhgef10l|Arfgef2|Arhgef17|Nrg1|Arhgef19|Farp1|Kank2|Prex1|Gpr4
GO Biological Processes	GO:0002821	positive regulation of adaptive immune response	M6	-1.9	11	H2-D1|H2-Q1|H2-T3|Hpx|Il12b|Il12rb1|Nectin2|Tnf|Traf6|Arid5a|H2-M10.5
GO Biological Processes	GO:1901018	potassium ion transmembrane	M6	-1.9	4	Gal|Trem2|Akap6|Lrrc38
GO Biological Processes	GO:0042594	response to starvation	M6	-1.9	12	Hspa5|Nprl3|Srebf1|Ulk1|Wrn|Map3k5|Slc39a4|Dapl1|Rrp8|Szt2|Tnrc6a|Lrp11
Reactome Gene Sets	R-MMU-194840	Rho GTPase cycle	M6	-1.9	10	Arhgef2|Pik3r2|Arhgap17|Arhgef10l|Arhgap8|Arhgap15|Gmip|Arhgef17|Arhgef19|Prex1
GO Biological Processes	GO:0001819	positive regulation of cytokine production	M6	-1.9	25	Cd6|Cebpg|Ifi204|Il12b|Il12rb1|Arhgef2|Lbp|Myd88|Ptpn22|Ccl2|Sphk1|Tlr6|Tnf|Traf6|Zfp64|Agpat1|Rgcc|Rtn4|Nfam1|Trem2|Trim6|Arfgef2|Arid5a|Nploc4|Psg22
GO Biological Processes	GO:0002819	regulation of adaptive immune response	M6	-1.9	14	Adcy7|Dpp4|H2-D1|H2-Q1|H2-T3|Hpx|Il12b|Il12rb1|Jak3|Nectin2|Tnf|Traf6|Arid5a|H2-M10.5
Reactome Gene Sets	R-MMU-71336	Pentose phosphate pathway	M6	-1.9	3	Rpia|Pgls|Prps1l1

Reactome Gene Sets	R-MMU-193639	p75NTR signals via NF-kB	M6	-1.9	3	Myd88|Traf6|Uba52
GO Biological Processes	GO:1903978	activation	M6	-1.9	3	Cst7|Sphk1|Trem2
GO Biological Processes	GO:0051938	L-glutamate import	M6	-1.9	3	Per2|Slc1a2|Tnf
GO Biological Processes	GO:0070307	lens fiber cell development	M6	-1.9	3	Bfsp1|Epha2|Tbc1d20
GO Biological Processes	GO:1903818	gated potassium channel	M6	-1.9	3	Trem2|Akap6|Lrrc38
KEGG Pathway	mmu05164	Influenza A	M6	-1.9	12	Ifnar2|Il12b|Irf9|Myd88|Pik3cd|Pik3r2|Ccl2|Tnf|Tmprss4|Tmprss13|Oas2|H2-Ea-ps
GO Biological Processes	GO:0032649	regulation of interferon-gamma production	M6	-1.9	9	Cebpg|Il12b|Il12rb1|Ptpn22|Tnf|Pglyrp2|Arid5a|Pglyrp4|Isg15
GO Biological Processes	GO:0019722	calcium-mediated signaling	M6	-1.9	14	Bst1|Sphk1|Tnf|Zap70|Homer3|Cherp|Treml1|Selenon|Trem2|Sri|Nrg1|Tpcn2|Akap6|Calm5
GO Biological Processes	GO:0042177	negative regulation of protein catabolic process	M6	-1.9	10	Cst3|Rps7|Ube2g2|Pdcl3|Trim39|Cdk5rap3|Laptm4b|Trim40|Nrg1|Lrig2
GO Biological Processes	GO:0034198	cellular response to amino acid starvation	M6	-1.8	5	Nprl3|Ulk1|Map3k5|Dapl1|Szt2
GO Biological Processes	GO:1902622	regulation of neutrophil migration	M6	-1.8	5	Bst1|Lbp|Myd88|Rtn4|Camk1d
KEGG Pathway	mmu05133	Pertussis	M6	-1.8	7	C2|C4b|Il12b|Myd88|Tnf|Traf6|Calm5
GO Biological Processes	GO:0007260	tyrosine phosphorylation of STAT protein	M6	-1.8	7	Crlf1|Hpx|Il12b|Jak3|Nf2|Tnf|Traf3ip1
GO Biological Processes	GO:0032507	maintenance of protein location in cell	M6	-1.8	7	Bard1|Hspa5|Rangap1|Taf8|Sun5|Tnrc6a|Syne2

GO Molecular Functions	GO:0008509	anion transmembrane transporter activity	M6	-1.8	19	Clcnka|Slc1a2|Slc23a1|Slc34a2|Slc4a3|Slc7a5|Slc7a7|Slc52a2|Clcnkb|Slco1c1|Pacc1|Slc52a3|Slc35b2|Slc35a5|Slco3a1|Slc5a5|Slco5a1|Slc26a11|Ano8
GO Biological Processes	GO:0046328	regulation of JNK cascade	M6	-1.8	13	Axin1|Myd88|Ptpn22|Tlr6|Tnf|Traf6|Map3k5|Cops5|Map4k4|Dusp3|Unc5cl|Tnxb|Taok3
GO Biological Processes	GO:1901381	potassium ion transmembrane transport	M6	-1.8	5	Gal|Kcnip2|Trem2|Akap6|Lrrc38
GO Biological Processes	GO:0001913	T cell mediated cytotoxicity	M6	-1.8	7	H2-D1|H2-Q1|H2-T3|Il12b|Nectin2|H2-M10.5|H60c
GO Molecular Functions	GO:0001540	amyloid-beta binding	M6	-1.8	6	Apbb1|Cst3|Gria2|Grin1|Pirb|Trem2
GO Biological Processes	GO:0008347	glial cell migration	M6	-1.8	6	Fn1|Grin1|Ccl2|Rtn4|Trem2|Syne2
GO Biological Processes	GO:0002822	regulation of adaptive immune response based on somatic recombination of immune receptors built from	M6	-1.8	13	Dpp4|H2-D1|H2-Q1|H2-T3|Hpx|Il12b|Il12rb1|Jak3|Nectin2|Tnf|Traf6|Arid5a|H2-M10.5
GO Cellular Components	GO:0048471	perinuclear region of cytoplasm	M6	-1.8	33	Prdx6|Apbb1|Axin1|Cobl|Cst3|Dst|Hmox1|Insl3|M6pr|Myo5b|Nf2|Nme2|Per2|Procr|Ptpn22|Rangap1|Ccl2|Sprr3|Tg|Tpd52|Traf6|Cops5|Cherp|Stx6|Taf8|Epn3|Cerkl|Tnrc6a|Akap6|Oas2|Ehd2|Ltbp1|Prex1

Reactome Gene Sets	R-MMU-381753	Olfactory Signaling Pathway	M6	-1.8	21	Olfr17|Olfr68|Rtp3|Olfr222|Olfr1034|Olfr420|Olfr657|Olfr554|Olfr692|Olfr677|Olfr698|Olfr661|Olfr556|Olfr473|Olfr640|Olfr589|Olfr641|Olfr552|Olfr555|Olfr681|Olfr151
GO Biological Processes	GO:0060314	sensitive calcium-release	M6	-1.8	3	Selenon|Sri|Akap6
Reactome Gene Sets	R-MMU-447115	Interleukin-12 family signaling	M6	-1.8	3	Crlf1|Il12b|Il12rb1
GO Molecular Functions	GO:0042834	peptidoglycan binding	M6	-1.8	3	Pglyrp2|Trem2|Pglyrp4
GO Biological Processes	GO:0098543	detection of other organism	M6	-1.8	3	Tlr6|Pglyrp2|Pglyrp4
Reactome Gene Sets	R-MMU-211979	Eicosanoids	M6	-1.8	3	Cyp4a12b|Ptgis|Cyp4f15
GO Biological Processes	GO:0016045	detection of bacterium	M6	-1.8	3	Tlr6|Pglyrp2|Pglyrp4
GO Biological Processes	GO:0031329	regulation of cellular catabolic process	M6	-1.8	35	Axin1|Cst3|Dvl1|Fabp1|Fbp1|Hmox1|Eif6|Nprl3|Myd88|Pik3r2|Ptpn22|Rps7|Srebf1|Trim21|Tfeb|Tnf|Ube2g2|Ulk1|Pik3cg|Pdcl3|Ankib1|Dapl1|Trim39|Cdk5rap3|Trem2|Rab3gap2|Laptm4b|Lzts1|Bag2|Dlgap1|Thrap3|Tnrc6a|Tpcn2|Lrig2|Tmem150b
GO Biological Processes	GO:0002230	positive regulation of defense response to virus by host	M6	-1.8	4	Il12b|Il12rb1|Ptpn22|Trim6
Reactome Gene Sets	R-MMU-445355	Smooth Muscle Contraction	M6	-1.8	4	Acta2|Myl7|Myl9|Itga1
GO Biological Processes	GO:0050766	positive regulation of phagocytosis	M6	-1.8	7	C2|Lbp|Ccl2|Tnf|Trem2|Camk1d|Myo18a
GO Cellular Components	GO:0005901	caveola	M6	-1.8	8	Hmox1|Ptgis|Tfpi|Pacsin2|Plvap|Cavin3|Akap6|Ehd2

GO Biological Processes	GO:0043506	regulation of JUN kinase activity	M6	-1.8	8	Axin1|Ptpn22|Tlr6|Tnf|Traf6|Map3k5|Tnxb|Taok3
GO Biological Processes	GO:0001704	formation of primary germ layer	M6	-1.8	8	Axin1|Col5a1|Epha2|Fn1|Nf2|Pou5f1|Atoh8|Arid1a
GO Cellular Components	GO:0016459	myosin complex	M6	-1.8	6	Myl7|Myo15|Myo5b|Myo7b|Myl9|Myo18a
GO Biological Processes	GO:0032874	positive regulation of stress-activated MAPK cascade	M6	-1.8	12	Axin1|Mid1|Myd88|Sphk1|Tlr6|Tnf|Traf6|Xdh|Map3k5|Map4k4|Unc5cl|Taok3
KEGG Pathway	mmu04150	mTOR signaling pathway	M6	-1.8	11	Dvl1|Nprl3|Pik3cd|Pik3r2|Slc7a5|Tnf|Ulk1|Wnt8b|Telo2|Atp6v1d|Tti1
GO Biological Processes	GO:0034340	response to type I interferon	M6	-1.8	5	Ifnar2|Myd88|Trim6|Oas2|Isg15
GO Biological Processes	GO:0051898	negative regulation of protein kinase B signaling	M6	-1.8	5	Epha2|Pou5f1|Xdh|Cavin3|Bank1
GO Molecular Functions	GO:0019207	kinase regulator activity	M6	-1.8	13	Angpt4|Ccnd3|Csnk2b|Pik3r2|Wars|Tcl1b5|Ccnl2|Rgcc|Gprc5d|Inka2|Spred2|Nrg1|Gprc5a
GO Cellular Components	GO:0005813	centrosome	M6	-1.8	27	Cep131|Dync1h1|Mak|Nin|Procr|Rbbp6|Rps7|Wrn|Nubp2|Cep63|Exoc7|Keg1|Rgcc|Ckap2l|Mvb12a|Kif2c|Atp6v1d|Traf3ip1|Map10|Cdk5rap3|Ift140|Crocc|Tmem201|Ankrd26|Nphp4|Syne2|Cep170

