А



Merkel 1,045 99.2 Longitudinal 2 .2 lanceolate 6 Club-like .6 Total 1,053 4.0 ± .8 3.6 ± .8 3.3 ± 1.3 3.6 ± .3 4.7 ± .9 4.9 .6 5.1 .7 3.1 ± 1.0 79+ 5.8 ± 1.3 70 10 10 3. Х 5.3 5.3 ± .5 3.9 ± .6 6.1 ± 1.0 ¥ TrkC^{CreER};Rosa^{Ai32} 4 Cck^{Cre};Rosa^{Ai32} Number of units 1 0 2 4 6 8 Mean latency (ms)

Count

%



Rate of change of moment, Mo ' (N-m ms⁻¹)

Figure S2



Figure S3



Figure S4



Figure S5



Figure S6



Figure S7

Table S1: Meta-data and assignment of neurons to analyses

Recording ID	Mouse ID	Sex	Mouse line	Recording Date	Туре	ldentified Merkel	Receptive field	Whisker length	Whisker base radius	Whisking and touch sensitivity	Fitted by viscoelastic	Appearances - Main Figures						Appearances - Supplemental Figures						Other notes	
						afferent		(mm)	(µm)		model														
												Fig. 1	Fig. 2	2 Fig. 3	Fig. 4	Fig. 5 Fig.	6 Fig. 7	Fig. S	1 Fig. S	2 Fig. S3	Fig. S4	Fig. S5	Fig. S	6 Fig. S7	
"Touch" re	ordings,	with b	oth whisker-pole cont	act and whis	king in	air																			
217F	KSt95	М	TrKC CroER ;Rosa Al32	04/29/15	RA		r	27.4	37.5	WT*	N.A.		С	C,D		C-E	B,G		A-E	A-D		A,B,D,F	В	A	
227A	KSt107	F	TrKC CreER ;Rosa Al32	05/15/15	RA		r	19.4	41.0	WT	N.A.		С	C,D			В		A-E			A,B,D,F		A	
145B	KSt76	М	TrKC CreER ;Rosa Al32	09/27/14	RA		C3	11.7	30.5	WT	N.A.		С	C,D			В		A-E			A,B,D,F		A	
194A	KSt88	М	TrKC CroER ;Rosa Al32	03/20/15	RA		r	29.7	43.0	WT	N.A.		С	C,D			В		A-E			A,B,D,F		A	
202A	KSt92	M	TrKC CreER ;Rosa Also	04/05/15	RA		C2	17.2	38.5	WT	N.A.		C	C,D			В		A-E			A,B,D,F	_	A	
163B	KSt//	M	TrKC Criter ;Rosa All	07/11/14	RA		r C1	25.6	45.0	T	N.A.		C	C,D			В		A-E			A,B,D,F		A	
120B	KS100	E	TrKC CriteR ;Rosa All	07/11/14	RA CA		0	24.0	41.5	1	N.A.		c	C,D	C	C F	B C		A-E	A D		A-F	D	A	
221B 225D	KSt100	F	TrKC CreER ;Rosa Al32	05/14/15	SA		p C2	20.3	39.0	WT*	r V	B	C	BCDH	C	C-E	B,G		A-E	A-D		A, B, D, F	B	A A	
132A	KSt69	M	TrKC CreER Rosa Alaz	07/25/14	SA		<u>в</u>	27.7	46.5	WT*	Y		c	C.D.	c	C-E	B.G	_	A-E	A-D		ABDF	B	A	
256B	KSt119	M	TrKC CroER : Rosa Al32	07/06/15	SA		C1	23.2	44.5	WT*	Y		C	C,D	C	C-E	B,G		A-E	A-D		A,B,D,F	В	A	
223B	KSt101	F	TrKC CroER ;Rosa Al32	05/11/15	SA		r	25.2	44.0	WT	Y		С	C,D	С		в		A-E			A,B,D,F		A	Example in Video S1
161A	KSt77	М	TrKC CroER ;Rosa AI32	11/10/14	SA		D1	23.7	44.0	WT*	Y		С	C,D	С	C-E	B,G		A-E	A-D		A,B,D,F	в	A	
167A	KSt82	М	TrKC CreER ;Rosa Al32	12/08/14	SA		C1	25.0	42.0	WT*	Y		С	C,D	С	C-E	B,G		A-E	A-D		A,B,D,F	В	A	
128D	KSt66	М	TrKC CreER ;Rosa AI32	07/18/14	SA		r	28.2	41.5	WT*	N.A.		С	C,D,I		C-E	B,G		A-E	A-D		A,B,D,F	в	A	
221C	KSt106	F	TrKC CreER ;Rosa AI32	05/14/15	SA		β	28.3	44.5	WT	Y		С	C,D	С		в		A-E			A,B,D,F		A	
198B	KSt89	F	TrKC CreER ;Rosa Al32	03/31/15	SA		r	24.4	42.0	WT	Y		С	C,D	С		В		A-E			A,B,D,F		A	
216D	KSt97	M	CCK ^{Cre} ; Rosa ^{Al32}	04/27/15	SA		C3	11.1	28.0	Т	Y		C	C,D	C		В	_	A-E	_		A,B,D,F		A	
211A	KSt96	F	TrKC CreER ;Rosa Also	04/20/15	SA		B2	14.1	28.5	Т	Y		С	C,D,I	С		В		A-E			A,B,D,F		A	
2208	KSt99	M	TrKC Green ;Rosa Alaz	05/06/15	SA	Y	C1	23.1	43.0	VV 1*	Y		B,C	C,D	C	C-E	B,G	C,D	A-E	A-D		A,B,D,F	В	A	
200A	KSt127	F	TrKC Crieff ;Rosa All	09/09/16	SA	Y	B2	15.0	37.0	WT*	Y		0	C,D	0	A-E	B,G	C,D	A-E	A-D		A,B,D,F	в	A	
251B	KSt117	м	TrKC Rosa	06/20/15	SA	T V	p 82	20.1	41.0	WT*	r V		C	CDH	B-D	C-E	B,G	C.D	A-E	A-D		A, B, D, F	A-C	A .	
254C	KSt119	M	TrKC CreER - Rosa Alaz	07/03/15	SA	v	ß	21.4	44.0	WT	Y		c	C.D.	C	0.5	B	C.D	A-E	A-D		ABDE		A	
207A	KSt91	M	TrKC CroER - Rosa Alaz	04/13/15	SA	Y	C4	8.6	23.5	WT	Y		c	C.D	c		В	C.D	A-F			ABDF		A	
154B	KSt80	F	TrKC CreER : Rosa Al32	10/25/14	SA	Y	δ	25.2	47.0	WT	Y		C	C,D	C		В	C,D	A-E			A,B,D,F		A	
265A	KSt122	М	TrKC CroER ;Rosa Al32	07/19/15	SA	Y	D4	10.3	30.5	WT	Y		С	C,D	С		в	C,D	A-E			A,B,D,F		A	
234A	KSt111	М	TrKC CroER ;Rosa AI32	05/29/15	SA	Y	C4	8.4	26.5	WT	Y		С	C,D	С		в	C,D	A-E			A,B,D,F		A	
231A	KSt109	F	TrKC CreER ;Rosa Al32	05/21/15	SA	Y	C1	18.5	41.0	WT*	Y		С	C,D	С	C-E	B,G	C,D	A-E	A-D		A,B,D,F	в	A	
243B	KSt112	М	TrKC CreER ;Rosa AI32	06/10/15	SA	Y	D2	20.1	38.0	WT	Y		С	C,D	С		в	C,D	A-E			A,B,D,F		A	
266B	KSt124	F	TrKC CreER ;Rosa Al32	07/21/15	SA	Y	B1	24.2	44.5	WT	Y		С	C,D,I	С		В	C,D	A-E			A,B,D,F		A	
220C	KSt99	м	TrKC CroER ;Rosa Al32	05/06/15	SA	Y	B3	11.3	27.0	WT	Y	D-F	С	C,D	С		В	C,D	A-E			A,B,D,F		A	
282A	KSt126	м	TrKC Creek ;Rosa Alsz	08/31/16	SA	Y	B3	8.1	22.5	Т	Y		С	C,D	С		В	C,D	A-E		_	A,B,D,F		A	
Touch re	coraings	exciua			ntiny tag	ging method	a (rigure S1)	00.0	44.0	MT								0.0							I wait of another another another in a second and inclusion allows have
2144	KSt94	F	TrKC CreER - Rosa Ala2	04/24/15	SA	Y	6 B1	20.3	39.0	WT	N.A.							C.D		_					Lack of rostral-caudal sensitivity prevented inclusion elsewhere
2714	KSt123	F	TrKC CroER - Rosa Alaz	07/29/15	SA	Y	D1	22.8	40.0	N.A.	N.A.							C.D							Whisker tracking errors prevented inclusion elsewhere
"Cut whisk	r only" r	ecordi	ngs obtained after the	relevant whi	isker w	as cut (cf. Fi	gure 7F)											-,-							
199B	KSt89	F	TrKC CroER ;Rosa AI32	04/01/15	SA	Y	D1 🔀	N.A.	N.A.	putative WT*	N.A.						B,F,G	C,D				A,B,D,F			
206A	KSt91	М	TrKC CroER ;Rosa AI32	04/13/15	SA	Y	A1 🔀	N.A.	N.A.	putative WT*	N.A.						B,F,G	C,D				A,B,D,F			
209A	KSt93	М	TrKC CreER ;Rosa Al32	04/16/15	SA	Y	A1 🔀	N.A.	N.A.	putative WT*	N.A.						B,F,G	C,D				A,B,D,F			
277A	KSm31	М	Rosa ^{Ai32}	08/24/16	SA		E4 3<	N.A.	N.A.	putative WT*	N.A.						B,F,G					A,B,D,F			