GO Biological Processes	GO:0070304	positive regulation of stress-activated protein kinase signaling cascade	M6	-1.8	12	Axin1|Mid1|Myd88|Sphk1|Tlr6|Tnf|Traf6|Xdh|Map3k5|Map4k4|Unc5cl|Taok3
GO Biological Processes	GO:0032675	regulation of interleukin-6 production	M6	-1.7	11	Arhgef2|Lbp|Myd88|Ptpn22|Tlr6|Tnf|Traf6|Zfp64|Trem2|Arid5a|Bank1
GO Biological Processes	GO:0002260	lymphocyte homeostasis	M6	-1.7	7	Jak3|Pik3cd|Pirb|Spta1|Tcirg1|Tnfrsf13b|Dock10
KEGG Pathway	mmu04970	Salivary secretion	M6	-1.7	7	Adcy7|Bst1|Chrm3|Cst3|Plcb2|Gucy1b2|Calm5
GO Biological Processes	GO:0042058	growth factor receptor signaling pathway	M6	-1.7	6	Ptprf|Dusp3|Mvb12a|Itga1|Chmp6|Gprc5a
GO Biological Processes	GO:0035023	regulation of Rho protein signal transduction	M6	-1.7	10	F2rl2|Arhgef2|Lpar2|Arhgef10l|Arhgef17|Arhgef19|Farp1|Kank2|Prex1|Gpr4
GO Biological Processes	GO:0051896	regulation of protein kinase B signaling	M6	-1.7	11	Epha2|Gcnt2|Pou5f1|Tnf|Xdh|Gdf15|Pik3cg|Rtn4|Cavin3|Nrg1|Bank1
GO Biological Processes	GO:0051186	cofactor metabolic process	M6	-1.7	27	Prdx6|Fbp1|Fdxr|Fpgs|Got1|Gsr|Hbb-y|Hebp1|Hmox1|Hpx|Eif6|Ldhb|Pemt|Pklr|Rpia|Spta1|Nubp2|Pgls|Coq8a|Acss1|Glyat|Atic|Nadk|Dhtkd1|Nmrk1|Pdk1|Far2
GO Biological Processes	GO:0001774	microglial cell activation	M6	-1.7	5	Cst7|Sphk1|Tlr6|Tnf|Trem2
GO Biological Processes	GO:0002269	leukocyte activation involved in inflammatory response	M6	-1.7	5	Cst7|Sphk1|Tlr6|Tnf|Trem2
GO Biological Processes	GO:0070306	lens fiber cell differentiation	M6	-1.7	4	Bfsp1|Epha2|Nf2|Tbc1d20

Reactome Gene Sets	R-MMU-196807	Nicotinate metabolism	M6	-1.7	4	Bst1|Ptgis|Nadk|Nmrk1
Reactome Gene Sets	R-MMU-917729	Required For Transport (ESCRT)	M6	-1.7	4	Uba52|Mvb12a|Vps37c|Chmp6
GO Biological Processes	GO:0002825	immune response	M6	-1.7	4	Il12b|Il12rb1|Jak3|Arid5a
Reactome Gene Sets	R-MMU-196849	Metabolism of water-soluble vitamins and cofactors	M6	-1.7	9	Bst1|Fpgs|Ptgis|Slc23a1|Slc52a2|Pccb|Slc52a3|Nadk|Nmrk1
Reactome Gene Sets	R-MMU-397014	Muscle contraction	M6	-1.7	12	Acta2|Kcnk5|Myl7|Scn10a|Abcc9|Tnnt2|Corin|Scn2b|Kcnip2|Myl9|Sri|Itga1
GO Biological Processes	GO:0045410	interleukin-6 biosynthetic	M6	-1.7	3	Tlr6|Tnf|Traf6
GO Molecular Functions	GO:0015347	anion transmembrane	M6	-1.7	3	Slco1c1|Slco3a1|Slco5a1
Reactome Gene Sets	R-MMU-210993	Tie2 Signaling	M6	-1.7	3	Angpt4|Dok2|Pik3r2
GO Biological Processes	GO:0071786	network organization	M6	-1.7	3	Use1|Rtn4|Rab3gap2
GO Biological Processes	GO:0002922	immune response	M6	-1.7	3	Hpx|Acod1|Tnf
Reactome Gene Sets	R-MMU-1482925	Acyl chain remodelling of PG	M6	-1.7	3	Pla2g2e|Pla2g2f|Lpcat1
GO Biological Processes	GO:0070571	projection regeneration	M6	-1.7	3	Map4k4|Rtn4|Lrig2
GO Biological Processes	GO:0050671	positive regulation of lymphocyte proliferation	M6	-1.7	10	Bst1|Cd6|Il12b|Il12rb1|Jak3|Myd88|Ptpn22|Spta1|Traf6|Zap70
GO Biological Processes	GO:0032760	positive regulation of tumor necrosis factor production	M6	-1.7	8	Il12b|Arhgef2|Lbp|Myd88|Ccl2|Zfp64|Arfgef2|Arid5a
GO Biological Processes	GO:0042102	positive regulation of T cell proliferation	M6	-1.7	8	Cd6|Il12b|Il12rb1|Jak3|Ptpn22|Spta1|Traf6|Zap70
GO Biological Processes	GO:0051403	stress-activated MAPK cascade	M6	-1.7	16	Axin1|Mid1|Myd88|Ptpn22|Sphk1|Tlr6|Tnf|Traf6|Xdh|Map3k5|Cops5|Map4k4|Dusp3|Unc5cl|Tnxb|Taok3

GO Molecular Functions	GO:0051879	Hsp90 protein binding	M6	-1.7	5	Cyp2b10|Ppef2|Ulk1|Telo2|Unc45a
GO Biological Processes	GO:1990928	response to amino acid starvation	M6	-1.7	5	Nprl3|Ulk1|Map3k5|Dapl1|Szt2
GO Biological Processes	GO:0098754	detoxification	M6	-1.7	5	Prdx6|Mt4|Tnf|Acaa1a|Szt2
GO Biological Processes	GO:0010799	regulation of peptidyl-threonine phosphorylation	M6	-1.7	5	Axin1|Ppef2|Sphk1|Trim6|Spred2
KEGG Pathway	mmu05152	Tuberculosis	M6	-1.7	12	Cebpg|Il12b|Lbp|Myd88|Rfxank|Sphk1|Tlr6|Tnf|Traf6|Tcirg1|Calm5|H2-Ea-ps
KEGG Pathway	mmu04650	Natural killer cell mediated cytotoxicity	M6	-1.7	9	H2-D1|Ifnar2|Klra4|Klra7|Klra9|Pik3cd|Pik3r2|Tnf|Zap70
KEGG Pathway	mmu01200	Carbon metabolism	M6	-1.7	9	Fbp1|Got1|Pklr|Rpia|Pgls|Pccb|Acss1|Tktl2|Prps1l1
GO Biological Processes	GO:0043537	vessel endothelial cell migration	M6	-1.7	4	Angpt4|Csnk2b|Pik3r2|Rgcc
GO Biological Processes	GO:0032755	positive regulation of interleukin-6 production	M6	-1.7	8	Arhgef2|Lbp|Myd88|Tlr6|Tnf|Traf6|Zfp64|Arid5a
GO Biological Processes	GO:1903557	positive regulation of tumor necrosis factor superfamily cytokine production	M6	-1.7	8	Il12b|Arhgef2|Lbp|Myd88|Ccl2|Zfp64|Arfgef2|Arid5a
GO Biological Processes	GO:0046579	positive regulation of Ras protein signal transduction	M6	-1.7	6	F2rl2|Map4k4|Lpar2|Rtn4|Nrg1|Gpr4
GO Biological Processes	GO:0032946	positive regulation of mononuclear cell proliferation	M6	-1.7	10	Bst1|Cd6|Il12b|Il12rb1|Jak3|Myd88|Ptpn22|Spta1|Traf6|Zap70

GO Biological Processes	GO:1990266	neutrophil migration	M6	-1.7	9	Bst1|Lbp|Myd88|Ccl2|Ccl7|Rtn4|Itga1|Camk1d|Prex1
GO Molecular Functions	GO:0022804	active transmembrane transporter activity	M6	-1.7	20	Abcb4|Slc1a2|Slc23a1|Slc34a2|Slc4a3|Slc5a1|Abcc9|Tcirg1|Slco1c1|Slc15a3|Abca14|Atp6v1d|Slc24a3|Slc45a4|Slco3a1|Slc5a5|Slco5a1|Slc26a11|Slc47a2|Abca17
GO Biological Processes	GO:0002456	T cell mediated immunity	M6	-1.7	10	Dpp4|H2-D1|H2-Q1|H2-T3|Il12b|Nectin2|Traf6|Arid5a|H2-M10.5|H60c
GO Biological Processes	GO:0042176	regulation of protein catabolic process	M6	-1.6	21	Axin1|Cst3|Dvl1|Rps7|Tnf|Ube2g2|Pdcl3|Ankib1|Fam83d|Trim39|Cdk5rap3|Trem2|Nkd1|Laptm4b|Trim40|Chmp6|Lpcat1|Nrg1|Bag2|Dlgap1|Lrig2
GO Molecular Functions	GO:0051184	transporter activity	M6	-1.6	3	Hpx|Slc23a1|Flvcr1
GO Molecular Functions	GO:0030676	exchange factor activity	M6	-1.6	3	Arhgef2|Farp1|Prex1
GO Biological Processes	GO:0043252	anion transport	M6	-1.6	3	Slco1c1|Slco3a1|Slco5a1
GO Biological Processes	GO:2000810	junction assembly	M6	-1.6	3	Epha2|Tnf|Nphp4
GO Biological Processes	GO:0045088	regulation of innate immune response	M6	-1.6	17	Hpx|Ifi204|Il12b|Acod1|Lbp|Myd88|Ptpn22|Nectin2|Tfeb|Tlr6|Tnf|Rtn4|Trem2|Trim6|Nploc4|9830107B12Rik|H60c