305A	KSt137	М	Rosa Alaz	10/18/16	SA		α 🔀	N.A.	N.A.	putative WT*	N.A.						B,F,G					A,B,D,F			
"Whisking	n air with	out to	uch" recordings, whish	ker-pole cont	tacts n	ot analyzed o	due to too many	y whiskers	s in video							0.5				1.5					
24UA	KSt112	M	TrKC Green ;Rosa Alaz	06/06/15	SA		B2	N.A.	N.A.	putative WT*	N.A.					U-E	B,G			A-D		A,B,D,F	В	-	
200A	which		IING "Rosa"	01/02/15	DA hout un	hisker-nole o	ontact	IV.A.	IV.A.	putative vv i -	n.A.					U-E	B,G			A-D		A, D, U, F	D		
278B	KSm30	M	Poss ^{A32}	08/31/16	SA	naker-pole c	B2	12.2	24.0	putative W/T*	N.A.					F-G	B-F-G					ABDE	В		
288C	KSt128	M	TrKC CreER : Rose Alaz	09/13/16	SA		B3 → ×	10.7	27.0	putative WT*	N.A.					E-G	B-E.G	-	-			A.B.D.F	B	-	
295C	KSt131	M	TrKC CreER :Rosa Ai32	09/23/16	SA		D1 → ≫	21.1	30.0	putative WT*	N.A.			1		B,E-G	B-E,G					A,B,D,F	в		Example in Video S2 - Episode 1
303A	KSt137	М	Rosa ^{Al32}	10/15/16	SA		$D1 \rightarrow >$	24.4	43.5	putative WT*	N.A.					E-G	B-E,G					A,B,D,F	в		
304B	KSt137	М	Rosa ^{Al32}	10/17/16	SA		$B2 \rightarrow >$	17.1	35.0	putative WT*	N.A.					E-G	B-E,G					A,B,D,F	в		
305B	KSt137	М	Rosa ^{Al32}	10/18/16	SA		$B1 \rightarrow imes$	24.7	44.5	putative WT*	N.A.					E-G	B-E,G					A,B,D,F	в		
309B	KSt135	М	TrKC CreER ;Rosa Ai32	10/24/16	SA		$D2 \rightarrow >$	17.6	38.0	putative WT*	N.A.					D-G	B-E,G					A,B,D,F	в		
311C	KSt135	М	TrKC CreER ;Rosa Al32	10/27/16	SA		$C4 \rightarrow >$	9.8	24.5	putative WT*	N.A.					C,E-G	B-E,G					A,B,D,F	В		Example in Video S2 - Episode 2
313A	KSt138	м	TrKC CreER ;Rosa Ai32	11/20/16	SA		$\Upsilon \rightarrow \times$	21.5	46.5	putative WT*	N.A.			-		E-G	B-E,G			_		A,B,D,F	В	_	
318A	KSt140	M	TrKC CreER ;Rosa Al32	12/01/16	SA		C1 → ≫	22.2	39.5	putative WT*	N.A.	-	-		-	E-G	B-E,G	-	-		-	A,B,D,F	В		
321A	KSt140	M	T KC CreER D 4/32	12/05/16	SA			22.3	45.0	putative W1*	N.A.					E-G	B-E,G					A,B,D,F	в	-	
2954	KSt130	M	TrKC CreER Roos Alaz	12/05/16	RA		$\cup J \rightarrow X$ D1 $\rightarrow Y$	9.0	28.5	putative WT*	N.A.					E-G	B-E,G					A B D F	B		
EMG record	linas du	rina w	hisking in air	53723/10	NA.			.0.0	20.0	porduve vv i						2-0	0-2,0					, 0, 0, F	5		
7A	KSm6	M	Rosa ^{Al32}	06/02/16	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.						A,D.F	3			D				intrinsic protractor
8A	KSm8	м	Rosa ^{Al32}	06/04/16	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.						A,D,F.O	3			D				intrinsic protractor
9A	KSm9	М	CCK ^{CreER} ;Rosa ^{Al32}	06/10/16	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.						A,D,F,C	3			B,C,D	1			intrinsic protractor
11A	KSm11	F	Rosa ^{Aig}	06/16/16	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.						A,D,F,C	3			F,G,H				extrinsic retractor