GO Biological Processes	GO:0051091	positive regulation of DNA-binding transcription factor activity	M6	-1.6	15	Arhgef2|Myd88|Sphk1|Trim21|Tlr6|Tnf|Traf6|Cops5|Rgcc|Nfam1|Adgrf1|Card14|Trim31|Pprc1|Camk1d
GO Biological Processes	GO:0031572	G2 DNA damage checkpoint	M6	-1.6	4	Mbd4|Babam1|Cdk5rap3|Taok3
Reactome Gene Sets	R-MMU-1483166	Synthesis of PA	M6	-1.6	4	Pla2g2f|Agpat1|Ddhd1|Lpcat1
GO Biological Processes	GO:0045672	osteoclast differentiation	M6	-1.6	4	Il12b|Tnf|Traf6|Trem2
GO Biological Processes	GO:0002486	presentation of endogenous peptide antigen via MHC class	M6	-1.6	4	H2-D1|H2-Q1|H2-T3|H2-M10.5
GO Biological Processes	GO:1903827	regulation of cellular protein localization	M6	-1.6	27	Cep131|Bard1|Dvl1|Epha2|Myo5b|Nf2|Pik3r2|Ptpn22|Rangap1|Ccl2|Srebf1|Tnf|Ube2g2|Stx6|Pdzk1|Rtn4|C2cd5|Mrap|Cdk5rap3|Trem2|Sec16b|Maged1|Trim40|Nrg1|Crocc|Lrig2|Epb41
GO Biological Processes	GO:0042088	T-helper 1 type immune response	M6	-1.6	5	Il12b|Il12rb1|Jak3|Traf6|Arid5a
GO Biological Processes	GO:0002718	production involved in immune response	M6	-1.6	7	Hmox1|Jak3|Tnf|Traf6|Rtn4|Trim6|Arid5a
GO Biological Processes	GO:0019932	second-messenger-mediated signaling	M6	-1.6	23	Adcy7|Bst1|Gal|Guca1a|Insl3|Nme2|Pde9a|Sphk1|Tnf|Zap70|Homer3|Cherp|Treml1|Selenon|Mrap|Adgrf1|Trem2|Sri|Nrg1|Tpcn2|Akap6|Gucy1b2|Calm5

GO Molecular Functions	GO:0015077	monovalent inorganic cation transmembrane transporter activity	M6	-1.6	20	Cox6c|Gria2|Kcnk5|Scn10a|Slc1a2|Slc23a1|Slc34a2|Slc5a1|Abcc9|Tcirg1|Kcnj1|Slc15a3|Scn2b|Atp6v1d|Kcnip2|Kcnn1|Slc24a3|Slc45a4|Slc5a5|Lrrc38
Reactome Gene Sets	R-MMU-6794361	Neurexins and neuroligins	M6	-1.6	4	Homer3|Nlgn1|Dlgap1|Epb41
GO Biological Processes	GO:0002484	presentation of endogenous peptide antigen via MHC class	M6	-1.6	4	H2-D1|H2-Q1|H2-T3|H2-M10.5
GO Biological Processes	GO:0032660	regulation of interleukin-17 production	M6	-1.6	4	Il12b|Myd88|Sphk1|Arid5a
GO Biological Processes	GO:0002476	presentation of endogenous peptide antigen via MHC class	M6	-1.6	4	H2-D1|H2-Q1|H2-T3|H2-M10.5
Reactome Gene Sets	R-MMU-432720	Lysosome Vesicle Biogenesis	M6	-1.6	4	Ap1m1|M6pr|Ap4b1|Dnajc6
GO Biological Processes	GO:0032635	interleukin-6 production	M6	-1.6	11	Arhgef2|Lbp|Myd88|Ptpn22|Tlr6|Tnf|Traf6|Zfp64|Trem2|Arid5a|Bank1
GO Biological Processes	GO:0009064	glutamine family amino acid metabolic process	M6	-1.6	6	Fpgs|Got1|Slc7a7|Ddah2|Dglucy|Lgsn
GO Biological Processes	GO:0009408	response to heat	M6	-1.6	8	Hspa5|Hmox1|Hspa4|Ier5|Pklr|Ccl2|Slc52a3|Lrp11
GO Biological Processes	GO:0002367	cytokine production involved in immune response	M6	-1.6	8	Hmox1|Il12b|Jak3|Tnf|Traf6|Rtn4|Trim6|Arid5a
GO Molecular Functions	GO:0004252	serine-type endopeptidase activity	M6	-1.6	12	C2|Dpp4|Cfb|Tpsg1|Prss30|Corin|Cela1|Prss27|Tmprss4|Tmprss13|Tmprss11f|Tmprss11c
GO Biological Processes	GO:0021535	cell migration in hindbrain	M6	-1.6	3	Ulk1|Rere|Rbfox2

GO Biological Processes	GO:0033173	calcineurin-NFAT signaling cascade	M6	-1.6	5	Tnf|Homer3|Cherp|Nrg1|Akap6
Reactome Gene Sets	R-MMU-193648	NRAGE signals death through JNK	M6	-1.6	5	Arhgef2|Arhgef10l|Arhgef17|Arhgef19|Prex1
GO Biological Processes	GO:0007254	JNK cascade	M6	-1.6	13	Axin1|Myd88|Ptpn22|Tlr6|Tnf|Traf6|Map3k5|Cops5|Map4k4|Dusp3|Unc5cl|Tnxb|Taok3
GO Molecular Functions	GO:0019887	protein kinase regulator activity	M6	-1.6	11	Angpt4|Ccnd3|Csnk2b|Tcl1b5|Ccnl2|Rgcc|Gprc5d|Inka2|Spred2|Nrg1|Gprc5a
GO Biological Processes	GO:0034504	protein localization to nucleus	M6	-1.6	16	Bard1|Dvl1|Nf2|Pik3r2|Ptpn22|Rangap1|Wrn|Taf8|Cdk5rap3|Maged1|Trim40|Sprn|Tmem201|Tor1aip2|Syne2|1700015F17Rik
GO Biological Processes	GO:0043087	regulation of GTPase activity	M6	-1.6	17	Epha2|Ptprn2|Rangap1|Ccl2|Ccl7|Map4k4|Tbc1d20|Tbc1d9|Arhgap15|Trappc6b|Rab3gap2|Plxnb2|Dock10|Arhgef19|Prex1|Lrch1|Iqgap2
GO Cellular Components	GO:0043198	dendritic shaft	M6	-1.6	6	Gria2|Arhgef2|Slc1a2|Nlgn1|Lzts1|Prex1
GO Biological Processes	GO:0050710	negative regulation of cytokine secretion	M6	-1.6	6	Fn1|Ptpn22|Tlr6|Tnf|Rgcc|Bank1
GO Biological Processes	GO:0032680	regulation of tumor necrosis factor production	M6	-1.6	11	Il12b|Arhgef2|Lbp|Myd88|Ptpn22|Ccl2|Tlr6|Zfp64|Trem2|Arfgef2|Arid5a
GO Biological Processes	GO:0030865	cortical cytoskeleton organization	M6	-1.5	5	Tnf|Cavin3|Nlgn1|Ehd2|Epb41

GO Biological Processes	GO:0043405	regulation of MAP kinase activity	M6	-1.5	17	Axin1|Ptpn22|Tlr6|Tnf|Traf6|Gdf15|Map3k5|Pik3cg|Lpar2|Dusp3|Cdk5rap3|Tnxb|Maged1|Itga1|Spred2|Taok3|Nek10
GO Biological Processes	GO:0048194	Golgi vesicle budding	M6	-1.5	4	Tbc1d20|Sec24a|Sec16b|Myo18a
GO Biological Processes	GO:0006739	NADP metabolic process	M6	-1.5	4	Fdxr|Rpia|Pgls|Nadk
GO Biological Processes	GO:0002428	presentation of peptide antigen via MHC class Ib	M6	-1.5	4	H2-D1|H2-Q1|H2-T3|H2-M10.5
GO Biological Processes	GO:0050764	regulation of phagocytosis	M6	-1.5	8	C2|Lbp|Ccl2|Sphk1|Tnf|Trem2|Camk1d|Myo18a
GO Biological Processes	GO:0070665	positive regulation of leukocyte proliferation	M6	-1.5	10	Bst1|Cd6|Il12b|Il12rb1|Jak3|Myd88|Ptpn22|Spta1|Traf6|Zap70
GO Biological Processes	GO:0032606	type I interferon production	M6	-1.5	7	Acod1|Irf9|Myd88|Ptpn22|Zfp64|Traf3ip1|Nploc4
GO Biological Processes	GO:0048002	antigen processing and presentation of peptide antigen	M6	-1.5	6	H2-D1|H2-Q1|H2-T3|Traf6|Trem2|H2-M10.5
Reactome Gene Sets	R-MMU-6794362	Protein-protein interactions at synapses	M6	-1.5	6	Grin1|Ptprf|Homer3|Nlgn1|Dlgap1|Epb41
GO Biological Processes	GO:1903829	positive regulation of cellular protein localization	M6	-1.5	17	Cep131|Epha2|Myo5b|Pik3r2|Ptpn22|Ccl2|Tnf|Pdzk1|Rtn4|C2cd5|Cdk5rap3|Trem2|Sec16b|Nrg1|Crocc|Lrig2|Epb41
GO Cellular Components	GO:0044292	dendrite terminus	M6	-1.5	3	Cobl|Rgs11|Rtn4
GO Biological Processes	GO:0034143	4 signaling pathway	M6	-1.5	3	Acod1|Lbp|Ptpn22
GO Biological Processes	GO:0002523	inflammatory response	M6	-1.5	3	Lbp|Ccl2|Rtn4
GO Molecular Functions	GO:0005402	activity	M6	-1.5	3	Slc23a1|Slc5a1|Slc45a4

Reactome Gene Sets	R-MMU-912526	signaling	M6	-1.5	3	Jak3|Pik3cd|Pik3r2
GO Biological Processes	GO:1903555	regulation of tumor necrosis factor superfamily cytokine production	M6	-1.5	11	Il12b|Arhgef2|Lbp|Myd88|Ptpn22|Ccl2|Tlr6|Zfp64|Trem2|Arfgef2|Arid5a
KEGG Pathway	mmu04141	Protein processing in endoplasmic reticulum	M6	-1.5	11	Hspa5|Rpn2|Ube2g2|Map3k5|Sec24a|Bag2|Ckap4|Nploc4|Ubqln3|Ubqlnl|Uggt1
GO Biological Processes	GO:0007032	endosome organization	M6	-1.5	5	Stx6|Pi4k2b|Fam160a2|Arfgef2|Laptm4b
Reactome Gene Sets	R-MMU-72695	complex, and subsequently, the 43S complex	M6	-1.5	5	Rps18|Rps7|Eif3g|Rps21|Eif2s2
GO Biological Processes	GO:0045089	positive regulation of innate immune response	M6	-1.5	14	Hpx|Ifi204|Il12b|Acod1|Lbp|Myd88|Ptpn22|Nectin2|Tlr6|Tnf|Rtn4|Trim6|Nploc4|H60c
GO Biological Processes	GO:0002831	regulation of response to biotic stimulus	M6	-1.5	10	Il12b|Il12rb1|Acod1|Ptpn22|Nectin2|Tfeb|Traf6|Traf3ip1|Trim6|Nploc4
GO Biological Processes	GO:0032640	tumor necrosis factor production	M6	-1.5	11	Il12b|Arhgef2|Lbp|Myd88|Ptpn22|Ccl2|Tlr6|Zfp64|Trem2|Arfgef2|Arid5a
GO Biological Processes	GO:0060142	formation by plasma	M6	-1.5	4	Nfe2|Gdf15|Trem2|Ehd2
GO Biological Processes	GO:0009187	cyclic nucleotide metabolic process	M6	-1.5	4	Adcy7|Epha2|Pde1a|Pde9a
GO Molecular Functions	GO:0048365	Rac GTPase binding	M6	-1.5	6	Dvl1|Arhgef2|Arhgap17|Farp1|Prex1|Iqgap2