Supplemental Figures

Figure S1. Specific labeling of Merkel afferents in TrkC^{CreER} mouse, related to Figure 1.

(A) Confocal stack projections of whisker follicles from two TrkC^{CreER}; Rosa^{Ai9} mice (Mouse 1: top 4 rows; Mouse 2, bottom 4 rows). Green channel (left column, tdTomato) shows labeled afferent processes selected for classification of ending type (arrows). Endings that could not be identified by their morphology as a known whisker follicle ending type were "unclassified" (indicated by asterisks). In top left image, anatomical regions of the whisker are labeled: whisker shaft (arrowhead), ringwulst (RW), ring sinus (RS), and rete ridge collar (RRC). Merkel cells (middle column, magenta) were stained with anti-cytokeratin 8 (Krt8). Merged images (right column) were used to determine association of afferent endings with Merkel cells. All images are oriented with skin surface at the top. (B) Merkel cellassociated afferents are specifically labeled in whisker follicles of TrkC^{CreER}; Rosa^{Ai9} mice (counts included all tdTomato⁺ afferents in 3 whisker pads from 3 mice). Of classified Merkel afferents, the vast majority (994 of 1,045) were located in the Merkel dense region rather than the rete ridge collar. (C) Mean spike waveforms evoked by light (blue: TrKC^{CreER}; Rosa^{Ai32} mice; green: Cck^{Cre}; Rosa^{Ai32}) shown superimposed on those evoked by mechanical stimulation (black). Spike latency is indicated above each waveform (mean \pm SD from time of light onset to spike peak or trough, in ms). All identified Merkel afferents are shown (n = 19 from $TrKC^{CreER}$: $Rosa^{Ai32}$ in blue, and n = 1 from Cck^{Cre};Rosa^{Ai32}in green; Table S1). Three putative WT* afferents from Figure 7F, obtained after whisker cutting, are indicated with scissors icons. To help characterize our optogenetic tagging method, also shown are 3 afferents (bottom row, right-most) for which lack of rostral-caudal direction selectivity or whisker tracking errors prevented inclusion in other figures or analyses (Table S1). Spike waveforms presumably vary in part to electrode position with respect to the cell body and axon of these pseudounipolar neurons. (D) Histogram of mean spike latencies for the neurons in (C).

Figure S2. Tuning to contact forces and bending moment, related to Figure 3 and Figure 4.