GO Molecular Functions	GO:0015291	secondary active transmembrane transporter activity	M6	-1.5	14	Slc1a2|Slc23a1|Slc34a2|Slc4a3|Slc5a1|Slco1c1|Slc15a3|Slc24a3|Slc45a4|Slco3a1|Slc5a5|Slco5a1|Slc26a11|Slc47a2
GO Biological Processes	GO:0097720	calcineurin-mediated signaling	M6	-1.5	5	Tnf|Homer3|Cherp|Nrg1|Akap6
GO Biological Processes	GO:0043268	positive regulation of potassium ion transport	M6	-1.5	5	Gal|Kcnip2|Trem2|Akap6|Lrrc38
KEGG Pathway	mmu05014	Amyotrophic lateral sclerosis (ALS)	M6	-1.5	5	Gria2|Grin1|Slc1a2|Tnf|Map3k5
KEGG Pathway	mmu05150	Staphylococcus aureus infection	M6	-1.5	5	C2|C4b|Cfb|Dsg1c|H2-Ea-ps
GO Biological Processes	GO:0072698	protein localization to microtubule cytoskeleton	M6	-1.5	5	Cep131|Dvl1|Mid1|Cep63|Fam83d
GO Biological Processes	GO:0051057	GTPase mediated signal transduction	M6	-1.5	6	F2rl2|Map4k4|Lpar2|Rtn4|Nrg1|Gpr4
GO Biological Processes	GO:0071902	positive regulation of protein serine/threonine kinase activity	M6	-1.5	16	Axin1|Ccnd3|Tlr6|Tnf|Traf6|Gdf15|Map3k5|Pik3cg|Lpar2|Rgcc|Telo2|Maged1|Itga1|Akap6|Taok3|Nek10
GO Biological Processes	GO:0015813	transport	M6	-1.5	3	Per2|Slc1a2|Tnf
GO Biological Processes	GO:0002577	processing and presentation	M6	-1.5	3	Ptpn22|Trem2|Ythdf1
GO Biological Processes	GO:1900017	production involved in inflammatory response	M6	-1.5	3	Cd6|Myd88|Tlr6
GO Molecular Functions	GO:0044183	protein folding	M6	-1.5	3	Hspa5|Pdcl3|Calr3
GO Biological Processes	GO:0007095	checkpoint	M6	-1.5	3	Mbd4|Cdk5rap3|Taok3
Reactome Gene Sets	R-MMU-912631	Regulation of signaling by CBL	M6	-1.5	3	Pik3cd|Pik3r2|Uba52
GO Biological Processes	GO:0008356	asymmetric cell division	M6	-1.5	3	Arhgef2|Pou5f1|Stra8
KEGG Pathway	mmu05143	African trypanosomiasis	M6	-1.5	4	Il12b|Myd88|Plcb2|Tnf

KEGG Pathway	mmu04270	Vascular smooth muscle contraction	M6	-1.5	9	Acta2|Adcy7|Cyp4a12b|Plcb2|Pla2g2e|Pla2g2f|Myl9|Gucy1b2|Calm5
GO Biological Processes	GO:0001910	regulation of leukocyte mediated cytotoxicity	M6	-1.5	8	H2-D1|H2-Q1|H2-T3|Il12b|Nectin2|Ccl2|H2-M10.5|H60c
GO Biological Processes	GO:0071706	tumor necrosis factor superfamily cytokine production	M6	-1.5	11	Il12b|Arhgef2|Lbp|Myd88|Ptpn22|Ccl2|Tlr6|Zfp64|Trem2|Arfgef2|Arid5a
GO Biological Processes	GO:0061900	glial cell activation	M6	-1.5	5	Cst7|Sphk1|Tlr6|Tnf|Trem2
GO Biological Processes	GO:0003341	cilium movement	M6	-1.4	6	Dync1h1|Tekt2|Dnah10|Cfap53|Kif27|Ccdc63
GO Biological Processes	GO:0042509	phosphorylation of STAT protein	M6	-1.4	6	Crlf1|Hpx|Il12b|Nf2|Tnf|Traf3ip1
GO Biological Processes	GO:0051056	regulation of small GTPase mediated signal transduction	M6	-1.4	15	F2rl2|Fbp1|Arhgef2|Map4k4|Lpar2|Rtn4|Arhgef10l|Arfgef2|Arhgef17|Nrg1|Arhgef19|Farp1|Kank2|Prex1|Gpr4
Reactome Gene Sets	R-MMU-5653656	Vesicle-mediated transport	M6	-1.4	28	Ap1m1|Dync1h1|Fnbp1|Hpx|M6pr|Spta1|Tpd52|Uba52|Ulk1|Pacsin2|Cops5|Stx6|Necap2|Use1|Tbc1d20|Ap4b1|Dnajc6|Mvb12a|Kif2c|Kif27|Sec24a|Trappc6b|Sec16b|Rab3gap2|Vps37c|Chmp6|Rabepk|Apol7e

GO Cellular Components	GO:0043197	dendritic spine	M6	-1.4	12	Apbb1|Dvl1|Gria2|Grin1|Myl7|Myo5b|Slc1a2|Arfgef2|Sri|Nlgn1|Dock10|Lzts1
KEGG Pathway	mmu04380	Osteoclast differentiation	M6	-1.4	9	Ifnar2|Irf9|Mitf|Pik3cd|Pik3r2|Pirb|Tnf|Traf6|Trem2
GO Molecular Functions	GO:0019955	cytokine binding	M6	-1.4	9	Crlf1|Ifnar2|Il12b|Il12rb1|Lifr|Pou5f1|Cops5|Hjv|Ltbp1
GO Biological Processes	GO:0001776	leukocyte homeostasis	M6	-1.4	8	Jak3|Pik3cd|Pirb|Ccl2|Spta1|Tcirg1|Tnfrsf13b|Dock10
Reactome Gene Sets	R-MMU-202733	Cell surface interactions at the vascular wall	M6	-1.4	8	Angpt4|Dok2|Fn1|Pik3r2|Procr|Slc7a5|Slc7a7|Psg22
GO Biological Processes	GO:0031669	cellular response to nutrient levels	M6	-1.4	12	Hspa5|Nprl3|Srebf1|Ulk1|Wrn|Map3k5|Slc39a4|Dapl1|Rrp8|Szt2|Tnrc6a|Kank2
GO Biological Processes	GO:0009108	coenzyme biosynthetic process	M6	-1.4	12	Fbp1|Fdxr|Fpgs|Eif6|Pklr|Coq8a|Acss1|Atic|Nadk|Dhtkd1|Nmrk1|Pdk1
GO Molecular Functions	GO:0043394	proteoglycan binding	M6	-1.4	4	Col5a1|Fn1|Ptprf|Psg22
GO Biological Processes	GO:0045601	differentiation	M6	-1.4	4	Notch4|Tnf|Xdh|Atoh8
GO Biological Processes	GO:0001782	B cell homeostasis	M6	-1.4	4	Pik3cd|Pirb|Tnfrsf13b|Dock10
GO Biological Processes	GO:0031341	regulation of cell killing	M6	-1.4	9	H2-D1|H2-Q1|H2-T3|Il12b|Nectin2|Ccl2|H2-M10.5|Pglyrp4|H60c

GO Cellular Components	GO:0030175	filopodium	M6	-1.4	7	Apbb1|Dync1h1|Nf2|Cd302|Nlgn1|Syne2|Iqgap2
GO Biological Processes	GO:0032964	collagen biosynthetic process	M6	-1.4	5	Col5a1|Got1|Ccl2|Rgcc|Ltbp1
GO Biological Processes	GO:0019882	antigen processing and presentation	M6	-1.4	8	H2-D1|H2-Q1|H2-T3|Ptpn22|Traf6|Trem2|H2-M10.5|Ythdf1
GO Biological Processes	GO:0043410	positive regulation of MAPK cascade	M6	-1.4	26	Acta2|Axin1|Gcnt2|Mid1|Myd88|Ptpn22|Ccl2|Ccl7|Sphk1|Tlr6|Tnf|Traf6|Xdh|Gdf15|Map3k5|Map4k4|Pik3cg|Lpar2|Unc5cl|Trem2|Maged1|Cavin3|Itga1|Bank1|Taok3|Nek10
GO Biological Processes	GO:2000010	localization to cell surface	M6	-1.4	3	Tnf|Nrg1|Lrig2
GO Molecular Functions	GO:0090482	transporter activity	M6	-1.4	3	Slc23a1|Slc52a2|Slc52a3
GO Molecular Functions	GO:0008483	transaminase activity	M6	-1.4	3	Bcat1|Got1|Got1l1
GO Molecular Functions	GO:0031420	alkali metal ion binding	M6	-1.4	3	Pklr|Slc34a2|Kcnj1
GO Biological Processes	GO:0046641	beta T cell proliferation	M6	-1.4	3	Il12b|Ptpn22|Zap70
GO Biological Processes	GO:0002706	regulation of lymphocyte mediated immunity	M6	-1.4	12	Dpp4|H2-D1|H2-Q1|H2-T3|Hpx|Il12b|Nectin2|Tnf|Traf6|Arid5a|H2-M10.5|H60c
KEGG Pathway	mmu04918	Thyroid hormone synthesis	M6	-1.4	6	Adcy7|Gsr|Hspa5|Plcb2|Tg|Slc5a5
GO Molecular Functions	GO:0030971	receptor tyrosine kinase binding	M6	-1.4	6	Angpt4|Dok2|Pik3r2|Ptprf|Dusp3|Nrg1

GO Biological Processes	GO:0006732	coenzyme metabolic process	M6	-1.4	18	Fbp1|Fdxr|Fpgs|Eif6|Ldhb|Pemt|Pklr|Rpia|Pgls|Coq8a|Acss1|Glyat|Atic|Nadk|Dhtkd1|Nmrk1|Pdk1|Far2
Reactome Gene Sets	R-MMU-6798695	Neutrophil degranulation	M6	-1.4	26	Aga|Prdx6|Ap1m1|Bst1|Csnk2b|Cst3|Dync1h1|H2-Q1|Ifi204|Nme2|Pirb|Ptprn2|Tcirg1|Rnase2b|Hebp2|Psmd11|Vps35l|Atp6v1d|Nfam1|Acaa1a|Lpcat1|Ckap4|H2-M10.5|Enpp4|Psg22|Iqgap2
GO Biological Processes	GO:0061512	protein localization to cilium	M6	-1.4	5	Atp6v1d|Arl13a|Ift140|Crocc|Nphp4
GO Cellular Components	GO:0001533	cornified envelope	M6	-1.4	5	Sprr2d|Sprr2e|Sprr3|Lelp1|Kazn
Reactome Gene Sets	R-MMU-202403	TCR signaling	M6	-1.4	5	Pik3r2|Ptpn22|Traf6|Uba52|Zap70
GO Biological Processes	GO:1902475	transmembrane transport	M6	-1.4	4	Per2|Slc1a2|Slc7a5|Tnf
KEGG Pathway	mmu04960	reabsorption	M6	-1.4	4	Pik3cd|Pik3r2|Kcnj1|Nr3c2
GO Biological Processes	GO:0002475	antigen processing and presentation via MHC class Ib	M6	-1.4	4	H2-D1|H2-Q1|H2-T3|H2-M10.5
GO Biological Processes	GO:0046854	phosphatidylinositol phosphorylation	M6	-1.4	4	Pik3cd|Pik3r2|Pik3cg|Pi4k2b
GO Biological Processes	GO:0006778	compound metabolic process	M6	-1.4	4	Hebp1|Hmox1|Hpx|Spta1
GO Biological Processes	GO:0070570	regeneration	M6	-1.4	4	Ptprf|Map4k4|Rtn4|Lrig2
GO Biological Processes	GO:0072595	maintenance of protein localization in organelle	M6	-1.4	4	Bard1|Hspa5|Rangap1|Taf8

GO Biological Processes	GO:0032101	regulation of response to external stimulus	M6	-1.4	36	Adcy7|Bst1|Cd6|Cst7|Dvl1|Fn1|Grin1|Il12b|Il12rb1|Acod1|Lbp|Myd88|Ptgis|Ptpn22|Ptprf|Ccl2|Sphk1|Tfeb|Tfpi|Tlr6|Tnf|Traf6|Pik3cg|Pglyrp2|Rtn4|Dusp3|Traf3ip1|Trem2|Trim6|Nploc4|Enpp4|Camk1d|Ythdf1|Kank2|Zswim8|Lrig2
GO Biological Processes	GO:0071900	regulation of protein serine/threonine kinase activity	M6	-1.4	22	Axin1|Ccnd3|Ptpn22|Tesk1|Tlr6|Tnf|Traf6|Gdf15|Map3k5|Pik3cg|Lpar2|Rgcc|Telo2|Dusp3|Cdk5rap3|Tnxb|Maged1|Itga1|Spred2|Akap6|Taok3|Nek10
GO Biological Processes	GO:0042116	macrophage activation	M6	-1.4	7	Cst7|Lbp|Sphk1|Tlr6|Tnf|Trem2|Myo18a
GO Biological Processes	GO:0002705	positive regulation of leukocyte mediated immunity	M6	-1.4	11	H2-D1|H2-Q1|H2-T3|Hpx|Il12b|Nectin2|Tnf|Traf6|Arid5a|H2-M10.5|H60c
GO Cellular Components	GO:0044309	neuron spine	M6	-1.4	12	Apbb1|Dvl1|Gria2|Grin1|Myl7|Myo5b|Slc1a2|Arfgef2|Sri|Nlgn1|Dock10|Lzts1
GO Biological Processes	GO:0042108	positive regulation of cytokine biosynthetic process	M6	-1.4	6	Cebpg|Lbp|Myd88|Tlr6|Tnf|Traf6

GO Molecular Functions	GO:0008047	enzyme activator activity	M6	-1.4	23	Angpt4|Fn1|Guca1a|Guca2a|Nprl3|Rangap1|Rgs9|Tcl1b5|Rgs11|Rgcc|Tbc1d20|Arhgap17|Tbc1d9|Arhgef10l|Arhgap8|Arhgap15|Gmip|Gprc5d|Rab3gap2|Nrg1|Arhgef19|Gprc5a|Tor1aip2
GO Cellular Components	GO:0005903	brush border	M6	-1.4	9	Myo5b|Myo7b|Pemt|Prom1|Slc23a1|Slc34a2|Slc5a1|Pdzk1|Myo18a
KEGG Pathway	mmu00360	Phenylalanine metabolism	M6	-1.4	3	Got1|Keg1|Glyat
GO Biological Processes	GO:1902884	to oxidative stress	M6	-1.4	3	Tlr6|Tnf|Selenon
GO Biological Processes	GO:0051457	location in nucleus	M6	-1.4	3	Bard1|Rangap1|Taf8
GO Biological Processes	GO:0002719	production involved in immune	M6	-1.4	3	Hmox1|Jak3|Tnf
GO Molecular Functions	GO:0005540	hyaluronic acid binding	M6	-1.4	3	Ncan|Hapln3|Hapln4
GO Biological Processes	GO:0002827	1 type immune response	M6	-1.4	3	Il12b|Il12rb1|Arid5a
GO Biological Processes	GO:0006733	oxidoreduction coenzyme metabolic process	M6	-1.4	11	Fbp1|Fdxr|Eif6|Ldhb|Pklr|Rpia|Pgls|Coq8a|Nadk|Dhtkd1|Nmrk1
Reactome Gene Sets	R-MMU-917937	Iron uptake and transport	M6	-1.4	5	Hmox1|Uba52|Tcirg1|Atp6v1d|Flvcr1
GO Biological Processes	GO:0035456	response to interferon-beta	M6	-1.4	5	Ifi204|Ifnar2|Acod1|Ube2g2|Trim6
GO Biological Processes	GO:0034765	regulation of ion transmembrane transport	M6	-1.4	24	Clcnka|Gal|Per2|Ptpn22|Rgs9|Scn10a|Ccl2|Tnf|Tcirg1|Pik3cg|Clcnkb|Kcnj1|Pdzk1|1810037I17Rik|Scn2b|Selenon|Kcnip2|Trem2|Sri|Nlgn1|Tpcn2|Akap6|Lrrc38|Catsper4

Reactome Gene Sets	R-MMU-425407	SLC-mediated transmembrane transport	M6	-1.4	13	Slc34a2|Slc4a3|Slc5a1|Slc7a5|Slc7a7|Slco1c1|Slc29a1|Slc15a3|Slc39a4|Slc35b2|Slco3a1|Sri|Slc26a11
GO Molecular Functions	GO:0003712	transcription coregulator activity	M6	-1.4	23	Aebp2|Ifi204|Mak|Nme2|Per2|Pou5f1|Scand1|Sin3b|Tcp10b|Cops5|Brd7|Spen|Insm2|Med31|Rere|Med30|Kdm5b|Rbfox2|Maged1|Nrg1|Arid5a|Pprc1|Thrap3
Reactome Gene Sets	R-MMU-425393	cations/anions and amino acids/oligopeptides	M6	-1.4	7	Slc34a2|Slc4a3|Slc7a5|Slc7a7|Slc15a3|Sri|Slc26a11
GO Biological Processes	GO:0002483	presentation of endogenous peptide antigen	M6	-1.4	4	H2-D1|H2-Q1|H2-T3|H2-M10.5
GO Biological Processes	GO:0019885	presentation of endogenous peptide antigen via MHC class	M6	-1.4	4	H2-D1|H2-Q1|H2-T3|H2-M10.5
GO Biological Processes	GO:0060337	pathway	M6	-1.4	4	Ifnar2|Myd88|Trim6|Oas2
GO Biological Processes	GO:0071357	interferon	M6	-1.4	4	Ifnar2|Myd88|Trim6|Oas2
GO Biological Processes	GO:0044088	regulation of vacuole organization	M6	-1.4	4	Nprl3|Ulk1|Rab3gap2|Laptm4b
GO Biological Processes	GO:1901224	positive regulation of NIK/NF-kappaB signaling	M6	-1.3	6	Ptp4a3|Sphk1|Tnf|Traf6|Trem2|Nr3c2
GO Biological Processes	GO:0031668	cellular response to extracellular stimulus	M6	-1.3	13	Hspa5|Nprl3|Slc1a2|Srebf1|Ulk1|Wrn|Map3k5|Slc39a4|Dapl1|Rrp8|Szt2|Tnrc6a|Kank2
GO Biological Processes	GO:0048016	inositol phosphate-mediated signaling	M6	-1.3	5	Tnf|Homer3|Cherp|Nrg1|Akap6
GO Cellular Components	GO:0001917	photoreceptor inner segment	M6	-1.3	5	Guca1a|Mak|Rgs9|Cerkl|Crocc

Reactome Gene Sets	R-MMU-6809371	Formation of the cornified envelope	M6	-1.3	8	Krt19|Sprr2d|Sprr2e|Sprr3|Lelp1|Kazn|Lipk|Cdsn
GO Biological Processes	GO:2000181	negative regulation of blood vessel morphogenesis	M6	-1.3	8	Angpt4|Epha2|Pik3r2|Ccl2|Xdh|Rgcc|Rtn4|Gpr4
GO Biological Processes	GO:0010506	regulation of autophagy	M6	-1.3	14	Hmox1|Nprl3|Pik3r2|Ptpn22|Srebf1|Trim21|Tfeb|Ulk1|Dapl1|Trem2|Rab3gap2|Lzts1|Tpcn2|Tmem150b
GO Biological Processes	GO:0072523	catabolic process	M6	-1.3	4	Pde1a|Pde9a|Xdh|Enpp4
GO Biological Processes	GO:0032620	interleukin-17 production	M6	-1.3	4	Il12b|Myd88|Sphk1|Arid5a
GO Biological Processes	GO:0006636	biosynthetic process	M6	-1.3	4	Ptgis|Sphk1|Decr2|Scd3
KEGG Pathway	mmu04975	Fat digestion and absorption	M6	-1.3	4	Fabp1|Pla2g2e|Pla2g2f|Agpat1
Reactome Gene Sets	R-MMU-512988	GM-CSF signaling	M6	-1.3	4	Jak3|Pik3cd|Pik3r2|Uba52
GO Biological Processes	GO:0019068	virion assembly	M6	-1.3	3	Tbc1d20|Mvb12a|Chmp6
GO Biological Processes	GO:0098869	cellular oxidant detoxification	M6	-1.3	3	Prdx6|Tnf|Szt2
GO Molecular Functions	GO:0016769	transferring nitrogenous	M6	-1.3	3	Bcat1|Got1|Got1l1
GO Cellular Components	GO:0030057	desmosome	M6	-1.3	3	Kazn|Dsg1c|Cdsn
GO Cellular Components	GO:0036452	ESCRT complex	M6	-1.3	3	Mvb12a|Vps37c|Chmp6
GO Biological Processes	GO:0050670	regulation of lymphocyte proliferation	M6	-1.3	13	Bst1|Cd6|Gal|Il12b|Il12rb1|Jak3|Myd88|Ptpn22|Spta1|Traf6|Zap70|Pla2g2f|Tnfrsf13b
GO Cellular Components	GO:0045121	membrane raft	M6	-1.3	19	Cd79a|Cntn1|H2-D1|Hmox1|Ldhb|Nf2|Ptgis|Tfpi|Tlr6|Tnf|Zap70|Pacsin2|Pdzk1|Nfam1|Plvap|Cavin3|Itga1|Akap6|Ehd2