(A) Systematic evaluation of the performance of Generalized Additive Models (GAMs) fitted by different combinations of variables (shown in title of each plot) during contact periods for each neuron (gray lines; n = 33afferents in each plot). The r value given in the title is the median Pearson correlation coefficient across neurons for the level of smoothing yielding highest performance. "Full" models include all dynamic variables (M_0 , F_{ax} , F_{lat}) and their rates of change (M_0', F_{ax}', F_{lat}) , plus four kinematic variables $(\theta, \omega, \alpha, \zeta)$. The performance of each model (gray crosses) was quantified as the Pearson correlation coefficient (r; y-axis) between predicted spike rate and the recorded spikes smoothed by Gaussian kernels with a range of sizes (in standard deviation, σ ; x-axis). Box plots depict distribution of r values across neurons within each smoothing condition (medians: red lines; 25^{th} and 75^{th} percentiles: lower and upper box boundaries; outliers marked by red plus symbols; MATLAB "boxplot"). Most models achieved best performance with $\sigma = 4$ ms. (B) Evaluation of Generalized Linear Models (GLMs) for the same data showing similar relationships between model performance and the smoothing parameter. Conventions as in (A), (C) Heatmaps showing r values ($\sigma = 4$ ms) for GAMs (top) and GLMs (bottom) based on different combinations of mechanical variables (along rows) for each neuron (columns). Similar to Figure 3D but including additional models. Afferents are sorted and labeled along the x-axis identically to Figure 2C, and are also listed by name to allow identification in Table S1. Conventions as in Figure 2C. GAMs outperform GLMs overall. (D) Same as in (C) but with performance quantified using deviance explained (%), which does not depend on smoothing. (E) Tuning surfaces for moment and its rate of change, for all touch recordings (n = 33). Dashed lines indicate the origin of each axis and are colored by afferent type (blue: Merkel; gray: SA; red: RA). The color scale for each surface ranges from 0 Hz to a maximum spike rate indicated by text above the surface (in Hz). Viscoelastic model was fitted to all Merkel and SA afferents except for 128D (for which the fitting algorithm failed). Red scale bars indicate 5 x 10^{-7} N-m and 5 x 10^{-8} N-m ms⁻¹ for M_0 and M_0' , respectively. Magenta scale bars indicate 5 x 10⁻⁸ N-m and 5 x 10⁻⁹ N-m ms⁻¹ for M_0 and M_0' , respectively. Bins with fewer than 25 observations are white.

Figure S3. Phase tuning during whisking in air across amplitudes, frequencies and setpoints, related to Figure 5.

(A) Tuning surfaces for each afferent (n = 15 WT* afferents, arrayed vertically), showing spike rate binned by both phase (x-axis) and whisk amplitude (y-axis; scale bars: 10°). Color scale for each surface spans 0 Hz to a maximum firing rate (in Hz) indicated to the right of each panel. Vertical dashed lines mark phase of 0 and are colored according to afferent type (blue: Merkel; gray: SA; red: RA). (B) Tuning surfaces for the same neurons (rows aligned with A) but with spike rate binned by phase (x-axis) and frequency (y-axis; scale bars: 10 Hz). (C) Tuning surfaces for the

same neurons (rows aligned with A), but with spike rate binned by phase (x-axis) and setpoint (y-axis; scale bars: 20°). (D) Phase tuning curves normalized and in Cartesian coordinates (mean \pm SEM spike rate) for each neuron (rows aligned with A). Axes are colored by afferent type as in (A). Unit names are listed to allow identification in Table S1.

Figure S4. Electromyogram (EMG) recordings from muscles that drive whisking, related to Figure 7.

(A) Schematic of chronic EMG recording procedure targeting intrinsic protractor muscle. During implantation of electrodes at this site, current stimulation resulted in whisker protraction. (B) Example EMG signal recorded together with high-speed whisker video during exploratory whisking. Rectified EMG signals were averaged into 2 ms bins. Intrinsic protractor activity peaked while velocity (ω) was positive, prior to peak position (θ). (C) Tuning surface for intrinsic protractor recording in (B), showing mean rectified EMG as a function of whisk phase (x-axis) and amplitude (y-axis, scale bar: 10°) measured from high-speed video (30 equally spaced bins for both phase and amplitude). Color ranges from 0 (black) to 0.08 mV. (D) Traces of mean rectified EMG (black curves) as a function of phase, for each of three intrinsic protractor recordings. Traces of mean whisker velocity as a function of phase were split into positive (red) and negative (blue) values, rectified and overlaid for each recording. Pearson correlation coefficients shown at right indicate that intrinsic protractor muscles and positive velocity were highly correlated within whisk cycles. (E) Schematic of chronic EMG recording procedure to target the extrinsic retractor muscle m. nasolabialis. During electrode implantation, passing current resulted in whisker pad retraction. (F) Example EMG signal for m. nasolabialis, with whisker velocity and position from high-speed video. Motor unit spikes were prevalent in this recording. Extrinsic retractor activity peaked while velocity was negative, just after peak position. (G) Same as (C), but based on motor unit spike rate. Color ranging from 0 (black) to 247 Hz. (H) Same as D, but for m. nasolabialis recording, showing high correlation with negative velocity within whisk cycles.