GO Biological Processes	GO:0046394	carboxylic acid biosynthetic process	M6	-1.3	19	Bcat1|Ccnd3|Fbp1|Fpgs|Got1|Eif6|Ldhb|Per2|Pklr|Ptgis|Sphk1|Srebf1|Decr2|Scd3|Acss1|Got1l1|Atic|Dhtkd1|Lgsn
GO Cellular Components	GO:0016607	nuclear speck	M6	-1.3	17	Bard1|Brd2|Ifi204|Mbd4|Ogg1|Rbbp6|Wrn|Pacsin2|Tfip11|Zc3h13|Ddx39|Rreb1|Kazn|Unc45a|U2af1|Ckap4|Thrap3
Reactome Gene Sets	R-MMU-72702	Ribosomal scanning and start codon recognition	M6	-1.3	5	Rps18|Rps7|Eif3g|Rps21|Eif2s2
Reactome Gene Sets	R-MMU-72649	Translation initiation complex formation	M6	-1.3	5	Rps18|Rps7|Eif3g|Rps21|Eif2s2
GO Biological Processes	GO:0044380	protein localization to cytoskeleton	M6	-1.3	5	Cep131|Dvl1|Mid1|Cep63|Fam83d
GO Cellular Components	GO:0098802	plasma membrane receptor complex	M6	-1.3	11	Cd6|Cd79a|Gria2|Grin1|Il12rb1|Tlr6|Traf6|Zap70|Hjv|Itga1|Nlgn1
GO Biological Processes	GO:0050688	regulation of defense response to virus	M6	-1.3	6	Il12b|Il12rb1|Ptpn22|Traf3ip1|Trim6|Nploc4
GO Biological Processes	GO:0032088	kappaB transcription factor activity	M6	-1.3	6	Acod1|Ptgis|Trim21|Cdk5rap3|Trim40|Nwd1
GO Biological Processes	GO:0032729	positive regulation of interferon-gamma production	M6	-1.3	6	Cebpg|Il12b|Il12rb1|Ptpn22|Tnf|Arid5a
GO Biological Processes	GO:2001259	positive regulation of cation channel activity	M6	-1.3	6	Gal|Rgs9|Ccl2|Trem2|Akap6|Lrrc38
GO Biological Processes	GO:0009582	detection of abiotic stimulus	1Yr	-3.7	8	Gnb1|Hpn|Htr7|Pkdrej|Arrb1|Asic3|Trpv1|Cngb1
GO Biological Processes	GO:0009581	detection of external stimulus	1Yr	-3.7	8	Gnb1|Hpn|Htr7|Pkdrej|Arrb1|Asic3|Trpv1|Cngb1

Reactome Gene Sets	R-MMU-446107	assembly	1Yr	-3.7	3	Col17a1|Dst|Lama3
GO Cellular Components	GO:0030056	hemidesmosome	1Yr	-3.7	3	Col17a1|Dst|Lama3
GO Molecular Functions	GO:0099094	ligand-gated cation channel activity	1Yr	-3.6	7	Chrng|Kcnj9|P2rx5|Asic3|Trpv1|Kcnj14|Cngb1
KEGG Pathway	mmu04514	Cell adhesion molecules (CAMs)	1Yr	-3.6	9	Cd6|Cntn1|H2-Q4|Madcam1|Nectin2|Cldn13|Cldn15|H2-M10.5|Nfasc
Reactome Gene Sets	R-MMU-1500931	Cell-Cell communication	1Yr	-3.2	6	Col17a1|Dst|Lama3|Nectin2|Parva|Kirrel
GO Biological Processes	GO:0051606	detection of stimulus	1Yr	-3.2	10	Gnb1|Hpn|Htr7|Pkdrej|Tlr6|Tas1r2|Arrb1|Asic3|Trpv1|Cngb1
Reactome Gene Sets	R-MMU-446728	Cell junction organization	1Yr	-2.9	5	Col17a1|Dst|Lama3|Nectin2|Parva
KEGG Pathway	mmu00770	biosynthesis	1Yr	-2.9	3	Bcat1|Enpp1|Ppcs
GO Biological Processes	GO:0046324	regulation of glucose import	1Yr	-2.9	5	Akt2|Enpp1|Slc1a2|C2cd5|Upk3b
GO Molecular Functions	GO:0015276	ligand-gated ion channel activity	1Yr	-2.9	7	Chrng|Kcnj9|P2rx5|Asic3|Trpv1|Kcnj14|Cngb1
GO Cellular Components	GO:0030864	cortical actin cytoskeleton	1Yr	-2.8	6	Actn2|Utrn|Myadm|Wipf2|Anln|Pdlim2
GO Molecular Functions	GO:0022834	ligand-gated channel activity	1Yr	-2.8	7	Chrng|Kcnj9|P2rx5|Asic3|Trpv1|Kcnj14|Cngb1
GO Cellular Components	GO:0005938	cell cortex	1Yr	-2.7	11	Actn2|Akt2|Fabp1|Utrn|Nlrp5|Myadm|Crip2|Wipf2|Anln|C2cd5|Pdlim2
GO Biological Processes	GO:0046323	glucose import	1Yr	-2.6	5	Akt2|Enpp1|Slc1a2|C2cd5|Upk3b
GO Molecular Functions	GO:0008483	transaminase activity	1Yr	-2.6	3	Bcat1|Got1l1|Kyat3

GO Cellular Components	GO:0005911	cell-cell junction	1Yr	-2.6	14	Dst|Hpn|Lama3|Abcb4|Nectin2|Myadm|Cldn13|Cldn15|Synpo|Kirrel|Pdlim2|Akap6|Nfasc|Cdsn
GO Molecular Functions	GO:0016769	transferring nitrogenous	1Yr	-2.5	3	Bcat1|Got1l1|Kyat3
GO Cellular Components	GO:0015629	actin cytoskeleton	1Yr	-2.5	14	Actn2|Dst|Abcb4|Tnni3|Utrn|Mprip|Myadm|Parva|Wipf2|Anln|Tax1bp3|Stk17b|Synpo|Pdlim2
GO Biological Processes	GO:0030865	organization	1Yr	-2.5	4	Wipf2|Anln|Synpo|Ehd2
GO Biological Processes	GO:0090630	activation of GTPase activity	1Yr	-2.5	5	Akt2|Tbc1d1|Tbc1d2b|Tbc1d9|Tax1bp3
GO Biological Processes	GO:0034113	heterotypic cell-cell adhesion	1Yr	-2.4	4	Gcnt2|Madcam1|Myadm|Parva
GO Biological Processes	GO:0010827	regulation of glucose transmembrane transport	1Yr	-2.4	5	Akt2|Enpp1|Slc1a2|C2cd5|Upk3b
GO Cellular Components	GO:0044448	cell cortex part	1Yr	-2.4	8	Actn2|Fabp1|Utrn|Nlrp5|Myadm|Wipf2|Anln|Pdlim2
GO Cellular Components	GO:0030055	cell-substrate junction	1Yr	-2.3	7	Actn2|Col17a1|Dst|Lama3|Abcb4|Map4k4|Parva
GO Biological Processes	GO:0007602	phototransduction	1Yr	-2.3	3	Gnb1|Arrb1|Cngb1
GO Molecular Functions	GO:0005261	cation channel activity	1Yr	-2.3	10	Chrng|Hpn|Kcnj9|Pkdrej|Scn3a|P2rx5|Asic3|Trpv1|Kcnj14|Cngb1
KEGG Pathway	mmu05032	Morphine addiction	1Yr	-2.2	5	Adcy7|Gnb1|Kcnj9|Pde1a|Arrb1
GO Cellular Components	GO:0030863	cortical cytoskeleton	1Yr	-2.2	6	Actn2|Utrn|Myadm|Wipf2|Anln|Pdlim2
Reactome Gene Sets	R-MMU-1296065	Inwardly rectifying K+ channels	1Yr	-2.2	3	Gnb1|Kcnj9|Kcnj14

GO Cellular Components	GO:0099568	cytoplasmic region	1Yr	-2.2	13	Actn2|Akt2|Camk2a|Fabp1|Utrn|Nlrp5|Myadm|Crip2|Wipf2|Anln|C2cd5|Pdlim2|Ccdc63
GO Biological Processes	GO:0007200	protein-coupled receptor signaling pathway	1Yr	-2.2	5	Actn2|F2rl2|Fpr2|Gnb1|P2ry12
Reactome Gene Sets	R-MMU-456926	proteinase activated receptors	1Yr	-2.1	3	F2rl2|Gnb1|Arrb1
GO Molecular Functions	GO:0003779	actin binding	1Yr	-2.1	12	Actn2|Capg|Dst|Tnni3|Utrn|Mprip|Parva|Wipf2|Anln|Ush1c|Synpo|Pdlim2
GO Biological Processes	GO:0050982	stimulus	1Yr	-2.1	4	Hpn|Htr7|Pkdrej|Asic3
GO Biological Processes	GO:0010657	muscle cell apoptotic process	1Yr	-2	5	Camk2a|Gnb1|Hmox1|Pde1a|Arrb1
GO Biological Processes	GO:0033363	secretory granule organization	1Yr	-2	3	Nectin2|Vps33b|Baiap3
GO Molecular Functions	GO:0005231	gated ion channel activity	1Yr	-2	3	Chrng|P2rx5|Trpv1
Reactome Gene Sets	R-MMU-198933	Immunoregulatory interactions between a Lymphoid and a non-Lymphoid cell	1Yr	-2	5	Col17a1|H2-Q4|Madcam1|Nectin2|H2-M10.5
GO Biological Processes	GO:0009416	response to light stimulus	1Yr	-2	9	Akt2|Ercc1|Gnb1|Slc1a2|Ctns|Synpo|Arrb1|Ccar2|Cngb1
Reactome Gene Sets	R-MMU-977444	GABA B receptor activation	1Yr	-2	3	Adcy7|Gnb1|Kcnj9
Reactome Gene Sets	R-MMU-991365	Activation of GABAB receptors	1Yr	-2	3	Adcy7|Gnb1|Kcnj9
GO Biological Processes	GO:1904659	glucose transmembrane transport	1Yr	-2	5	Akt2|Enpp1|Slc1a2|C2cd5|Upk3b
GO Biological Processes	GO:0043087	regulation of GTPase activity	1Yr	-1.9	9	Akt2|Map4k4|Tbc1d1|Tbc1d2b|Chn2|Tbc1d9|Tax1bp3|Arrb1|Rasgrp3
GO Biological Processes	GO:0008645	hexose transmembrane transport	1Yr	-1.9	5	Akt2|Enpp1|Slc1a2|C2cd5|Upk3b
GO Biological Processes	GO:2000379	oxygen species metabolic	1Yr	-1.9	5	Akt2|Fpr2|Tlr6|Xdh|Trpv1

GO Biological Processes	GO:0002711	positive regulation of T cell mediated immunity	1Yr	-1.9	4	H2-Q4|Nectin2|Arid5a|H2-M10.5
GO Molecular Functions	GO:0098631	cell adhesion mediator activity	1Yr	-1.9	3	Madcam1|Bcam|Nfasc
GO Biological Processes	GO:0015749	monosaccharide transmembrane transport	1Yr	-1.9	5	Akt2|Enpp1|Slc1a2|C2cd5|Upk3b
GO Biological Processes	GO:0034219	carbohydrate transmembrane transport	1Yr	-1.9	5	Akt2|Enpp1|Slc1a2|C2cd5|Upk3b
GO Biological Processes	GO:0008630	pathway in response to DNA damage	1Yr	-1.9	5	Bcl2a1c|Casp14|Hmox1|Bcl2l12|Ccar2
KEGG Pathway	mmu04725	Cholinergic synapse	1Yr	-1.9	5	Adcy7|Akt2|Camk2a|Gnb1|Kcnj14
Reactome Gene Sets	R-MMU-418346	Platelet homeostasis	1Yr	-1.9	4	Gnb1|Mrvi1|Pde1a|P2rx5
GO Cellular Components	GO:0016529	sarcoplasmic reticulum	1Yr	-1.9	4	Akt2|Mrvi1|Xdh|Akap6
GO Biological Processes	GO:0046326	import	1Yr	-1.9	3	Akt2|Slc1a2|C2cd5
GO Biological Processes	GO:1900015	production involved in	1Yr	-1.8	3	Adcy7|Cd6|Tlr6
GO Biological Processes	GO:0030866	organization	1Yr	-1.8	3	Wipf2|Anln|Ehd2
GO Cellular Components	GO:0031012	extracellular matrix	1Yr	-1.8	12	Col17a1|Lama3|Lgals4|Lrrn2|Rbp3|Sftpb|Hapln3|2300002M23Rik|Mepe|Prelp|Optc|Tgm4
GO Cellular Components	GO:0070161	anchoring junction	1Yr	-1.8	9	Actn2|Dst|Lama3|Abcb4|Nectin2|Map4k4|Parva|Pdlim2|Cdsn
GO Biological Processes	GO:0051261	protein depolymerization	1Yr	-1.8	5	Actn2|Capg|Mid1|Dnajc6|Eml4
GO Cellular Components	GO:0045111	intermediate filament cytoskeleton	1Yr	-1.8	6	Bfsp1|Casp14|Dst|Krt31|Ctns|Iffo2
GO Biological Processes	GO:0043154	type endopeptidase activity involved in apoptotic process	1Yr	-1.8	4	Akt2|Fabp1|Bcl2l12|Arrb1
Reactome Gene Sets	R-MMU-5576891	Cardiac conduction	1Yr	-1.7	5	Camk2a|Fxyd3|Scn3a|Tnni3|Kcnj14

GO Biological Processes	GO:0001774	microglial cell activation	1Yr	-1.7	3	Fpr2|Tlr6|Trpv1
GO Biological Processes	GO:0002534	inflammatory response	1Yr	-1.7	3	Adcy7|Cd6|Tlr6
GO Biological Processes	GO:0002269	inflammatory response	1Yr	-1.7	3	Fpr2|Tlr6|Trpv1
GO Biological Processes	GO:0002274	myeloid leukocyte activation	1Yr	-1.7	7	Fpr2|Hmox1|Pirb|Nectin2|Tlr6|Tac4|Trpv1
GO Biological Processes	GO:0043547	positive regulation of GTPase activity	1Yr	-1.7	7	Akt2|Map4k4|Tbc1d1|Tbc1d2b|Chn2|Tbc1d9|Tax1bp3
GO Cellular Components	GO:0044853	plasma membrane raft	1Yr	-1.7	5	Ms4a1|Hmox1|P2ry12|Akap6|Ehd2
GO Molecular Functions	GO:0022839	ion gated channel activity	1Yr	-1.7	9	Chrng|Hpn|Kcnj9|Scn3a|P2rx5|Asic3|Trpv1|Kcnj14|Cngb1
GO Biological Processes	GO:0045429	oxide biosynthetic process	1Yr	-1.7	3	Akt2|Tlr6|Trpv1
GO Molecular Functions	GO:0038024	cargo receptor activity	1Yr	-1.7	4	Cd6|Fpr2|Enpp1|Arrb1
GO Cellular Components	GO:0016528	sarcoplasm	1Yr	-1.7	4	Akt2|Mrvi1|Xdh|Akap6
GO Cellular Components	GO:0005882	intermediate filament	1Yr	-1.7	5	Bfsp1|Casp14|Dst|Krt31|Iffo2
GO Biological Processes	GO:0050974	stimulus involved in sensory	1Yr	-1.7	3	Hpn|Htr7|Asic3
GO Biological Processes	GO:1904407	oxide metabolic process	1Yr	-1.7	3	Akt2|Tlr6|Trpv1
GO Cellular Components	GO:0097517	bundle	1Yr	-1.7	4	Dst|Mprip|Synpo|Pdlim2
GO Biological Processes	GO:0007044	assembly	1Yr	-1.7	4	Actn2|Dst|Lama3|Map4k4
GO Biological Processes	GO:0001912	leukocyte mediated cytotoxicity	1Yr	-1.7	4	H2-Q4|Klrb1c|Nectin2|H2-M10.5
GO Biological Processes	GO:0009593	detection of chemical stimulus	1Yr	-1.7	4	Tlr6|Tas1r2|Asic3|Trpv1
GO Cellular Components	GO:0001725	stress fiber	1Yr	-1.7	4	Dst|Mprip|Synpo|Pdlim2
Reactome Gene Sets	R-MMU-397014	Muscle contraction	1Yr	-1.7	6	Actn2|Camk2a|Fxyd3|Scn3a|Tnni3|Kcnj14
GO Biological Processes	GO:0001916	mediated cytotoxicity	1Yr	-1.6	3	H2-Q4|Nectin2|H2-M10.5
GO Molecular Functions	GO:0008081	phosphoric diester hydrolase activity	1Yr	-1.6	4	Gnb1|Hmox1|Pde1a|Enpp1

GO Biological Processes	GO:2000117	type endopeptidase activity	1Yr	-1.6	4	Akt2|Fabp1|Bcl2l12|Arrb1
KEGG Pathway	mmu00230	Purine metabolism	1Yr	-1.6	6	Adcy7|Ampd3|Pde1a|Enpp1|Xdh|Polr3c
GO Biological Processes	GO:0031110	polymerization or	1Yr	-1.6	4	Dst|Mid1|Eml4|Gba2
GO Biological Processes	GO:0010828	transmembrane transport	1Yr	-1.6	3	Akt2|Slc1a2|C2cd5
GO Molecular Functions	GO:0022836	gated channel activity	1Yr	-1.6	9	Chrng|Hpn|Kcnj9|Scn3a|P2rx5|Asic3|Trpv1|Kcnj14|Cngb1
GO Biological Processes	GO:1901879	depolymerization	1Yr	-1.6	4	Actn2|Capg|Mid1|Eml4
Reactome Gene Sets	R-MMU-109582	Hemostasis	1Yr	-1.6	12	Actn2|F2rl2|Gnb1|H3f3a|Mrvi1|Pde1a|Ceacam9|P2ry12|P2rx5|Arrb1|Klc3|Ehd2
GO Biological Processes	GO:0009583	detection of light stimulus	1Yr	-1.6	3	Gnb1|Arrb1|Cngb1
Reactome Gene Sets	R-MMU-5578775	Ion homeostasis	1Yr	-1.6	3	Camk2a|Fxyd3|Tnni3
KEGG Pathway	mmu04144	Endocytosis	1Yr	-1.6	8	H2-Q4|Wipf2|Dnajc6|Vps37c|Arrb1|Psd4|H2-M10.5|Ehd2
GO Biological Processes	GO:0050906	detection of stimulus involved in sensory perception	1Yr	-1.6	5	Hpn|Htr7|Tas1r2|Asic3|Trpv1
KEGG Pathway	mmu04612	Antigen processing and presentation	1Yr	-1.6	4	H2-Q4|Rfxank|Rfxap|H2-M10.5
GO Biological Processes	GO:0015672	monovalent inorganic cation transport	1Yr	-1.6	11	Actn2|Akt2|Cntn1|Hpn|Kcnj9|Fxyd3|Scn3a|P2ry12|Asic3|Kcnj14|Akap6
GO Biological Processes	GO:0006813	potassium ion transport	1Yr	-1.6	7	Actn2|Hpn|Kcnj9|Fxyd3|P2ry12|Kcnj14|Akap6
GO Biological Processes	GO:0009791	post-embryonic development	1Yr	-1.6	5	Ercc1|Tbce|Atf5|Etnk2|Impad1
GO Cellular Components	GO:0099738	cell cortex region	1Yr	-1.6	3	Fabp1|Nlrp5|Anln

Reactome Gene Sets	R-MMU-977443	GABA receptor activation	1Yr	-1.6	3	Adcy7|Gnb1|Kcnj9
GO Biological Processes	GO:0061900	glial cell activation	1Yr	-1.6	3	Fpr2|Tlr6|Trpv1
Reactome Gene Sets	R-MMU-112314	and postsynaptic signal transmission	1Yr	-1.6	5	Actn2|Adcy7|Camk2a|Gnb1|Kcnj9
GO Biological Processes	GO:0051346	negative regulation of hydrolase activity	1Yr	-1.5	10	Akt2|Fabp1|Hpn|Mcm2|Slpi|Tnni3|Mprip|Serpina1f|Bcl2l12|Arrb1
GO Biological Processes	GO:0001914	cytotoxicity	1Yr	-1.5	3	H2-Q4|Nectin2|H2-M10.5
GO Biological Processes	GO:0043624	cellular protein complex disassembly	1Yr	-1.5	5	Actn2|Capg|Mid1|Dnajc6|Eml4
GO Biological Processes	GO:0016573	histone acetylation	1Yr	-1.5	5	Tcf3|Trrap|Arrb1|Arid5a|Brd1
GO Biological Processes	GO:0002709	regulation of T cell mediated immunity	1Yr	-1.5	4	H2-Q4|Nectin2|Arid5a|H2-M10.5
GO Cellular Components	GO:0005901	caveola	1Yr	-1.5	4	Hmox1|P2ry12|Akap6|Ehd2
GO Cellular Components	GO:0032432	actin filament bundle	1Yr	-1.5	4	Dst|Mprip|Synpo|Pdlim2
GO Cellular Components	GO:0043296	apical junction complex	1Yr	-1.5	5	Nectin2|Cldn13|Cldn15|Synpo|Nfasc
GO Cellular Components	GO:0031253	cell projection membrane	1Yr	-1.5	8	Akt2|Gnb1|Slc1a2|Utrn|P2ry12|C2cd5|Kirrel|Psd4
GO Molecular Functions	GO:0005216	ion channel activity	1Yr	-1.5	10	Chrng|Hpn|Kcnj9|Pkdrej|Scn3a|P2rx5|Asic3|Trpv1|Kcnj14|Cngb1
GO Biological Processes	GO:0071805	potassium ion transmembrane transport	1Yr	-1.5	6	Actn2|Hpn|Kcnj9|P2ry12|Kcnj14|Akap6
GO Biological Processes	GO:0071804	cellular potassium ion transport	1Yr	-1.5	6	Actn2|Hpn|Kcnj9|P2ry12|Kcnj14|Akap6
GO Biological Processes	GO:0007588	excretion	1Yr	-1.5	3	Htr7|Kirrel|Trpv1
Reactome Gene Sets	R-MMU-2022090	and other multimeric	1Yr	-1.5	3	Col17a1|Dst|Lama3
GO Cellular Components	GO:0042641	actomyosin	1Yr	-1.5	4	Dst|Mprip|Synpo|Pdlim2