Figure S5. Distributions of kinematics and degree of invariance of kinematics with phase, related to Figure 7.

(A) Traces in each panel show probability distributions of a kinematic variable (indicated under each plot) for individual recording sessions (n = 33 sessions). Colors indicate whisker arc (columnar identity in whisker array on face). (B) Traces show the mean velocity (left), acceleration (middle), or jerk (right) binned by phase (x-axis) for the recording sessions in (A). Green traces show one example session. Crosses indicate the phases at which positive (red) and negative (blue) peaks occur for individual traces. Corresponding circles and error bars show the mean \pm 3 SD of these peaks. (C) Mean kinematics binned by phase (x-axis) and amplitude (grayscale traces; bins indicated in legend at right) for the example session (green curves) in (B). Markers indicate the phases where positive (red) and negative (blue) peaks occur for low (cross), middle (triangle), and high (circle) amplitude bins, respectively. (D) For all sessions, phase (angular axis) and amplitude (radial axis) values of the peaks extracted as in (C). Color and symbol conventions as in (C). Peaks from the same sessions are connected by lines. Data from the example session in (B) are plotted with thick lines. (E, F) Similar to (C, D) but for whisk frequency instead of whisk amplitude. The phases where peaks in kinematics occur are largely invariant across amplitudes and frequencies, except for negative jerk.

Figure S6. Phase tuning in terms of instantaneous combinations of kinematic variables, related to Figure 7.

(A) Each row shows an overlay of the observed phase tuning curve (black, same in each row) for an example Merkel afferent and a tuning curve predicted from a GAM model (red) fitted to one of 15 possible combinations (indicated at left) of four kinematic variables (θ , whisker position; ω , velocity; α , acceleration; ζ , jerk) during whisking in air. Pearson correlation coefficient between observed and predicted curves, *r*, is shown to the right for each row. (B) Heatmap of *r* quantified as in (A) for each model type (kinematic variables listed at left) for all WT* neurons (columns). Gray indicates *r* values < 0.5. Arrow indicates the example afferent from (A). Afferent names along the x-axis are colored by afferent type (blue: Merkel; gray: SA; red: RA). Models containing at least acceleration and velocity (or jerk) produced good performance, while those lacking acceleration generally performed worse. (C) Spikes during whisking in air are triggered in a confined region of kinematic subspace, giving rise to phase tuning (inspired by Wallach et al. 2016). Left, Each point in the background is the instantaneous acceleration (y-axis), velocity (x-axis), and phase (color) for a random subset of frames (15,000 out of ~590,900 total) for the example afferent in (A). In the foreground, another random subset of frames were drawn (1,500 of ~590,900) and those with spikes were plotted as black dots. Right, Same as left panel but acceleration and jerk, and with different randomly chosen frames.

Figure S7. Uncertainty level of curvature change measurements, related to Figure 3.

The uncertainty or "noise" level (σ_{κ}) for the curvature measurement in each touch recording (n = 33) is the ratio of mean curvature change measured in the absence of contact to that measured in the presence of contact (STAR Methods). Afferents are sorted and labeled along the x-axis identically to Figure 2C, and are also listed by name to allow identification in Table S1. Conventions as in Figure 2C.

Table S1. Meta-data for all recordings and their assignment to analyses, related to STAR Methods.

Metadata for each afferent, including figure appearances. Scissors icons indicate a receptive field comprising a whisker cut to within ~1.2 mm or less from the face. T: sensitive to touch, but not to whisking. WT: sensitive to both whisking and touch. WT*: sensitive to both whisking and touch, with mean whisking in air spike rate >1 Hz and >1000 spikes. *N.A.*: not applicable.