GO Cellular Components	GO:0005912	adherens junction	1Yr	-1.5	8	Actn2|Dst|Lama3|Abcb4|Nectin2|Map4k4|Parva|Pdlim2
KEGG Pathway	mmu04713	Circadian entrainment	1Yr	-1.5	4	Adcy7|Camk2a|Gnb1|Kcnj9
GO Biological Processes	GO:0002708	positive regulation of lymphocyte mediated immunity	1Yr	-1.5	5	H2-Q4|Klrb1c|Nectin2|Arid5a|H2-M10.5
GO Biological Processes	GO:0018393	internal peptidyl-lysine acetylation	1Yr	-1.5	5	Tcf3|Trrap|Arrb1|Arid5a|Brd1
GO Biological Processes	GO:0044380	cytoskeleton	1Yr	-1.5	3	Mid1|Anln|4933427D14Rik
GO Cellular Components	GO:0045171	intercellular bridge	1Yr	-1.5	3	Rfxank|Tex14|Ehd2
GO Biological Processes	GO:0031343	positive regulation of cell killing	1Yr	-1.4	4	H2-Q4|Klrb1c|Nectin2|H2-M10.5
GO Biological Processes	GO:0010660	regulation of muscle cell apoptotic process	1Yr	-1.4	4	Camk2a|Hmox1|Pde1a|Arrb1
GO Biological Processes	GO:0008643	carbohydrate transport	1Yr	-1.4	5	Akt2|Enpp1|Slc1a2|C2cd5|Upk3b
Reactome Gene Sets	R-MMU-418594	G alpha (i) signalling events	1Yr	-1.4	9	Adcy7|Fpr2|Gnb1|Pde1a|Npy4r|Rbp3|P2ry12|Tas1r2|Cngb1
GO Biological Processes	GO:0050907	involved in sensory perception	1Yr	-1.4	3	Tas1r2|Asic3|Trpv1
GO Biological Processes	GO:0006475	internal protein amino acid acetylation	1Yr	-1.4	5	Tcf3|Trrap|Arrb1|Arid5a|Brd1
GO Biological Processes	GO:0030036	actin cytoskeleton organization	1Yr	-1.4	14	Actn2|Capg|Ran|Myadm|Parva|Wipf2|Anln|Ush1c|Synpo|Arrb1|Kirrel|Pdlim2|Gba2|Ehd2
Reactome Gene Sets	R-MMU-112315	Transmission across Chemical Synapses	1Yr	-1.4	6	Actn2|Adcy7|Camk2a|Gnb1|Kcnj9|Slc1a2

GO Molecular Functions	GO:0022838	substrate-specific channel activity	1Yr	-1.4	10	Chrng|Hpn|Kcnj9|Pkdrej|Scn3a|P2rx5|Asic3|Trpv1|Kcnj14|Cngb1
GO Cellular Components	GO:0045121	membrane raft	1Yr	-1.4	9	Ms4a1|Cntn1|Hmox1|Tlr6|Myadm|P2ry12|Kirrel|Akap6|Ehd2
GO Molecular Functions	GO:0051219	phosphoprotein binding	1Yr	-1.4	4	Mid1|Sh3bp2|Arrb1|Trpv1
GO Cellular Components	GO:0098857	membrane microdomain	1Yr	-1.4	9	Ms4a1|Cntn1|Hmox1|Tlr6|Myadm|P2ry12|Kirrel|Akap6|Ehd2
GO Molecular Functions	GO:0051015	actin filament binding	1Yr	-1.4	6	Actn2|Capg|Tnni3|Utrn|Wipf2|Ush1c
GO Biological Processes	GO:2000377	regulation of reactive oxygen species metabolic process	1Yr	-1.4	6	Akt2|Fpr2|Tlr6|Xdh|Ctns|Trpv1
GO Biological Processes	GO:1903426	species biosynthetic process	1Yr	-1.4	4	Akt2|Tlr6|Ctns|Trpv1
GO Biological Processes	GO:0009408	response to heat	1Yr	-1.4	4	Hmox1|Hsfy2|Asic3|Trpv1
GO Biological Processes	GO:1903428	oxygen species biosynthetic	1Yr	-1.4	3	Akt2|Tlr6|Trpv1
Reactome Gene Sets	R-MMU-9607240	FLT3 Signaling	1Yr	-1.4	6	Actn2|Akt2|Camk2a|Frs3|Arrb1|Rasgrp3
GO Biological Processes	GO:0042461	development	1Yr	-1.4	3	Ush1c|Cngb1|Mir182
GO Cellular Components	GO:0005925	focal adhesion	1Yr	-1.4	5	Actn2|Dst|Abcb4|Map4k4|Parva
GO Biological Processes	GO:0002699	positive regulation of immune effector process	1Yr	-1.4	7	H2-Q4|Hmox1|Klrb1c|Nectin2|Pgc|Arid5a|H2-M10.5
GO Biological Processes	GO:0046579	protein signal transduction	1Yr	-1.4	3	F2rl2|Map4k4|Arrb1
GO Biological Processes	GO:0018394	peptidyl-lysine acetylation	1Yr	-1.4	5	Tcf3|Trrap|Arrb1|Arid5a|Brd1
GO Biological Processes	GO:0043967	histone H4 acetylation	1Yr	-1.3	3	Tcf3|Trrap|Arrb1
GO Biological Processes	GO:0034605	cellular response to heat	1Yr	-1.3	3	Hmox1|Hsfy2|Trpv1

GO Biological Processes	GO:0002819	regulation of adaptive immune response	1Yr	-1.3	6	Adcy7|H2-Q4|Nectin2|Arid5a|H2-M10.5|Il27
GO Biological Processes	GO:0030029	actin filament-based process	1Yr	-1.3	15	Actn2|Capg|Ran|Myadm|Parva|Wipf2|Anln|Ush1c|Synpo|Arrb1|Kirrel|Pdlim2|Gba2|Akap6|Ehd2
GO Cellular Components	GO:0098589	membrane region	1Yr	-1.3	9	Ms4a1|Cntn1|Hmox1|Tlr6|Myadm|P2ry12|Kirrel|Akap6|Ehd2
GO Biological Processes	GO:0001910	regulation of leukocyte mediated cytotoxicity	1Yr	-1.3	4	H2-Q4|Klrb1c|Nectin2|H2-M10.5
GO Biological Processes	GO:0006612	protein targeting to membrane	1Yr	-1.3	4	Akt2|Zdhhc24|C2cd5|Vps37c
GO Biological Processes	GO:0150076	neuroinflammatory response	1Yr	-1.3	3	Fpr2|Tlr6|Trpv1
GO Biological Processes	GO:1901657	process	1Yr	-1.3	4	Ampd3|Ran|Trmt12|Gba2
GO Cellular Components	GO:0005924	cell-substrate adherens junction	1Yr	-1.3	5	Actn2|Dst|Abcb4|Map4k4|Parva

Appendix 5

Manuscript I: Genes with consistent differential methylation profiles between M6 and those identified previously in Massart et al. 2016

gene	M6Methylation = Massart Methylation	M6 Methylation Direction	Massart Methylation Direction
1700016C15Rik	TRUE	Hypo	Hypo
Abcc9	TRUE	Hypo	Hypo
Arfgef2	TRUE	Hypo	Hypo
Armc3	TRUE	Hypo	Hypo
Camk1d	TRUE	Hypo	Hypo
Ccdc154	TRUE	Hypo	Hypo
Coa5	TRUE	Hyper	Hyper
Col5a1	TRUE	Hypo	Hypo
Dapl1	TRUE	Hypo	Hypo
Dydc1	TRUE	Hypo	Hypo
Ehd2	TRUE	Hypo	Hypo
Eif3g	TRUE	Hypo	Hypo
Fabp1	TRUE	Hyper	Hyper
Fam184a	TRUE	Hyper	Hyper
Farp1	TRUE	Hypo	Hypo
Gprc5d	TRUE	Hypo	Hypo
Grin1	TRUE	Hypo	Hypo
Hfe2	TRUE	Hypo	Hypo
Kif2c	TRUE	Hypo	Hypo
Lrig2	TRUE	Hyper	Hyper
Lrrc49	TRUE	Hyper	Hyper
Mitf	TRUE	Hypo	Hypo
Mvb12a	TRUE	Hyper	Hyper
Ndufs8	TRUE	Hypo	Hypo
Nphp4	TRUE	Hypo	Hypo
Nr3c2	TRUE	Hyper	Hyper
Olfr517	TRUE	Hyper	Hyper
Olfr677	TRUE	Hyper	Hyper
Pde9a	TRUE	Hypo	Hypo
Pld5	TRUE	Hypo	Hypo
Prss27	TRUE	Hypo	Hypo
Ptp4a3	TRUE	Hypo	Hypo
Rps18	TRUE	Hyper	Hyper
Rtn4	TRUE	Hyper	Hyper
Scyl3	TRUE	Hypo	Hypo
Slc23a4	TRUE	Hypo	Hypo
Slc45a4	TRUE	Hypo	Hypo
Slco5a1	TRUE	Hyper	Hyper
Smco2	TRUE	Hypo	Hypo
Sult6b2	TRUE	Hypo	Hypo
Szt2	TRUE	Hypo	Hypo
Tectb	TRUE	Hypo	Hypo
Tfpi	TRUE	Hypo	Hypo
Tktl2	TRUE	Hypo	Hypo
Tmem88b	TRUE	Hypo	Hypo
Tmem9	TRUE	Hyper	Hyper
Trappc6b	TRUE	Hyper	Hyper
Tssk6	TRUE	Hyper	Hyper

Vangl1	TRUE	Hypo	Hypo
Vmn1r71	TRUE	Hyper	Hyper
Ythdf1	TRUE	Hyper	Hyper
Zbtb11	TRUE	Hyper	Hyper
Zbtb24	TRUE	Hyper	Hyper
Zfp57	TRUE	Hypo	Hypo
Zic5	TRUE	Hyper	Hyper
Zswim8	TRUE	Hypo	Hypo

Appendix 6

Manuscript I: Genes consistent with the predicted change in mRNA expression between M6 and those identified previously in Alvarado et al. 2013

gene	Meth=RNASeq	Methylation Direction	RNA Expression Direction
Camk1d	TRUE	Hypo	Increased
Cobl	TRUE	Hypo	Increased
Cst3	TRUE	Hyper	Decreased
Ddhd1	TRUE	Hypo	Increased
Dsg1c	TRUE	Hyper	Decreased
Grin1	TRUE	Hypo	Increased
Hnrnpab	TRUE	Hypo	Increased
Kcnip2	TRUE	Hypo	Increased
Rps21	TRUE	Hyper	Decreased
Serf2	TRUE	Hyper	Decreased
Snhg11	TRUE	Hyper	Decreased
Tmem201	TRUE	Hypo	Increased